UNIVERSITÉ DU QUÉBEC À RIMOUSKI

Écologie alimentaire du rorqual commun (*Balaenoptera physalus*) dans l'Estuaire et le Golfe du Saint-Laurent

Mémoire présenté

dans le cadre du programme de maîtrise en Gestion de la faune et de ses habitats

en vue de l'obtention du grade de maître ès sciences

PAR

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Août 2015

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Dépôt initial le : 31 août 2015 Dépôt final le : 26 mars 2016

À mes grands-parents, avec qui j'aurais tellement aimé pouvoir partager ce succès.

REMERCIEMENTS

J'aimerais tout d'abord remercier **Véronique Lesage**. Pour avoir accepté une étudiante sans bourse, qui n'avait comme bagage que de la motivation. Pour les opportunités de terrain que tu m'as offertes. Pour avoir été présente du début à la fin. Pour tes précieux conseils et pour ta rigueur scientifique.

Merci aussi à **Christian Nozais** d'avoir accepté une étudiante travaillant sur les baleines, alors que ce ne sont pas vraiment tes bibittes habituelles. Merci pour ta disponibilité, ton accessibilité et ton professionnalisme.

J'aimerais aussi remercier **Robert Michaud et toute l'équipe du GREMM** qui ont travaillé fort pour que j'aie une base de données complète ! Vous ayant côtoyés tout un été, je connais la valeur et l'implication de votre travail. Sans vous ma maîtrise n'aurait pu avoir lieu.

Merci à **Arnaud Mosnier** qui a réussi à démystifier plusieurs de mes problèmes avec R et ArcGis. La programmation n'est pas naturelle pour moi !

Un immense merci à **Alain Caron** pour ton aide judicieuse en statistiques. Pour ta patience, tes réponses rapides et ta disponibilité. Qu'est-ce que j'aurais fait sans toi !

Je souhaite aussi exprimer ma reconnaissance à **Joël Bêty** et **Gesche Winkler** qui, deux fois plutôt qu'une, ont accepté de siéger sur mon comité d'évaluation.

Merci à **Katherine Gavrilchuk** pour ton aide silencieuse. Sans le savoir, ton mémoire de maîtrise a été une référence et un guide pour le mien. Une idée concrète de ce vers quoi je devais me diriger.

J'aimerais aussi remercier **Claudie-Ann Michaud-Tremblay, Cristina Charrette et Véronique Caron,** parce que sans vous ça aurait été beaucoup plus difficile et surtout, pas mal moins le fun. Vous étiez les seules à vraiment comprendre. Merci pour votre présence et pour tous les bons moments.

J'aimerais aussi exprimer toute ma gratitude à **ma famille**. À mes parents**,** pour votre soutien sans limite. Pour le support moral et financier. Pour votre présence et vos encouragements. Papa et Maman, je ne vous le dirai probablement jamais assez, mais sans vous ceci n'aurait pas été possible. Merci infiniment. Merci aussi à ma petite sœur, **Marie-Sarah.** Surtout pour tes mauvais coups (eh oui), ils ont mis du piquant et bien du rire dans mon quotidien. Merci pour ta tendresse de petite sœur, tu as une place importante dans mon cœur.

RÉSUMÉ

La niche écologique est un concept théorique fondamental de l'écologie et de l'évolution des espèces pouvant être abordé sous différents angles : du point de vue trophique, spatial, temporel ou encore comportemental. L'étude des niches trophiques, soit l'ensemble des ressources alimentaires qu'un individu sélectionne et utilise, est primordiale pour établir son rôle écologique en tant que consommateur, mais aussi pour évaluer les impacts des changements écosystémiques sur cet animal. Bien que les méthodes permettant d'étudier cette niche trophique sont nombreuses, les dernières années ont vu la popularité des analyses d'isotopes stables et d'acides gras exploser, surtout considérant leurs avantages relativement aux méthodes traditionnelles. La présente étude s'est penchée sur l'écologie alimentaire du rorqual commun (*Balaenoptera physalus*) dans l'Estuaire du Saint-Laurent pour la période 1998-2006 et avait pour objectif d'établir la composition de sa diète, et d'examiner les variabilités interindividuelle, interannuelle et saisonnière de celle-ci. Une analyse de groupement a permis de regrouper les individus selon la similarité de leurs signatures isotopiques ($\delta^{13}C$ et $\delta^{15}N$). Les contributions relatives des proies à la diète du rorqual commun ont été établies à l'aide de SIAR, un modèle de mélange isotopique Bayésien. Les profils d'acides gras du lard des rorquals communs ont été utilisés qualitativement pour bonifier la discrimination entre les proies et la résolution des résultats. Cette étude montre que le rorqual commun est une espèce généraliste, c'est-à-dire pouvant exploiter plusieurs espèces de proies. De la variabilité interindividuelle a été observée, certains individus étant plus spécialisés que d'autres. Le krill arctique (*Thysanoessa raschii*) représentait invariablement la proie dominante du rorqual commun, même si le krill nordique (*Meganyctiphanes norvegica*), et diverses espèces de petits poissons pélagiques pouvaient également être consommés à des niveaux variables selon les individus. Les analyses isotopiques, et dans une moindre mesure celles des acides gras, ont par ailleurs révélé un changement dans la composition de la diète du rorqual commun entre les saisons et au cours de la période d'étude (1998-2006). À partir de l'année 2000, l'importance du krill Arctique a diminué au profit du krill nordique et des poissons (capelan et hareng) dans la diète des rorquals communs, soulevant un certain nombre de questions concernant l'influence de la variabilité du climat sur le régime alimentaire, la distribution, la condition physique et le succès reproducteur (*fitness*) de cette espèce.

Mots clés: rorqual commun · écologie alimentaire · niche trophique · isotopes stables · $\delta^{13}C$ · $\delta^{15}N$ · acides gras · modèles Bayésiens

ABSTRACT

The ecological niche is a fundamental theoretical concept of ecology and evolution of species which can be approached from different angles: from a trophic, spatial, temporal or behavioral perspective. Trophic ecology is central to understanding animal ecology, defining their role in ecosystems, and assessing potential impacts of environmental changes. Although methods for studying trophic niches are numerous, stable isotopes and fatty acids analyzes are increasingly used, especially considering their advantages over traditional methods. This study focuses on the feeding ecology of fin whales (*Balaenoptera physalus*) in the St. Lawrence Estuary during the period 1998-2006 with the aim of documenting the composition of their diet and examining inter-individual, inter-annual and seasonal variability. Individuals were grouped according to the similarity of their isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) using a cluster analysis. Proportional contribution of each prey was determined using SIAR, a Bayesian isotopic mixing model. The fatty acid profiles of their blubber were used qualitatively as a complement to isotope analysis to increase discrimination among prey and resolution of the results. The study demonstrates that fin whale is a generalist species, i.e. it exploits a variety of prey. Some within-species variability was observed, with some individuals being more specialized than others. Arctic krill (*Thysanoessa raschii*) was invariably the dominant prey of fin whale, although northern krill (*Meganyctiphanes norvegica*), and various species of small pelagic fish could be consumed to varying levels depending on individuals. Stable isotopes and to a lesser extent fatty acids also revealed a change in diet between seasons and during the study period (1998-2006). Starting around the year 2000, a decline in the importance of Arctic krill to the benefit of an increase in that of northern krill and fish (capelin and herring) was observed in the diet of fin whales. This raises a number of questions about the potential influence of climate variability on diet, distribution, body condition and fitness of this species.

Key words: fin whale · feeding ecology · trophic niche · stable isotopes · $\delta^{13}C$ · $\delta^{15}N$ · fatty acids · Bayesian models

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ANOVA	Analysis of variance – Analyse de la variance
BHT	Butylated hydroxytoluene – Hydroxytoluène butylé
CC	Calibration coefficient – Coefficient de calibration
COSEPAC	Comité sur la situation des espèces en péril au Canada
COSEWIC	Committee on the status of endangered wildlife in Canada
DMSO	Dimethyl sulfoxide – Diméthylsulfoxyde
EC	Ester wax – Ester de cire
EGSL	Estuary and Gulf of St. Lawrence – Estuaire et Golfe du Saint-Laurent
FA - AG	Fatty acid - Acide gras
FAME	Fatty acid methyl ester – Ester méthylique d'acide gras
FID	Flame ionization detector - Détecteur à ionisation de flamme
GAM	Generalized Additive Model – Modèle additif généralisé
GSL	Gulf of St. Lawrence – Golfe du Saint-Laurent
MANOVA	Multivariate analysis of variance – Analyse de variance multivariée
MUFA	Monounsaturated fatty acid – Acide gras monoinsaturé
PCA	Principal component analysis – Analyse en composantes principales
PL	Phospholipe – Phospholipide
POM	Particulate organic matter – Matière organique particulaire

PUFA Polyunsaturated fatty acid – Acide gras polyinsaturé

QFASA Quantitative fatty acid signatures analysis – Analyse quantitative des profils d'acides gras

SD Standard deviation – Écart-type

SI – IS Stable Isotope – Isotope stable

SFA Saturated fatty acid – Acide gras saturé

SIAR Stable Isotopes Analysis in R – Analyse d'isotopes stables dans R

TAG Triacylglycerol – Triacylglycérol

TDF Trophic discrimination factor – Facteur de discrimination trophique

LISTE DES SYMBOLES

δ	Delta notation - Notation delta

INTRODUCTION GÉNÉRALE

Niche écologique

La niche écologique est un concept théorique fondamental de l'écologie et de l'évolution des espèces employé dans divers domaines : utilisation des ressources, diversité géographique, composition et structure des communautés biologiques, etc. (McGill *et al.*, 2006). Malgré son importance, le concept de niche écologique peut renvoyer à plusieurs définitions (Leibold, 1995; Schoener, 2009; Polechová et Storch, 2010). Le fait que la niche écologique soit difficile à mesurer ajoute aussi à l'ambiguïté entourant ce concept (Newsome *et al.*, 2007). Tout d'abord, la niche écologique peut être définie comme la réponse ou les exigences des espèces face à leur environnement, tel que décrit par Grinnell (1917) (niche de Grinnell). La niche écologique peut aussi référer à l'impact des espèces et de leur utilisation des ressources sur leur environnement. Cette définition, d'abord développée par Elton (1927) (niche d'Elton) puis par MacArthur et Levins (1967), se fonde sur le rôle fonctionnel de l'espèce au sein de son environnement. Finalement, la niche écologique peut être un concept plus dynamique, combinant les deux définitions précédentes. En effet, Hutchinson (1957) a postulé que la niche écologique est un hypervolume dans un espace écologique multidimensionnel. Cet espace serait non seulement défini par les exigences (biotiques ou abiotiques) de l'espèce assurant sa reproduction et sa survie, mais aussi par le rôle fonctionnel des espèces dans leur communauté puisque les interactions entre les espèces (ex. compétition) peuvent modifier la position des niches dans l'espace multidimensionnel (Hutchinson, 1957, 1965). Ainsi, deux définitions de la niche écologique peuvent être développées : la niche *fondamentale* et la niche *réalisée* (Hutchinson, 1957, 1965). La niche fondamentale est définie comme réunissant l'ensemble des composantes et conditions environnementales dont une espèce a besoin pour survivre (Hutchinson, 1957; Newsome *et al.*, 2007). La niche réalisée représente quant à elle l'espace que cette même espèce est contrainte d'utiliser du fait

d'interactions intra et interspécifiques; autrement dit, du fait de la compétition (Hutchinson, 1957, 1965). De ce fait, la niche réalisée est souvent incluse dans la niche fondamentale. La niche écologique peut être abordée sous différents angles : du point de vue trophique, spatial, temporel ou encore comportemental. Ces *sous-niches* sont donc des subdivisions de la niche écologique. Par exemple, la niche trophique vise spécifiquement les ressources alimentaires sélectionnées par les individus et les populations alors que la niche spatiale est liée à leur utilisation et à l'occupation de l'espace (taille des territoires, migrations, répartition spatiale).

Selon le principe de Gause, aussi nommé principe d'exclusion compétitive, dans un milieu homogène deux espèces sympatriques ne peuvent occuper une même niche écologique de manière viable, sauf dans le cas de symbiotes, puisqu'il en résulte inévitablement de la compétition (Gause, 1934). Les lois de la sélection naturelle tendent à favoriser l'espèce la mieux adaptée, ou ayant le meilleur *fitness*[1], et éventuellement à exclure l'autre (Hardin, 1960; Tilman, 1982; Chesson, 2000). Cependant, l'action conjointe de *mécanismes de stabilisation* et *d'égalisation* peut mener à une coexistence stable entre deux espèces, les premiers permettant de compenser pour les inégalités de *fitness* alors que les seconds réduisent l'amplitude de cette différence (Chesson, 2000). Par exemple, une boucle de rétroaction densité-dépendante ou une réduction du chevauchement des ressources partagées (< 100%) peuvent être considérées comme des mécanismes de stabilisation alors qu'une différence de taux de mortalité ou un compromis entre la capacité de concurrence et la susceptibilité à la prédation seront considérés comme des mécanismes d'égalisation (Chesson, 2000). Néanmoins, le nombre d'espèces cohabitant dans une même et unique communauté sera ultimement défini par la capacité des espèces à se répartir les ressources disponibles dans le temps et l'espace (Chesson, 2000; Amarasekare, 2003; Chave, 2004; Tilman, 2004; Kadmon et Allouche, 2007).

[1] *Fitness* : capacité à croître et à se reproduire assez rapidement, malgré une faible disponibilité des ressources, pour compenser la mort des tissus et la mortalité, lesquels sont affectées par des facteurs tels que la prédation.

Les dimensions d'une niche écologique varient d'une espèce à l'autre et peuvent être plus ou moins flexibles. Les espèces occupant des niches étroites (spécialistes) ont de fortes exigences écologiques et dépendent d'un nombre limité de ressources alors que les espèces possédant une niche plus large (généralistes) seront plus souples dans leurs exigences et donc moins restreintes dans leur sélection des ressources (MacArthur et Levins, 1964; Newsome *et al.*, 2007). Dans le cas particulier de la niche trophique, les espèces spécialistes sont composées d'individus se nourrissant tous du même type de proies, donc très efficaces pour exploiter leur ressource de prédilection (Stilmant *et al.*, 2008). Les espèces généralistes peuvent quant à elles présenter deux patrons d'alimentation : (1) les individus exploitent une large gamme de proies ou (2) chaque individu est spécialisé pour un type de proies en particulier, cette spécialité variant entre les individus (Van Valen, 1965; Grant *et al.*, 1976; Bearhop *et al.*, 2004). Alors que ce dernier patron d'alimentation mène à une grande variation interindividuelle de la diète, les individus généralistes du premier type peuvent présenter une diète très uniforme (Bearhop *et al.*, 2004) ou très variable (Huckstadt *et al.*, 2012) puisqu'ils pourraient tous consommer exactement les mêmes proies ou utiliser des gammes de proies complètement différentes.

De nombreuses études ont démontré, chez divers taxons et une grande variété d'écosystèmes, que les espèces spécialistes ont plus de difficulté à faire face aux fluctuations dans leur environnement, y compris une perte d'habitat, un changement des conditions climatiques, une modification dans la disponibilité des proies ou dans la structure trophique (ex. Carlson, 2000; Warren *et al.*, 2001; Munday, 2004; Goulson *et al.*, 2005; Rand et Tscharntke, 2007; Clavel *et al.*, 2010). Les espèces généralistes devraient par contre être moins vulnérables à ces changements, et donc présenter un risque d'extinction moins élevé (Wilson *et al.*, 2008).

Le rorqual commun

Le rorqual commun (*Balaenoptera physalus*) est, après le rorqual bleu (*B. musculus*), le deuxième plus grand prédateur au monde (Mizroch *et al.*, 1984), et il partage avec celui-ci certaines ressources alimentaires. Contrairement aux rorquals bleus, qui semblent se spécialiser dans l'alimentation d'euphausiacés (krill), les rorquals communs seraient également en mesure d'utiliser d'autres types de proies comme de petits poissons pélagiques tels que le capelan, le hareng et le lançon ainsi que des copépodes (Sergeant, 1977; Overholtz et Nicolas, 1979; Kawamura, 1980; Tershy *et al.*, 1993; Pauly *et al.*, 1998b; Flinn *et al.*, 2002) ce qui suggère que cette espèce serait généraliste. S'il advenait un changement environnemental important dans son écosystème, le rorqual commun étant apte à modifier son régime alimentaire pourrait être favorisé, contrairement aux cétacés qui possèdent une diète plus spécialisée, tel que le rorqual bleu (Gavrilchuck *et al.*, 2014).

Le rorqual commun est distribué mondialement, de l'Arctique à l'Antarctique (Sergeant, 1977), et séjourne chaque année dans l'Estuaire et le Golfe du Saint-Laurent (EGSL). Il y coexiste spatio-temporellement de manière saisonnière avec trois autres espèces de *Balaenopteridae*: le rorqual bleu (*B. musuculus*), le petit rorqual (*B. acutorostrata*) et le rorqual à bosse (*Megaptera novaeangliae*) (Doniol-Valcroze *et al.*, 2007; Lesage *et al.*, 2007). La principale caractéristique des *Balaenopteridae* est d'utiliser une stratégie alimentaire unique, nommée engouffrement (Pivorunas, 1979). En étirant leur poche ventrale, les rorquals augmentent le volume de leur cavité buccale ce qui leur permet d'engouffrer de grandes quantités de proies de petite taille (Pivorunas, 1979). Ils requièrent donc une concentration élevée de proies afin de combler leurs besoins énergétiques (Brodie *et al.*, 1978; Piatt *et al.*, 1989; Piatt et Methven, 1992; Tershy, 1992; Wishner *et al.*, 1995). Ces quatre espèces quittent leurs aires d'hivernage et de reproduction pour venir s'alimenter pendant l'été (Sergeant, 1977; Lockyer et Brown, 1981; Lesage *et al.*, 2007; Parrott *et al.*, 2011) dans les eaux très productives du Saint-Laurent (El-Sabh et Silverberg, 1990; Therriault, 1991; Le Fouest *et al.*, 2005; Dufour et Ouellet, 2007).

L'Estuaire et le Golfe du Saint-Laurent

La grande productivité du Saint-Laurent résulte principalement de la combinaison de deux processus océanographiques : le mélange des eaux douces et salées provoqué par l'effet des marées et la remontée des eaux froides riches en sels nutritifs causée par la dénivellation marquée du sol marin à la tête du chenal Laurentien (El-Sabh et Silverberg, 1990; Dufour et Ouellet, 2007). Sur moins de 20 km, la profondeur du chenal passe de plus de 320 m à moins de 40 m face à l'embouchure du Saguenay (Trites et Walton, 1975).

Les deux dernières décennies ont été le théâtre de changements majeurs dans plusieurs des écosystèmes du monde notamment en raison de la surpêche et de l'effondrement des stocks de poissons de fond (ex. Pauly *et al.*, 1998a; Myers et Worm, 2003, 2005; Heithaus *et al.*, 2008). L'EGSL ne fait pas exception avec l'effondrement de plusieurs de ses stocks de poissons démersaux dans les années 1990 (Myers *et al.*, 1997; Savenkoff *et al.*, 2007; Bundy *et al.*, 2009; Morissette *et al.*, 2009; Plourde *et al.*, 2013) et les changements concomitants dans l'abondance, la distribution et la phénologie des petits poissons pélagiques, des crustacés et du plancton (Worm et Myers, 2003; Frank *et al.*, 2005; Savenkoff *et al.*, 2007; Plourde *et al.*, 2013). Vers le milieu des années 1980 l'écosystème du Saint-Laurent était dominé par des poissons de fond piscivores, principalement la morue atlantique (*Gadus morhua*), alors que cent ans plus tard (milieu des années 1990) il était plutôt dominé par de petits poissons pélagiques à courte durée de vie tels que le capelan (*Mallotus villosus*), le hareng (*Clupea harengus*) et le maquereau (*Scomber scombrus*) (Bundy *et al.*, 2009; Morissette *et al.*, 2009). La dernière décennie des années 1900 ainsi que le milieu et la fin des années 2000 ont aussi été des périodes de profonds changements dans l'écosystème de l'EGSL, notamment au niveau de l'abondance et la phénologie du plancton (Plourde *et al.*, 2013). Depuis 2003-2004, les espèces de plancton de grande taille telles que *Calanus hyperboreus* ont vu leur biomasse augmenter alors que celles des espèces côtières arctiques et d'eaux froides (*Calanus glacialis, Metridia longa*) ont diminué. Les changements dans la phénologie du plancton sont principalement attribuables à des modifications au niveau de la taille et de la saison de recrutement de *Calanus finmarchicus* (Plourde *et al.*, 2013). Parallèlement, une diminution générale des

biomasses du maquereau et du hareng ainsi qu'une augmentation de celle du capelan ont été documentées (Plourde *et al.*, 2013). Au cours des dernières années, des changements dans l'environnement physique ont aussi été relevés : une augmentation significative de la température de surface ainsi qu'une diminution notable de l'indice de couvert de glace (Plourde *et al.*, 2013).

Il existe trois grands facteurs de changements (*regime shifts*) dans les écosystèmes marins : les processus abiotiques (ex. stratification de la colonne d'eau), les processus biotiques (ex. dynamique du réseau alimentaire internes) et les changements à l'habitat structurel (ex. type de fond) (DeYoung *et al.*, 2008). Ces facteurs peuvent être d'origine naturelle ou anthropique et agissent souvent en synergie ce qui rend difficile leur distinction. Les plus fréquents sont généralement associés à des contraintes climatiques à effet *bottom-up*, à l'impact de la pêche commerciale qui a un effet *top-down* ou encore à une combinaison des deux (DeYoung *et al.*, 2004; Steele, 2004; DeYoung *et al.*, 2008). L'effet *top-down* implique le contrôle par la prédation (incluant la pêche) alors qu'un effet *bottom-up* sous-entend un contrôle *via* l'abondance de nourriture (proies primaires à la base de la chaîne alimentaire), abondance qui est elle-même influencée par le climat ainsi que par la charge en éléments nutritifs (Frederiksen *et al.*, 2006).

Dans l'EGSL, l'environnement physique de même que l'abondance, la composition et la phénologie du plancton ont subi des changements graduels et constants suivant une période de stabilité, ce qui suggère que l'écosystème serait en état de transition (Plourde *et al.*, 2013). Cette cohérence entre les indices suggère une propagation du signal à travers la chaîne alimentaire typique d'un effet *bottom-up* (Greene *et al.*, 2013; Plourde *et al.*, 2013). Les indices de biomasse des poissons démersaux et pélagiques ont pour leur part révélé des changements plus marqués résultant potentiellement de processus naturels (recrutement et mortalité), mais aussi de la surpêche (effet *top-down*).

Justification de l'étude

Les changements écosystémiques au sein de l'EGSL ne manqueront pas d'affecter tous les maillons de la chaîne alimentaire, incluant les mammifères marins qui ont une importance économique et culturelle significatives dans la région (Michaud et Giard, 1997). Alors que les populations de certains prédateurs supérieurs comme le phoque gris et le phoque du Groenland se sont fortement accrue depuis les années 1970-80 (Mohn et Bowen, 1996; Bowen *et al.*, 2003; Hammill et Stenson, 2005), les conséquences et l'étendue de tels changements sur la structure trophique de cet écosystème et sur l'alimentation des grands prédateurs comme le rorqual commun demeurent incertaines.

Une étude récente menée sur les rorquals dans le golfe du Saint-Laurent a examiné leur ségrégation trophique et a démontré que les quatre espèces (rorqual bleu, rorqual commun, rorqual à bosse et petit rorqual) consomment des proportions différentes des proies partagées (Gavrilchuck *et al.*, 2014). Concernant le rorqual commun, cette étude n'a pu déterminer avec certitude s'il consomme à la fois du krill et des poissons, ou exclusivement du krill. Cette même étude a mis en lumière l'existence de variations interannuelles dans la diète du rorqual commun de même que de variations interindividuelle de cette diète d'un degré qui demeure ambigüe (Gavrilchuck *et al.*, 2014).

C'est donc dans l'optique de mieux comprendre l'alimentation de cette espèce et ses variations en fonction des secteurs fréquentés et des proies disponibles que cette étude a été entreprise. Une meilleure connaissance de la diète du rorqual commun et des variations spatio-temporelles de celle-ci permettra également de mieux prédire les effets de changements écosystémiques sur cette espèce (Best *et al.*, 2003). L'impact de ce prédateur sur son environnement (rôle écologique) pourra aussi être évalué plus précisément (Knox, 1994; Pauly *et al.*, 1998b; Hooker *et al.*, 2001; Santos *et al.*, 2001; Best *et al.*, 2003). Par exemple, une baleine à fanons consommant de grandes quantités de krill réduira la biomasse de celui-ci ce qui pourrait avoir un effet cascade sur les producteurs primaires ou les autres espèces dépendant de cette ressource. En l'absence de données précises sur la dynamique des populations de proies, le rorqual commun pourrait même servir d'indicateur de l'état des ressources qu'il consomme (Brodie *et al.*, 1978; Bowen *et al.*, 2006; Moore,

2008). Qui plus est, la population Atlantique, dont font partie les rorquals communs séjournant dans le Saint-Laurent, détient un statut préoccupant selon le COSEPAC (COSEWIC, 2011). En vertu du plan de gestion développé dans le cadre de la Loi sur les Espèces en Péril, l'habitat (incluant l'alimentation) et les aires de concentrations de telles populations devraient être décrits (Gouvernement du Canada, 2012). Dans cette perspective, une analyse approfondie de leur diète est d'autant plus justifiée.

Étude des niches trophiques

Dans le cas d'espèces cryptiques[2] vivant dans des environnements difficiles d'accès, tel le milieu marin, l'étude des niches trophiques peut s'avérer particulièrement pénible et laborieuse (Brown, 1995). Différentes stratégies peuvent être utilisées pour étudier la niche trophique des mammifères marins telles que l'observation du comportement d'alimentation (ex. Tershy *et al.*, 1993; Caraveo-Patiño et Soto, 2005) et l'analyse des contenus stomacaux et fécaux (ex. Nemoto, 1959; Nemoto et Kasuya, 1965; Overholtz et Nicolas, 1979; Kawamura, 1980; Jonsgård, 1982; Kawamura, 1982; Ichii et Kato, 1991; Smith et Whitehead, 2000; Flinn *et al.*, 2002; Jarman *et al.*, 2002). Ces techniques traditionnelles reflètent le régime alimentaire à un moment et un endroit précis (Bowen et Iverson, 2013). Les données obtenues à partir de ces techniques fournissent une description détaillée de la composition de la diète ainsi que la fréquence d'ingestion des proies et de l'information au sujet du poids, de la longueur, et parfois du sexe de ces proies (Berg, 1979; Hyslop, 1980; Polito *et al.*, 2011). Les analyses de contenus stomacaux et fécaux peuvent aussi fournir de l'information sur l'écologie des proies, leur distribution (Clarke, 1980), leurs fluctuations saisonnières et leur croissance (Clarke, 1993) ainsi que la biomasse de leur population (Clarke, 1987). L'observation du comportement d'alimentation et l'analyse des contenus stomacaux et fécaux présentent aussi de nombreuses limitations, tout particulièrement au sein d'espèces ne pouvant être capturées et passant la majeure partie de leur vie sous l'eau et loin des côtes, comme c'est le cas pour plusieurs cétacés. En effet, dans de telles

[2] Espèce cryptique : dont la coloration leur permet de se fondre dans leur habitat.

circonstances, l'observation directe du comportement d'alimentation est plutôt rare, de même que l'accès à des fèces ou des contenus stomacaux. L'échantillonnage de ces derniers étant généralement réalisé sur des animaux morts, captifs ou échoués, il en résulte un risque élevé de récolter des données non représentatives d'une population en santé (Smith *et al.*, 2011). Ces deux techniques donnent de l'information sur ce qui a été ingéré et non sur ce qui a été assimilé et intégré dans les tissus de l'animal (Jobling et Breiby, 1986; Jobling, 1987; Bowen et Iverson, 2013). Elles ne tiennent donc pas compte des prises accidentelles ou occasionnelles et peuvent restreindre l'identification des espèces de proie à une zone près du lieu d'échantillonnage (Smith *et al.*, 2011). Finalement, les conclusions tirées des analyses des contenus stomacaux et fécaux sont souvent biaisées vers les proies possédant des composantes solides ou chitineuses (ex. coquilles des crustacés, otolithes et os des poissons, becs des céphalopodes), celles-ci étant plus difficiles à digérer (Da Silva et Neilson, 1985; Jobling et Breiby, 1986; Jobling, 1987; Pierce *et al.*, 1991; Iverson *et al.*, 2004; Dehn *et al.*, 2007; Smith *et al.*, 2011). À l'inverse, les proies à corps mou subissent une digestion rapide et très peu de résidus, voire aucun, sont présents et identifiables dans les échantillons prélevés. Ces proies risquent d'être considérées comme absentes de la diète ou du moins leur contribution à celle-ci risque d'être grandement sous-estimée (Iverson *et al.*, 2004; Dehn *et al.*, 2007; Smith *et al.*, 2011).

L'analyse des rapports de certains isotopes stables (IS) et des acides gras du lard (AG) font partie des méthodes alternatives permettant de déterminer la composition du régime alimentaire des mammifères marins. Ces techniques présentent des avantages par rapport aux méthodes traditionnelles. Elles ont le potentiel de documenter la diète sur une plus longue période de temps que les méthodes traditionnelles puisqu'elles présentent l'analyse de l'ensemble des ressources qui ont été assimilées et intégrées dans les tissus plutôt que ce qui a été ingérés récemment (Jobling, 1987; Hobson *et al.*, 1996; Iverson *et al.*, 1997; Iverson *et al.*, 2004; Dalerum et Angerbjörn, 2005; Newsome *et al.*, 2010; Smith *et al.*, 2011).

Les isotopes stables

Dans le milieu naturel, les éléments du tableau périodique sont présents sous plusieurs formes, nommées isotopes. Ces isotopes se distinguent par leur masse atomique, plus précisément par leur nombre de neutrons, et peuvent être classés en deux catégories : stables ou instables (radioactifs) (Hoefs, 1980; Sulzman, 1994; Fry, 2006). Par exemple, seulement deux isotopes du carbone et deux de l'azote sont considérés stables alors qu'ils en possèdent respectivement 15 et 16 (Hoefs, 1980; Audi *et al.*, 2003). Les isotopes stables les plus légers (ici ^{12}C et ^{14}N) sont largement majoritaires dans l'environnement (Fry, 2006; Ben-David et Flaherty, 2012), mais puisque les énergies de dissociation des molécules dépendent de la masse relative des éléments les constituant, ils sont habituellement métabolisés (et éliminés) plus rapidement que leurs homologues lourds (^{13}C et ^{15}N), faisant en sorte que les tissus des organismes vivants s'enrichissent en isotopes lourds (Hoefs, 1980; Fry et Sherr, 1984; Minagawa et Wada, 1984; Fry, 2006). Cet enrichissement trophique résulte du fractionnement isotopique ou discrimination isotopique (Newsome *et al.*, 2010) et peut varier en raison des différences d'assimilation métabolique des composants alimentaires entre les différents tissus (ex. : lipides, protéines, hydrates de carbone, etc.), mais aussi en fonction de la variation du taux de croissance de l'animal et de la qualité nutritionnelle de son alimentation, des différences dans sa composition en acides aminés et en lipides (Newsome *et al.*, 2010). Le fait que les isotopes stables lourds soient plus rares et qu'ils soient en quelque sorte accumulés par les organismes vivants fait de ces marqueurs biochimiques de bons traceurs de l'alimentation.

La valeur du ratio isotopique ou signature isotopique de l'azote ($^{15}N/^{14}N$ ou $\delta^{15}N$) est utilisée pour déterminer le niveau trophique occupé par une espèce, car le ^{15}N s'accumule progressivement d'un maillon à l'autre de la chaîne alimentaire (2‰-5‰) (DeNiro et Epstein, 1981; Minagawa et Wada, 1984; Owens, 1987; Peterson et Fry, 1987; France et Peters, 1997; Vander Zanden et Rasmussen, 2001; Post, 2002; Vanderklift et Ponsard, 2003; Caut *et al.*, 2009; Newsome *et al.*, 2010). Cette accumulation étant beaucoup plus faible pour le ^{13}C, soit d'environ 1‰ (DeNiro et Epstein, 1978; France et Peters, 1997; Vander Zanden et Rasmussen, 2001; Post, 2002; Caut *et al.*, 2009; Newsome

et al., 2010), la signature isotopique du carbone ($^{13}C/^{12}C$ ou $\delta^{13}C$) est plutôt utilisée afin d'identifier la source, ou l'origine, du carbone alimentaire (Fry et Sherr, 1984). Ainsi, les rapports isotopiques stables permettent d'obtenir de l'information sur l'origine et la transformation de la matière.

Par convention, les ratios isotopiques sont exprimés en notation delta (δ) en fonction de normes établies à l'échelle internationale tels que $\delta^{13}C$ ou $\delta^{15}N$ (‰) = $[(R_{échantillon} / R_{standard}) - 1] \times 1000$, où $R_{échantillon}$ est le ratio $^{13}C:^{12}C$ ou $^{15}N:^{14}N$ de l'échantillon et $R_{standard}$ est celui de la norme de référence appropriée (Ben-David et Flaherty, 2012). Les normes de référence pour le carbone et l'azote étant respectivement les carbonates de Vienne Peedee bélemnite (APB) calcaire (en utilisant l'échelle de Vienne APB) et l'azote atmosphérique (N_2).

Méthode d'analyses des signatures isotopiques

Les dernières années ont vu la popularité des isotopes stables exploser (Phillips *et al.*, 2014). Puisque la signature isotopique du carbone et de l'azote d'un consommateur est principalement déterminée par celle de la nourriture qu'il assimile (Fry, 2006; Newsome *et al.*, 2010) et que les isotopes stables sont incorporés de manière prévisible dans les tissus des consommateurs (DeNiro et Epstein, 1978, 1981), il est possible d'inférer la diète des animaux et d'établir l'étendue de leur niche trophique (Bearhop *et al.*, 2004) à partir de cette signature.

Les modèles de mélange isotopiques (Phillips et Gregg, 2003; Phillips, 2012) permettent de déterminer la contribution proportionnelle d'une source (proie) à la diète d'un consommateur (Moore et Semmens, 2008; Parnell *et al.*, 2010). Récemment, de tels modèles ont été développés dans un cadre statistique Bayésien (SIAR dans R et MixSIR dans Matlab) ce qui permet l'ajout d'incertitude sur tous les paramètres d'entrée. Étant donné leur ajustement hiérarchique, ces modèles offrent une grande flexibilité dans l'ajout de complexité (Parnell *et al.*, 2010; Hopkins et Ferguson, 2012). De plus, l'approche

bayésienne permet d'incorporer un grand nombre de proies de même que de l'information connue *a priori* ce qui permet d'accentuer la précision des estimations des proportions alimentaires (Parnell *et al.*, 2010).

Les modèles bayésiens comportent néanmoins trois prérequis importants. (1) Toutes les proies susceptibles de contribuer de manière significative à la diète du prédateur doivent être incluses dans le modèle et (2) être « isotopiquement » distinctes entre elles (Phillips, 2001). Il est également nécessaire de s'assurer que (3) le facteur d'enrichissement trophique, aussi appelé facteur de discrimination, soit adéquat pour le tissu et l'espèce considérée (Tarroux *et al.*, 2010a; Caut *et al.*, 2011).

Les analyses isotopiques documentent la diète sur une période de temps plus ou moins longue selon le tissu échantillonné. Le temps d'intégration isotopique (*turnover*)[3], sera plus court pour les tissus dont le métabolisme des protéines tissulaires est plus élevé (ex. sérum du sang et foie) que pour ceux dont ce métabolisme est plus faible (ex. muscle et peau). D'autres tissus, comme les os et les dents, représenteront plutôt une période ciblée de la vie de l'animal correspondant à la période de croissance du tissu en question (Tieszen *et al.*, 1983; Koch, 2007; Wolf *et al.*, 2009; Newsome *et al.*, 2010). La quantité de lipides et de protéines, la composition en acides aminés, la taille du corps, le taux de croissance et le taux de renouvellements des protéines influencent aussi le *turnover* ce qui peut mener à des différences de composition isotopique entre plusieurs échantillons provenant d'un seul et même individu (Newsome *et al.*, 2010). Finalement, il faut également tenir compte du fait que la niche isotopique n'est qu'une approximation de la niche trophique puisque c'est une approche indirecte (Newsome *et al.*, 2007).

Les acides gras

Les acides gras (AGs) sont les composantes de base de la majorité des lipides retrouvés dans les organismes vivants (Iverson *et al.*, 2004; Budge *et al.*, 2006; Smith *et al.*, 2011). Ils sont constitués d'une chaîne droite d'atomes de carbone, dont l'une des

[3] *Turnover* : temps nécessaire pour que les valeurs isotopiques du bol alimentaire se reflètent dans celles des tissus de l'animal (Newsome *et al.*, 2010).

extrémités se termine d'un méthyle (CH_3) et l'autre d'un carboxyle (-COOH). Cette chaîne carbonée possède en règle générale un nombre pair de carbones ainsi qu'un certain nombre de liaisons doubles (Budge *et al.*, 2006). Toutefois, sa longueur varie d'un acide gras à l'autre. En effet, certaines ressources alimentaires, comme le lait des mammifères ruminants, présentent des acides gras courts, soit possédant entre 4-6 carbones alors que d'autres, comme le lait de certains animaux monogastriques (ex. rongeurs, lagomorphes et primates, incluant l'humain) ainsi que les lipides de certaines graines en présentent de longueur moyenne, c'est-à-dire ayant de 8-12 carbones (Iverson et Oftedal, 1992; Budge *et al.*, 2006). À l'autre extrémité, il existe aussi des AGs ayant plus de 24 atomes de carbone et plus de 6 doubles liaisons, mais ceux-ci sont présents seulement en quantités infimes et en tant qu'intermédiaires dans la plupart des organismes (Voss *et al.*, 1991). Dans les chaînes alimentaires marines et terrestres impliquant des carnivores de niveau trophique supérieur, les AGs courts (moins de 14 atomes de carbone) sont rarement présents au-dessus de l'état de traces et représentent souvent moins de 0.1% du total des AGs (Budge *et al.*, 2006). Ils sont souvent présents dans des proportions considérables dans les tissus adipeux de plusieurs membres de la famille des odontocètes (baleines à dents), mais ils ne sont pas liés à l'alimentation, car ils sont généralement formés *de novo* par le prédateur (Budge *et al.*, 2006). À l'opposé, les AGs très longs, soit possédant plus de 24 atomes de carbone existent aussi, mais seulement à l'état de traces (Budge *et al.*, 2006). Ainsi, seuls les AGs de 14 à 24 atomes de carbone et contenant de 0 à 6 doubles liaisons sont représentatifs des gammes de longueur et d'insaturation pertinentes pour l'étude de la plupart des prédateurs. Le profil d'AGs d'un prédateur résulte de deux sources métaboliques : (1) les AGs provenant de l'alimentation, qui peuvent être déposés avec peu (ex. élongation de la chaîne de carbones ou ajout de doubles liaisons) ou pas de modification dans les tissus adipeux et (2) les AGs endogènes synthétisés *de novo* par le prédateur (Cook, 1991; Budge *et al.*, 2006). Étant donné qu'un nombre relativement limité d'AGs peuvent être biosynthétisés (Cook, 1991), il est possible de faire la distinction entre ceux-ci et ceux provenant de l'alimentation (voir Iverson *et al.*, 2004), qui par conséquent constituent la principale source d'AGs d'un animal.

Il existe une grande diversité de lipides dans lesquels on peut retrouver les AGs. Dans le milieu marin, plus de 70 d'entre eux peuvent être identifiés et quantifiés (Iverson *et al.*, 2004; Budge *et al.*, 2006), les plus communs étant les triacylglycérols (TAGs), les esters de cire (ECs) et les phospholipides (PLs). Le fait que les AGs n'existent que rarement à l'état libre explique que ces trois catégories soient toutes des lipides acyles, c'est-à-dire des lipides possédant au minimum un acide gras estérifié (Budge *et al.*, 2006). Les TAGs, qui comportent trois AGs estérifiés à un squelette de glycérol, représentent la forme la plus commune de lipides de réserve et constituent la majorité des lipides dans les tissus adipeux et le lard des animaux. Ces derniers mobilisent les TAGs stockés si leurs exigences en AGs ne sont pas comblées par l'alimentation ou, au contraire, vont les déposer lorsque l'apport alimentaire en AGs et en énergie dépasse ces exigences. Ainsi, la composition des AGs de type TAG dans les tissus graisseux est relativement dynamique et largement influencée par le régime alimentaire (Budge *et al.*, 2006). Les ECs se composent d'un AG estérifié à un alcool gras et sont un second type de lipide acyle pertinent dans les études de l'alimentation. En réalité, leurs fonctions sont plus ou moins bien connues, mais tout comme les TAGs, on estime qu'ils sont impliqués dans le stockage d'énergie chez certaines espèces de crustacés, de poissons et de mammifères marins (Budge *et al.*, 2006). Les PLs sont la troisième classe d'acyle lipidique commune. Ils consistent en deux AGs estérifiés à une molécule de glycérol qui contient également un dérivé de l'acide phosphatidique polaire. Les PLs sont un composant structurel de toutes les membranes cellulaires. En raison des fonctions spécialisées de celles-ci, les PLs ne sont que peu sensibles aux changements alimentaires et sont donc un piètre indicateur de la diète chez les prédateurs supérieurs (Budge *et al.*, 2006). D'autres classes de lipides acyles existent (ex. glycolipides, sphingolipides, céramides), mais ils sont relativement rares et contribuent peu à la composition globale en AGs des organismes. Harwood et Russel (1984) ainsi que Gunstone *et al.* (1986) ont fourni des descriptions complètes de ces lipides.

Les AGs sont le plus souvent nommés suivant la notation abrégée C:Dn-x, où C indique le nombre d'atomes de carbone, D le nombre de liaisons doubles et n-x l'emplacement de celle se trouvant la plus proche du méthyle terminal (Iverson *et al.*, 2004; Budge *et al.*, 2006).

Méthode d'analyses des profils d'acides gras

La signature ou profil d'AGs d'un organisme réfère à la distribution quantitative de tous les AGs mesurés pour ce même organisme. C'est un outil de plus en plus utilisé dans divers domaines de recherche particulièrement en ce qui a trait au régime alimentaire, aux interactions trophiques et à la structure des écosystèmes (ex. Grahl-Nielsen et Mjaavatten, 1991; Iverson *et al.*, 1997; Dahl *et al.*, 2000; Hooker *et al.*, 2001; Best *et al.*, 2003; Bradshaw *et al.*, 2003; Budge *et al.*, 2008; Thiemann *et al.*, 2008; Smith *et al.*, 2011; Pomerleau *et al.*, 2014). Largement conservés et déposés dans les tissus adipeux de manière prévisible, les AGs subissent peu de changements biochimiques lors de leur passage dans les chaînes alimentaires.

De nombreuses études ont démontré que des assemblages d'AGs spécifiques sont transférés des proies aux prédateurs à partir de la base de la chaîne alimentaire (ex. Sargent *et al.*, 1987; Fraser *et al.*, 1989; Graeve *et al.*, 1994; Navarro *et al.*, 1995; St. John et Lund, 1996; Kirsch *et al.*, 1998). Les AGs polyinsaturés à longue chaîne carbonée (PUFAs) sont biosynthétisés exclusivement par les producteurs primaires et sont transférés de manière quasi intacte le long de la chaîne alimentaire (Sargent *et al.*, 1987). Par exemple, les AGs 20:5n-3 et 22:6n-3 sont respectivement des marqueurs typiques des diatomées et des dinoflagellés (Kates et Volcani, 1966; Ying *et al.*, 2000)**.** Les AGs mono-insaturés à longue chaîne carbonée (MUFAs), tels que 20:1 et 22:1, sont pour leur part formés uniquement *de novo* chez les copépodes calanoides (Kattner et Hagen, 2009) et leur présence indique une consommation directe de ces derniers ou encore leur ingestion via leur prédateur. Bien qu'il arrive que certains AGs à origine unique soient utilisés comme marqueurs désignant l'ingestion d'une proie ou d'un taxon spécifique, ceci est plutôt rare étant donné

l'omniprésence des AGs dans les milieux marins et terrestres (Iverson, 1993; Budge *et al.*, 2006). En règle générale c'est plutôt l'abondance relative de certains AGs qui est utilisée pour inférer les relations prédateur-proie, identifier les espèces ingérées et la structure du réseau trophique (ex. Iverson *et al.*, 1997; Dahl *et al.*, 2000; Hooker *et al.*, 2001; Best *et al.*, 2003; Dalsgaard *et al.*, 2003; Iverson *et al.*, 2004; Budge *et al.*, 2006; Thiemann *et al.*, 2008).

En bref, puisqu'ils sont conservés et déposés selon un schéma attendu et que la plupart sont synthétisés par des organismes de bas niveau trophique, les AGs permettent d'inférer l'écologie alimentaire des prédateurs soit de manière qualitativement ou quantitativement en agissant en tant que biomarqueurs (Dalsgaard *et al.*, 2003; Iverson *et al.*, 2004; Budge *et al.*, 2006; Budge *et al.*, 2008). Des conclusions qualitatives peuvent être tirées de l'examen d'une série d'AG, c'est-à-dire la signature ou profil d'AGs (Iverson, 1993) et d'une comparaison des individus ou des groupes de consommateurs et de leurs proies potentielles grâce à des techniques statistiques multivariées. De l'information quantitative peut aussi être dérivée des données d'AGs, QFASA (Iverson *et al.*, 2004) étant la seule méthode disponible à ce jour.

Les mammifères marins, en particulier les cétacés, présentent une autre limitation importante en ce qui a trait aux analyses d'AGs, soit une stratification verticale des AGs dans la couche de graisse, couche qui sert à la thermorégulation, mais aussi de réserve énergétique (Iverson *et al.*, 1995). Une telle stratification a été documentée chez les pinnipèdes et les cétacés quoique celle-ci semble plus restreinte chez ces derniers (Ackman *et al.*, 1965; Ackman *et al.*, 1975; Koopman *et al.*, 1996; Hooker *et al.*, 2001; Best *et al.*, 2003; Koopman, 2003; Thiemann *et al.*, 2004; Koopman, 2007; Strandberg *et al.*, 2008; Thiemann *et al.*, 2008). La couche interne (la plus proche du muscle) est métaboliquement la plus active et donc indicatrice de l'alimentation (Budge *et al.*, 2008) puisque c'est là que le dépôt et le retrait des lipides sont les plus actifs (Lockyer *et al.*, 1984; Koopman *et al.*, 1996; Hooker *et al.*, 2001). Ainsi, il serait préférable d'échantillonner toute l'épaisseur de la couche graisseuse ce qui est difficile, voire impossible, avec des techniques de biopsie à

distance (Budge *et al.*, 2006) qui ne prélèvent que la peau et la couche externe de gras, c'est-à-dire de 1.5 à 2.5 cm de graisse (souvent moins d'un quart de l'épaisseur totale de celle-ci) (Hooker *et al.*, 2001). D'autres facteurs peuvent aussi influencer cette stratification : l'âge (Koopman *et al.*, 1996; Koopman, 2003), le statut reproducteur (Stull *et al.*, 1967; West *et al.*, 1979b), la condition physique (Koopman, 2003), le sexe (West *et al.*, 1979a), et l'endroit sur le corps de l'animal (Ackman et Lamothe, 1989; Koopman *et al.*, 1996). Néanmoins, puisque l'importance de cette stratification est moins importante chez les baleines à fanons, des inférences qualitatives peuvent être faites sans trop d'erreur, ce qui permet de documenter la diète sur une période allant de quelques semaines à des mois (Iverson *et al.*, 1995; Iverson *et al.*, 2004; Nordstrom *et al.*, 2008).

Utilisation combinée des isotopes stables et des acides gras

L'utilisation combinée des analyses d'isotopes stables et d'AGs pour déterminer le régime alimentaire des animaux offre une perspective prometteuse (Stowasser *et al.*, 2006; Guest *et al.*, 2008; Jaschinski *et al.*, 2008; Tucker *et al.*, 2008; Guest *et al.*, 2009; Bank *et al.*, 2011; Neubauer et Jensen, 2015). Jusqu'à présent, cette combinaison s'est avérée uniquement qualitative ou fondée sur la base de corrélations positives entre les résultats des deux méthodes. Les analyses d'isotopes stables sont limitées dans la résolution qu'elles peuvent fournir puisque seulement deux ou trois isotopes stables sont généralement mesurés. Le contraste qu'elles peuvent fournir est d'autant plus limité lorsque le nombre de proies augmente (Neubauer et Jensen, 2015). Grouper les proies permet de contourner le problème (Ward *et al.*, 2011; Phillips *et al.*, 2014), mais cela réduit l'étendue de l'interprétation qui peut devenir insatisfaisante, particulièrement pour les réseaux trophiques complexes. Néanmoins, un problème persiste : plus le nombre de proies potentielles augmente, plus l'interprétation des résultats peut devenir compliquée. En plus de permettre une meilleure discrimination entre les proies, la combinaison des deux techniques permet de décrire avec plus de précision les relations prédateur-proie. Le fractionnement trophique des isotopes stables (en particulier l'azote) permet de départager

les similarités de deux signatures découlant d'un chevauchement de la diète de celles résultant d'une prédation d'une espèce sur l'autre, alors que la technique exploitant les AGs est moins puissante à cet égard (Neubauer et Jensen, 2015). Finalement, l'utilisation conjointe des profils d'isotopes stables et d'AGs pourrait réduire l'erreur associée à l'estimation de la diète étant donné la quantité plus importante d'études menées sur les facteurs de discrimination trophiques que sur les coefficients de calibration (Neubauer et Jensen, 2015).

Objectifs

L'objectif principal de cette étude est de documenter le régime alimentaire du rorqual commun dans l'estuaire du Saint-Laurent. Plus spécifiquement, les objectifs sont d'examiner les variabilités interindividuelle, interannuelle et saisonnière de sa diète et d'approfondir les tendances dans sa dynamique trophique dans le contexte d'un climat changeant. L'atteinte de ces objectifs permettra de vérifier l'hypothèse selon laquelle le rorqual commun est une espèce généraliste. Pour atteindre ces objectifs, une combinaison d'analyses des signatures isotopiques et des profils d'AGs de rorquals communs échantillonnés entre 1998 et 2006 a été effectuée.

CHAPITRE 1

FEEDING ECOLOGY OF FIN WHALES IN THE ESTUARY AND GULF OF ST. LAWRENCE INFERRED FROM STABLE ISOTOPE AND FATTY ACID ANALYSES

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Résumé

Identifier le régime alimentaire d'un animal est fondamental pour établir son rôle écologique en tant que consommateur, mais aussi pour évaluer les impacts des changements écosystémiques sur cet animal. La présente étude s'est penchée sur l'écologie alimentaire du rorqual commun (*Balaenoptera physalus*) dans l'Estuaire du Saint-Laurent pour la période 1998-2006. La composition de sa diète de même que les variabilités interindividuelle, interannuelle et saisonnière de celle-ci ont été examinées. 101 individus ont été regroupés selon la similarité de leurs signatures isotopiques ($\delta^{13}C$ et $\delta^{15}N$) grâce à une analyse de groupements. Les contributions relatives de chaque proie potentielle à la diète du rorqual commun ont été établies à l'aide de SIAR, un modèle Bayésien mixte multi-isotopes. Les profils d'acides gras ont ensuite été utilisés qualitativement pour augmenter la discrimination entre les proies et affiner les résultats. Cette étude montre que le rorqual commun est une espèce généraliste, c'est-à-dire qui peut exploiter plusieurs espèces de proies. De la variabilité interindividuelle a été observée, certains individus étant plus spécialisés que d'autres. Le krill arctique (*Thysanoessa raschii*) représentait invariablement la proie dominante du rorqual commun, même si le krill nordique (*Meganyctiphanes norvegica*), et diverses espèces de petits poissons pélagiques pouvaient également être consommés à des niveaux variables selon les individus. Les analyses isotopiques, et dans une moindre mesure celles des acides gras, ont par ailleurs révélé un changement dans la composition de la diète du rorqual commun entre les saisons et au cours de la période d'étude (1998-2006). À partir de l'année 2000, l'importance du krill Arctique a diminué au profit du krill nordique et des poissons (capelan et hareng) dans la diète des rorquals communs, soulevant un certain nombre de questions concernant l'influence de la variabilité du climat sur le régime alimentaire, la distribution, la condition physique et le succès reproducteur (*fitness*) de cette espèce.

Mots clés: rorqual commun · écologie alimentaire · niche trophique · isotopes stables · $\delta^{13}C$ · $\delta^{15}N$ · acides gras · modèles Bayésiens

Abstract

Trophic ecology is central to understand better the ecology of animals and to define their role in ecosystems, but also to assess the impacts of environmental changes on them. This study focuses on the feeding ecology of fin whales (*Balaenoptera physalus*) in the Estuary of St. Lawrence during the period 1998-2006. The composition of their diet and the inter-individual, inter-annual and seasonal variabilities were examined. 101 individuals were grouped according to the similarity of their isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) using a cluster analysis. Proportional contribution of each prey to the diet of fin whale was determined using SIAR, a Bayesian isotopic mixing model. The fatty acid profiles were then used qualitatively to increase discrimination among prey and to refine results. The study demonstrates that fin whale is a generalist species, i.e. it exploits a variety of prey. Some within-species variability was observed, with some individuals being more specialized than others. Arctic krill (*Thysanoessa raschii*) was invariably the dominant prey of fin whale, although northern krill (*Meganyctiphanes norvegica*), and various species of small pelagic fish could be consumed to varying levels depending on individuals. Stable isotopes and to a lesser extent fatty acids also revealed a change in diet between seasons and during the study period (1998-2006). Starting around the year 2000, a decline in the importance of Arctic krill to the benefit of an increase in that of northern krill and fish (capelin and herring) was observed in the diet of fin whales. This raises a number of questions about the potential influence of climate variability on diet, distribution, body condition and fitness of this species.

Key words: fin whale · feeding ecology · trophic niche · stable isotopes · $\delta^{13}C$ · $\delta^{15}N$ · fatty acids · Bayesian models

Introduction

Trophic ecology, the study of the structure of feeding relationships among organisms in an ecosystem, is central to defining species ecological needs and role in ecosystems (Knox, 1994; Pauly *et al.*, 1998b; Hooker *et al.*, 2001; Santos *et al.*, 2001; Best *et al.*, 2003). Trophic niche is the set of resources that an individual or a population selects and uses. Specialist species are composed of individuals all feeding on the same type of prey and often very efficient in their acquisition and assimilation (Stilmant *et al.*, 2008), whereas generalist species may have two feeding patterns: (1) individuals exploit a broad range of prey or (2) individuals are each specialized for a particular prey type, this speciality varying between individuals (Van Valen, 1965; Grant *et al.*, 1976; Bearhop *et al.*, 2004). While that last feeding pattern leads to a high inter-individual variation in the diet, generalist individuals feeding according to the first scheme could have either a very uniform (Bearhop *et al.*, 2004) or variable diet (Huckstadt *et al.*, 2012) as they could all eat the same prey or use an entirely different range of prey. Nevertheless, both generalist feeding patterns reduce inter-individual competition and thus facilitate the acquisition of resources (Partridge et Green, 1985; Bolnick *et al.*, 2003). Numerous studies have demonstrated in various taxa and in a wide variety of ecosystems that specialist species have more difficulty coping with environmental changes, including habitat loss, climate variability, and modification in prey availability or trophic structure (eg. Carlson, 2000; Warren *et al.*, 2001; Munday, 2004; Goulson *et al.*, 2005; Rand et Tscharntke, 2007; Clavel *et al.*, 2010). Generalist species, on the other hand, are expected to be less vulnerable to these changes, and to the risk of extinction (Wilson *et al.*, 2008).

The last two decades have witnessed major changes in several marine ecosystems as a result of overfishing and groundfish population collapses (e.g. Pauly *et al.*, 1998a; Myers et Worm, 2003, 2005; Heithaus *et al.*, 2008). The Estuary and Gulf of St. Lawrence (EGSL), in eastern Canada, is no exception with the collapse of several demersal fish stocks (e.g. Atlantic cod, *Gadus morhua*) in the early 1990s (Myers *et al.*, 1997; Bundy *et al.*, 2009; Morissette *et al.*, 2009; Plourde *et al.*, 2013) that were concomitant with changes

in abundance, distribution or phenology of small pelagic fishes, crustaceans, and plankton (Worm et Myers, 2003; Frank *et al.*, 2005; Plourde *et al.*, 2013). During the 1990s, oceanographic conditions also have changed, and some top marine predators such as the harp and grey seals have increased in abundance (Mohn et Bowen, 1996; Bowen *et al.*, 2003; Hammill et Stenson, 2005). How these multiple changes have affected the trophic structure of this ecosystem and diet of these species and potential competitors remains unclear.

The fin whale (*Balaenoptera physalus*) is the second largest predator after the blue whale (*Balaenoptera musculus*) (Mizroch *et al.*, 1984), and shares some prey resources with the latter. In contrast to blue whales, which appear to specialize in feeding on euphausiids or krill, fin whales may also use other types of prey including small pelagic fish such as capelin, herring and sandlance, as well as copepods (Sergeant, 1977; Overholtz et Nicolas, 1979; Kawamura, 1980; Tershy *et al.*, 1993; Pauly *et al.*, 1998b; Flinn *et al.*, 2002). A recent study conducted on fin whales in the Gulf of St. Lawrence using stable isotopes alone was inconclusive in determining whether they ingested both euphausiids and fish or exclusively euphausiids, but identified inter-annual variability in diet and a long-term decline in their carbon isotopic signatures (Gavrilchuck *et al.*, 2014). Questions also remained as to the degree of inter-individual variability in the diet. Fin whales are far ranging, and may have access to a variety of prey from ecosystems that fundamentally differ in isotopic signatures (e.g. Ruiz-Cooley *et al.*, 2012).

Different strategies can be used to study trophic niches, including direct observation of feeding behavior (Tershy *et al.*, 1993; Caraveo-Patiño et Soto, 2005) or inferences from the analysis of stomach or fecal contents (e.g. Nemoto, 1959; Nemoto et Kasuya, 1965; Overholtz et Nicolas, 1979; Kawamura, 1980; Jonsgård, 1982; Kawamura, 1982; Ichii et Kato, 1991; Smith et Whitehead, 2000; Flinn *et al.*, 2002; Jarman *et al.*, 2002). These analyzes reflect diet at a particular time and place (Bowen et Iverson, 2013). They provide a detailed description of the diet composition as well as the ingestion frequency of prey, and information about their weight, length, and sometimes their sex (Berg, 1979; Hyslop,

1980; Polito *et al.*, 2011). Those techniques present several limitations (Bowen et Iverson, 2013), particularly with species that cannot be captured and that are spending most of their lives underwater and far from the coasts, as it is the case for several cetaceans. They may underestimate the importance of offshore feeding since sampling often occurs at haul-out sites or near land, and reflects only the last few meals. Sampling from dead individuals may also not be representative of a healthy population (Smith *et al.*, 2011). Finally, the conclusions made from stomach contents and fecal analyzes are often biased towards prey with hard or chitinous components (e.g. shells of crustaceans, fish otoliths and bones, beaks of cephalopods), the latter being more difficult to digest (Da Silva et Neilson, 1985; Jobling et Breiby, 1986; Jobling, 1987; Pierce *et al.*, 1991; Iverson *et al.*, 2004; Dehn *et al.*, 2007; Smith *et al.*, 2011). Conversely, soft-bodied prey undergo rapid digestion and very little residue, if any, are present and identifiable in the samples leading to an underestimation of their contribution to the animal's diet (Iverson *et al.*, 2004; Dehn *et al.*, 2007; Smith *et al.*, 2011).

Alternatives for assessing diet composition include the analysis of stable isotopes (SIs) and fatty acids (FAs). These techniques have advantages over traditional methods since they can document diet over various periods of time depending on the tissue used, and reflect the assimilated and not just recently ingested prey (Jobling, 1987; Hobson *et al.*, 1996; Iverson *et al.*, 1997; Iverson *et al.*, 2004; Dalerum et Angerbjörn, 2005; Newsome *et al.*, 2010; Smith *et al.*, 2011). Their common foundation is that these biochemical markers (SIs and FAs) are integrated in a predictable manner in the consumer tissues (DeNiro et Epstein, 1978, 1981; Iverson, 1993; Dalsgaard *et al.*, 2003; Bearhop *et al.*, 2004; Iverson *et al.*, 2004; Budge *et al.*, 2006).

Typically, the SI technique relies on isotopic measurements of two elements, i.e., nitrogen (N) and carbon (C). Stable nitrogen isotope ratios ($^{15}N/^{14}N$ or $\delta^{15}N$) are usually used as indicators of trophic position due to the 2 to 5‰ enrichment per trophic level observed in $\delta^{15}N$ (DeNiro et Epstein, 1981; Minagawa et Wada, 1984; Owens, 1987; Peterson et Fry, 1987; France et Peters, 1997; Vander Zanden et Rasmussen, 2001; Post, 2002; Vanderklift et Ponsard, 2003; Caut *et al.*, 2009; Newsome *et al.*, 2010). The

enrichment is lower for $\delta^{13}C$, at approximately 1 ‰ (DeNiro et Epstein, 1978; France et Peters, 1997; Vander Zanden et Rasmussen, 2001; Post, 2002; Caut *et al.*, 2009; Newsome *et al.*, 2010), making the carbon isotope ratio ($^{13}C/^{12}C$ or $\delta^{13}C$) an adequate tracer of carbon origin (Fry et Sherr, 1984). A common use of SI is to infer diet composition of a predator by comparing its isotopic signature and that of its potential prey. This can be accomplished through mixing models, which convert isotopic data into estimates of proportional contributions of individual prey species to the diet of a consumer (Phillips, 2012).

Recently, Bayesian mixing models have been developed allowing the incorporation of the following features: uncertainties, concentration dependence, large numbers of sources, external or known *a priori* information (Moore et Semmens, 2008; Parnell *et al.*, 2010; Phillips, 2012; Parnell *et al.*, 2013). Given their hierarchical adjustment, they offer great flexibility in adding complexity (Parnell *et al.*, 2010; Hopkins et Ferguson, 2012). However, these models have important prerequisites such as the need for all potential prey to be isotopically distinct and included into the model. Prey sampling needs to be adapted to the period of integration for the tissue sampled. Isotopic turnover rate for epidermal tissue is unknown for baleen whales, and is estimated at 70-75 days in belugas (*Delphinapterus leucas*) and bottlenose dolphins (*Tursiops truncatus*) (Hicks *et al.*, 1985; St-Aubin *et al.*, 1990). Turnover rate is expected to be similar or longer in large cetaceans, given their size and their associated lower metabolic rate (Ruiz-Cooley *et al.*, 2004; Lockyer, 2007). In cases where animals are likely to migrate among regions that are isotopically distinct, there is a need to account for the iso-scape characteristics in diet estimation (West *et al.*, 2010). Isotopic mixing models also require knowing the degree of metabolism (or trophic discrimination) associated with the deposition of each element in a particular tissue (Parnell *et al.*, 2013; Phillips *et al.*, 2014). To be accurately determined, trophic discrimination factors or TDFs (also expressed as $\Delta^{13}C$ and $\Delta^{15}N$) must be obtained through experiments on animals in captivity with known diets. However, TDFs are undefined for large cetaceans, and thus require using surrogate values developed for small cetaceans in captivity studies (Caut *et al.*, 2011), or values that were inferred from field studies of large or small cetaceans (Abend et Smith, 1995; Gendron *et al.*, 2001; Ruiz-

Cooley *et al.*, 2004; Borrell *et al.*, 2012; Gavrilchuck *et al.*, 2014), or from relationships between TDF and the isotopic value of the diet in marine species (Caut *et al.*, 2008).

Diet inferences can also be made using FAs, which represent the basic components of most lipids found in living organisms (Iverson *et al.*, 2004; Budge *et al.*, 2006; Smith *et al.*, 2011). Unlike other nutrients such as proteins, FAs are not easily broken down during digestion, being released directly from the ingested lipid molecules (Iverson, 1993; Dalsgaard *et al.*, 2003; Iverson *et al.*, 2004; Budge *et al.*, 2006). Many studies have shown that specific FAs pattern are transferred from prey to predators (e.g. Sargent *et al.*, 1987; Fraser *et al.*, 1989; Graeve *et al.*, 1994; Navarro *et al.*, 1995; St. John et Lund, 1996; Kirsch *et al.*, 1998). Qualitative inferences can be drawn from single FA known to be synthetized by a specific prey or by examining the overall FA composition, i.e., the FA signature or profile (Iverson, 1993) and comparing it among individuals or groups of individuals and their potential prey using multivariate statistical techniques. Diet can also be described with quantitative proportions using Quantitative Fatty Acid Signature Analysis or QFASA (Iverson *et al.*, 2004). In marine mammals, FAs are thought to reflect diet integrated over a period ranging from a few weeks to a few months (Iverson *et al.*, 1995; Iverson *et al.*, 2004; Nordstrom *et al.*, 2008).

Both SI and FA analyzes are realised from blubber samples which can be sampled remotely through biopsy techniques, but are often limited to the external and middle layers at best. Unfortunately, some vertical stratification of FAs exists in marine mammals, with more structural or saturated FAs being generally more abundant in the external layer compared to the inner layer (Koopman *et al.*, 1996; Thiemann *et al.*, 2004; Strandberg *et al.*, 2008). Thus, the innermost layer, which is the main site of lipids deposition and removal (Lockyer, 1984; Koopman *et al.*, 1996; Hooker *et al.*, 2001), should be more representative of diet as it is thought to be more metabolically active (Budge *et al.*, 2008). Stratification varies between species groups, and is highly influenced by factors such as : individual age (Koopman *et al.*, 1996; Koopman, 2003), reproductive status (Stull *et al.*, 1967; West *et al.*, 1979b), fitness (Koopman, 2003) and gender (West *et al.*, 1979a) as well

as the sampling site along the body (Ackman et Lamothe, 1989; Koopman *et al.*, 1996). Stratification is less pronounced in baleen whales than in small cetaceans (Ackman *et al.*, 1965; Ackman *et al.*, 1975; Koopman *et al.*, 1996; Hooker *et al.*, 2001; Best *et al.*, 2003; Koopman, 2003; Thiemann *et al.*, 2004; Koopman, 2007; Strandberg *et al.*, 2008; Thiemann *et al.*, 2008), making some degree of qualitative inferences possible based on the external and middle layer of the blubber.

The concomitant use of SIs and FAs to examine diet offers a promising perspective. Until now, they have been used in combination in qualitative studies (Guest *et al.*, 2009) or more quantitatively by examining positive correlation of results among the two methods (Tucker *et al.*, 2008). SI are limited in the resolution they can provide in diet estimation given the small number of elements they are based on (usually two or three stable isotopes) compared to FA techniques, which measures the abundance of several tens of FAs and exploit generally 15-20 for diet estimation (Neubauer et Jensen, 2015). In addition to providing increased discrimination power among potential prey items, the combination of the two techniques enables to examine predator-prey relationships through SI trophic enrichment and to reduce errors associated with diet estimates due to the larger body of research on TDFs compared to CCs (Neubauer et Jensen, 2015).

In this study, SI and FA analyses were jointly used in a relatively new way to examine diet composition of fin whales in the St. Lawrence Estuary. A quantitative estimation of diet composition using SI ratios was combined with a qualitative analysis of FA signatures to examine specific questions such as the degree of inter-annual, seasonal, and inter-individual variability in diet composition.

Methodology

2.1. Study area and isotopic features

The St. Lawrence system exhibits a subarctic climate and is considered highly productive (El-Sabh et Silverberg, 1990; Therriault, 1991; Le Fouest *et al.*, 2005; Dufour et Ouellet, 2007). Its drainage basin includes the Greats Lakes, making the EGSL the second most important North American source of freshwater for the North Atlantic Ocean (Le Fouest *et al.*, 2005; Dufour et Ouellet, 2007). The EGSL presents large spatial and temporal variations in its environmental and oceanographic conditions, resulting in diverse biological communities and complex trophic structures (Dufour et Ouellet, 2007).

The EGSL is naturally divided into three regions - the Upper and Lower Estuary , and the Gulf of St. Lawrence (GSL) (Fig. 1), which differ in bathymetry, salinity and water temperature (Trites et Walton, 1975; El-Sabh et Silverberg, 1990; Therriault, 1991; Galbraith, 2006; Dufour et Ouellet, 2007). A strong salinity gradient, from 0 to a maximum of 25 near the mouth of the Saguenay river, characterizes the Upper Estuary; a lesser gradient from ~26 to ~30ppm is observed in the Lower Estuary and northwestern GSL (Trites et Walton, 1975; Tan et Strain, 1979; El-Sabh et Silverberg, 1990). Waters are generally warmer and more turbid in the Upper Estuary than in the Lower Estuary or GSL (Trites et Walton, 1975; Galbraith, 2006; Dufour et Ouellet, 2007). The primary production varies greatly between the EGSL sub-regions. The spring bloom takes place four to eight weeks later in the Estuary than in the GSL where sometimes there is a second peak in the fall (Dufour et Ouellet, 2007). The relatively high productivity of the Lower Estuary originates from a combination of tidal mixing of fresh- and saltwater and the upwelling of cold mineral-rich waters at the head of the Laurentian channel (El-Sabh et Silverberg, 1990; Dufour et Ouellet, 2007). This is the area, along with northwestern and other parts of the Gulf, where a wide variety of marine mammals, from baleen whales to toothed whales and pinnipeds, gather seasonally to feed (Lesage *et al.*, 2007).

The variability in the physical oceanography and productivity among regions of the EGSL influence the isotopic characteristics of the food webs and communities (Dunton *et al.*, 1989; Lesage *et al.*, 2001). Primary producers show high variation in their $\delta^{13}C$ values,

with particulate organic matter (POM) being ^{13}C-depleted compared to benthic macroalgae (Fry et Sherr, 1984), with a difference in the order of 5.3-9.1‰ (Lesage *et al.*, 2001). Moreover, the $\delta^{13}C$ of a particular carbon source may differ between regions, which explain that consumers exploiting the same resource may have different ^{13}C signatures (Dunton *et al.*, 1989). POM in the Lower Estuary (ca –23‰) is generally enriched in ^{13}C by 2 to 3.5‰ compared to its counterpart in the Upper Estuary or GSL (ca –25‰), probably as a result of a higher carbon demand in the Lower Estuary, or differences in phytoplanktonic community structure among areas (Tan et Strain, 1979, 1983). The isotopic difference in ^{13}C is expected to propagate through the food chain, resulting in whales feeding in the Lower Estuary being ^{13}C-enriched relative to those feeding in the Upper Estuary or GSL (Tan et Strain, 1979, 1983), although this difference has been shown to attenuate with the increase in trophic position (Gavrilchuck *et al.*, 2014, Suppl. 2). In contrast, prey items of these three regions seem relatively comparable in their $\delta^{15}N$ values (Lesage *et al.*, 2001).

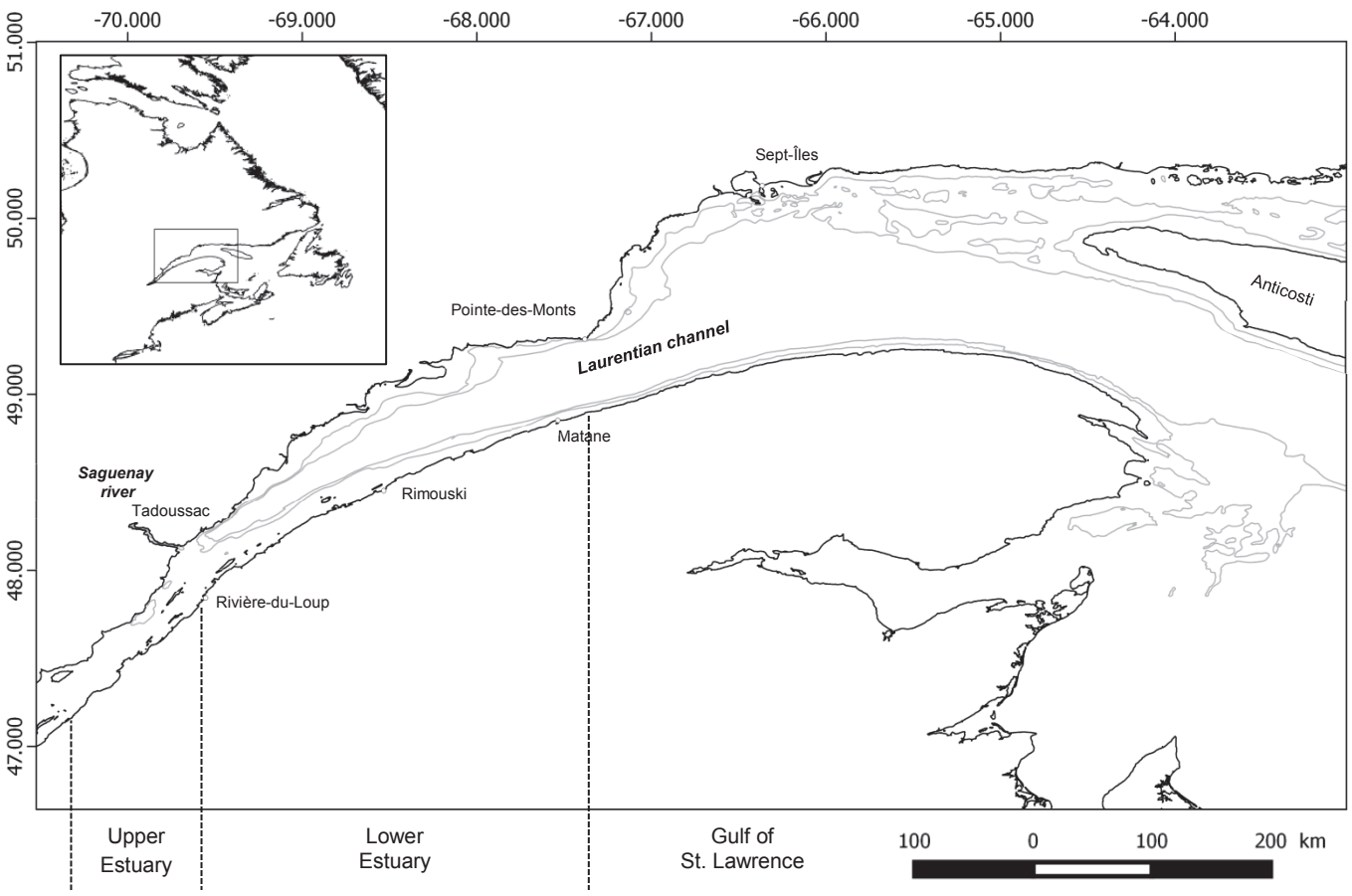


Fig. 1: Study area in the Estuary and northwestern Gulf of St Lawrence, eastern Canada. The light grey lines represent bathymetric lines of 100m and 200m

2.2. Field sampling

A total of 114 biopsies were collected from 101 fin whales in the Lower St. Lawrence Estuary between June and November of 1998-2006 (Appendix 1). Biopsies (consisting of skin and underlying fat) were obtained by remotely projecting a dart (40mm in length and 8mm in diameter) from a 5-8 m vessel. The skin was separated from the fat using a sterile scalpel. Skin samples taken between 1998 and 2001 were preserved in a dimethyl sulfoxide solution (DMSO, 20% v/v) of deionized water saturated with NaCl,

frozen at -20°C (Amos et Hoelzel, 1990), whereas fat samples were frozen directly at -20°C. Skin and fat collected between 2002 and 2006 were directly frozen as separate samples.

Several species of fish and zooplankton (Appendix 2), which may be part of the fin whale diet, were also sampled in the EGSL during various research cruises conducted by Fisheries and Oceans Canada largely over the same period as the whale sampling (between April and November of 1999-2005). Prey were collected following methods outlined in Lesage *et al.* (2010). Briefly, zooplankton samples were collected by vertically towing Bongo nets (1m diameter x 3m length) with a 333µm mesh size, and were kept alive overnight to allow gut content clearance, then sorted to the species and frozen. Fish were collected during bottom trawls or using weir nets deployed from a vessel or the coastline, depending on species, and frozen at -20°C.

2.3. Chemical analyses

2.3.1. Stable isotope analyses

The use of an external substance in preservation method (e.g. formalin and/or ethanol or DMSO) and chemical treatment may alter isotopic signatures of tissue samples (e.g. Hobson *et al.*, 1997; Todd *et al.*, 1997; Barrow *et al.*, 2008; Lesage *et al.*, 2010; Ruiz-Cooley *et al.*, 2011; Burrows *et al.*, 2014). While lipid-removal is highly recommended to avoid distorting isotopic carbon signatures, it is also known to inflate $\delta^{15}N$ values of marine organisms (e.g. Pinnegar et Polunin, 1999; Sotiropoulos *et al.*, 2004; Murry *et al.*, 2006; Sweeting *et al.*, 2006; Mintenbeck *et al.*, 2008). While specific corrections are available for some species, model applicability across taxa and tissues remains questionable (e.g. Sweeting *et al.*, 2006; Bodin *et al.*, 2007; Post *et al.*, 2007; Smyntek *et al.*, 2007; Logan *et al.*, 2008), and there is a general consensus to either apply species- and tissue-specific corrections, or to analyze aliquots separately for carbon (lipid-free) and nitrogen (bulk) isotopic characterization. Similarly, DMSO is known to alter isotopic signatures (e.g.

Hobson *et al.*, 1997; Todd *et al.*, 1997; Lesage *et al.*, 2010; Burrows *et al.*, 2014). Therefore, there is a need to account for this effect prior to data analysis.

Recent studies have examined the effect of lipid-removal and DMSO on the skin of whales and on some of their prey, and correction curves were developed to restore signatures to account for these effects. For instance, the effect of DMSO on baleen whale skin was quantified, and its effect removed by repeated water rinsing and lipid-extraction, and by applying a residual correction on both C and N isotopic signatures (Lesage *et al.*, 2010). Similarly, correction factors specific to baleen whale skin, and to fish muscles were developed for lipid-extracted samples to account for lipid effects on $\delta^{15}N$ values (Lesage et al. 2010; Lesage 2014).

DMSO-preserved samples were therefore processed following Lesage *et al.* (2010), and were repeatedly rinsed with deionized water and lipid-extracted. Skin tissues not preserved in DMSO (i.e., frozen), and prey samples (muscle for and most zooplankton samples except for copepods, which were analyzed whole) were also lipid-extracted, but not rinsed. Samples were first lyophilized until reaching a constant weight, reduced to a powder, then lipid-extracted using the Folch method (Folch *et al.*, 1957). Approximately 0.2 g of dried sample was homogenized with a chloroform/methanol (2:1, v/v) solvent in 10 ml glass tubes. The homogenate was sonicated for 10 min, gently stirred overnight at 4°C, and centrifuged for 10 min to collect the supernatant. This extraction was repeated three times, and the complete extraction of lipids was tested using the sulfophosphovanilline test (Folch *et al.*, 1957). The samples were dried by evaporation, rinsed with distilled water and then dried again overnight at 50°C and powdered. Approximately 1 mg (± 0.005 mg) of this powder was weighed and inserted in tin capsules. The isotope ratios of carbon ($^{13}C/^{12}C$ or $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$ or $\delta^{15}N$) were determined using a mass spectrometer coupled to a continuous flow Carlo Erba Elemental Analyzer (CHNS-O EA-1108, Environmental Isotope Laboratory, University of Waterloo, Canada). Replicates using laboratory standards indicated an analytical error of ±0.2 and ±0.3‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively, whereas

the average deviations observed between replicates of skin and prey samples (n = 101) were 0.11‰ for $\delta^{13}C$ and 0.12‰ for $\delta^{15}N$. The ratio of heavy to light isotope is presented in delta notation (δ) relative to reference standards, carbonates from Vienna PeeDee Belemnite (PDB) limestone (using the Vienna PDB scale) for carbon, and atmospheric N_2 for nitrogen, such that $\delta^{13}C$ or $\delta^{15}N$ (‰) = $[(R_{sample}/R_{standard}) - 1] \times 1000$, where R_{sample} is the $^{13}C:^{12}C$ or $^{15}N:^{14}N$ ratio of the sample and $R_{standard}$ is the ratio of the appropriate standard.

Once lipid-extracted, a final correction was applied to isotopic values of whale skin preserved in DMSO using curves developed by Lesage *et al.* (2010) in order to eliminate its effect in the case of carbon, and eliminate both its effect and that of lipid-extraction in the case of nitrogen :

$$\delta^{13}C_{lipid\text{-}free} = 0.911 \times \delta^{13}C_{lipid\text{-}free\ DMSO} - 1.548 \qquad (1)$$

$$\delta^{15}N_{bulk} = 0.960 \times \delta^{15}N_{lipid\text{-}free\ DMSO} + 0.371 \qquad (2)$$

For samples that were frozen directly, correction factors specific to the skin of *Balaenopteridae* (Lesage *et al.*, 2010), and those developed for fish muscle using 10 species of fish (n = 97 individuals), including potential prey of fin whales (Lesage, 2014) were applied to $\delta^{15}N$ values of lipid-extracted samples to account for lipid effects:

$$\delta^{15}N_{bulk} = 0.998 \times \delta^{15}N_{lipid\text{-}free} + 0.169 \qquad (3)\ \text{whales}$$

$$\delta^{15}N_{bulk} = 0.94704 \times \delta^{15}N_{lipid\text{-}extracted} - 0.03238 \qquad (4)\ \text{prey}$$

So far, there is currently no specific correction developed for zooplankton species. In the absence of data (and while we recognize that lipid content might affect lipid-correction), we assumed that the effect was of a similar amplitude among the range of zooplankton species as it was across the sampled fish species and thus, that the mean enrichment of $\delta^{15}N$ values caused by lipid-extraction was of 0.7‰ on average (Lesage, 2014). The uncertainty related to this correction was taken into account in data analyses (see below).

2.3.2. Fatty acid analyses

Lipids were extracted from a 1.5 g homogenate of fin whale blubber or whole prey sample using modified Folch procedures, as described in Budge *et al.* (2006). A solution of chloroform/methanol solvents (2:1, v/v) and BHT 0.01% (v/v/v) was added to the homogenate as an antioxidant. This mixture was washed with NaCl solution, and centrifuged to separate the lipid-containing chloroform layer, which was then dried with anhydrous sodium sulfate, and evaporated *in vacuo* with nitrogen and ultrasounds. The lipid extract was recovered by gravimetry.

The fatty acid methyl esters (FAMEs) were prepared from ≤ 100 mg of lipid extract using 3.0 ml of Hilditch reagent (0.5N H_2SO^4 in methanol) and 1.5 ml of methylene chloride, following Budge *et al.* (2006). In short, the lipid samples were heated to 100^{o}C for one hour under nitrogen, and FAMEs extracted in hexane, dried with anhydrous sodium sulfate, then evaporated under nitrogen. Highly pure hexane was added back to the FAME solution in order to obtain a concentration of 50 mg ml^{-1}. FAMEs were analyzed using capillary gas-liquid chromatography (Perkin-Elmer Autosystem II) and a flexible fused silica column (30 x 0.25 mm ID) coated with 50% cyanopropyl polysiloxane (film with a thickness of 0.25um, J & W DB-23, Folsom, CA). Helium was used as carrier gas and the gas line was equipped with an oxygen purifier. The temperature program for the gas chromatography is described in Budge *et al.* (2006). The chromatograph was connected to a flame ionization detector (FID) and the peaks identified by comparison with known mixtures. Samples containing large amounts of wax esters (e.g., copepods) were re-analyzed for their fatty alcohols and methylated and then combined with FAMEs as lipid acyl derivatives (Budge et Iverson, 2003), thereby providing the quantification of all lipid components of prey that have been assimilated.

FAs were expressed as mass % of all FAs in the subset of interest, and are named using shorthand nomenclature of C:D*n*-x, where C is the number of carbon atoms, D is the number of double bonds, and *n*-x denotes the position of the first double bond relative to

the terminal methyl end of the FA. Of the identified fatty acids, only the most abundant (contribution > 1% of total fatty acids) or most variable fatty acids, which were derived partially or completely from the diet, were retained for the analysis (Iverson *et al.*, 2004).

2.4. Data analyses

2.4.1. Stable isotopes

Sex differences in $\delta^{13}C$ and $\delta^{15}N$ values (54 females, 47 males) were examined using linear mixed-effects models with sampling year as a random effect to control for potential inter-annual variability (R package "lmerTest"). Trends over the study period (years) and among seasons (Julian days) were examined using Generalized Linear Models (GLM) while including sex as a covariate (R package "stats"). Generalized Additive Models (GAMs) were preferred over GLM when heterogeneity persisted in the residuals from the GLM (R package "mgcv"), and best model selection was confirmed using the Akaike Information Criterion (AIC). For the latter, penalized cubic regression splines, representing smoothed terms, were applied to temporal variables (Wood, 2006) to obtain the best fit possible while incorporating the least amount of error. Optimal degree of smoothing was determined using the Generalized Cross-Validation criterion (GCV).

A hierarchical cluster analysis (R package vegan) was used to reveal the natural grouping of individuals among the sampled whales. Grouping whales was done with the intent to obtain meaningful diets and to allow a better understanding of interindividual variability. As recommended by Hair et al. (1995), 10% of the individuals (n = 11 individuals) representing outliers were excluded from the analysis (Appendix 2) to avoid distorting cluster centroids (Hair *et al.*, 1995). The number of clusters was chosen according to Dunn's index (R package clv). Clustering results were validated using a discriminant function analysis (R package mass) and groupings cross-validated using the weighted k-nearest neighbor method (R package kknn).

Diet composition of each of those groups obtained through the hierarchical cluster analysis was estimated using SIAR, a multi-source, multi-isotope Bayesian mixing model (Parnell *et al.*, 2010; Phillips, 2012; Phillips *et al.*, 2014).

This requires estimation of TDF, and sampling of all potential prey of fin whales. To date, the only controlled experiment available for cetaceans was carried out on a killer whale and yielded TDF values of 2.4‰ and 3.2‰ for $\Delta^{13}C_{lipid\text{-}free}$ and $\Delta^{15}N_{bulk}$, respectively, for skin relative to their prey analysed whole and lipid-extracted only for carbon analyses (Caut *et al.*, 2011). However, the one whale used in this study was sick for three months prior to the experiment and died before the end of it. These TDF values appear high when compared to values inferred from field studies on *balaenopterids.* For instance, blue whales that are assumed to be feeding exclusively on *euphausiids* (undetermined species) had a skin-diet TDF of 1.3‰ for carbon and 1.7-1.9‰ for nitrogen (Gendron *et al.*, 2001). Borrell et al. (2012) obtained a similar value for carbon (1.3‰) with the skin of wild fin whales, also assumed to be feeding exclusively on *euphausiids*. Their nitrogen value was higher (2.8‰) compared to the 1.4-2.0‰ values reported for $\Delta^{15}N$ of the skin of wild pilot whales thought to be feeding on a mixture of mackerel and squid ($\Delta^{15}N$: 1.7‰ if diet is an equal mixture of both) (Abend et Smith, 1995). Sperm whales eating jumbo squid had skin-diet TDFs of 0.4 ± 1.8‰ for carbon and 1.6 ± 3.5‰ for nitrogen, with a notably high variability around estimated TDFs (Ruiz-Cooley *et al.*, 2004). Gavrilchuck *et al.* (2014) who studied four species of rorquals in the Gulf of St. Lawrence, including fin whales, used TDFs values for skin of 0.5 ± 0.5‰ and 1.7 ± 0.5‰ for carbon and nitrogen, respectively. The large standard deviations associated with the TDFs are meant to recognize the uncertainty associated with TDF values in large cetaceans. According to the relationship between the isotopic value of the diet, and that of the discriminant factor (Caut *et al.*, 2008), the estimated TDF value of fin whales for nitrogen should be no greater than 1.3-1.9‰. The relationship between the quality of the diet and the $\Delta^{15}N$ has also been investigated (Vanderklift et Ponsard, 2003; Robbins *et al.*, 2005). The variables most commonly used as a measure of food quality are the percentage in nitrogen content and the C/N ratio of food sources (Hobson et Clark, 1992; Hobson *et al.*, 1993;

Adams et Sterner, 2000; Vanderklift et Ponsard, 2003; Robbins *et al.*, 2005). These measures can be used as substitutes for protein content, which has itself been suggested as influencing the $\Delta^{15}N$ (Vanderklift et Ponsard, 2003). Caut *et al.* (2008) did not find any relationship between the TDF of nitrogen and the C:N ratio, probably because of the homogeneity of the diet they used, while Vanderklift and Ponsard (2003) found a weak relationship. For matter of consistency among studies conducted in the same general area (the St. Lawrence system), the same TDF values as Gavrilchuck *et al.* (2014) were used here, i.e 0.5 ± 0.5‰ and 1.7 ± 0.5‰ for carbon and nitrogen, respectively.

As fin whale diet is largely unknown in the EGSL, potential prey (Appendix 3-4) were selected based on local availability, as well as through an exhaustive review of the specie's diet in other parts of the world (Sergeant, 1977; Overholtz et Nicolas, 1979; Kawamura, 1980; Tershy *et al.*, 1993; Pauly *et al.*, 1998b; Flinn *et al.*, 2002). Not all prey were sampled each year and in sufficient number. As a result, isotopic signatures were averaged for each prey species. However, the effect of prey sampling site (Gulf, Estuary or Saguenay River) on isotopic signature was tested for each prey sampled at multiple sites. Prey sources were pooled *a priori* when their isotope signatures were not statistically different (ANOVA). Sources were combined *a posteriori* by summing the negatively correlated dietary proportions of the isotopic model for each iteration and recomputing posterior probability distributions (Parnell *et al.*, 2013) when their posterior distributions were highly negatively correlated (> - 0.65), indicating they were interchangeable in the models. In both cases (*a priori* and *a posteriori*), prey also had to be biologically or functionally related to be grouped.

2.4.2. Fatty acids

The diet-related FAs retained for the analysis were renormalized over 100% and transformed into centered log ratios (Aitchison, 1983, 1986): $x_t = \log (x_i / g(x))$, where x_i is a given FA expressed as percent of total, g(x) is the geometric mean of the FA data for the sample, and x_t represents the transformed FA data. This transformation standardized all

variables to a mean of 0 and a stable variance (~0.5 for whales and ~0.6 for prey) as PCA and cluster analysis are both highly sensitive to discordant scales (Hair *et al.*, 1995; Quinn et Keough, 2002). Only individuals with both SI and FA data were retained (n = 100 individuals) to allow for comparisons of the groups obtained using the two techniques.

A Principal Components Analysis (PCA; covariance matrix) was carried out on the selected transformed FAs to reduce the dataset to a set of uncorrelated principal components (PCs) that retained most of the variance. Indeed, in PCA collinear variables load on the same PC and PCs being orthogonal, they are uncorrelated with one another. Only the PCs with eigenvalues greater than one (Kaiser-Guttman criterion) were retained and a VARIMAX rotation was applied to maximise the variance between them and to simplify matrix structure and its interpretation. This rotation maximises the loadings of variables correlated with one PC and reduces (near zero) those of variables that are only mildly correlated with it.

The FA data was examined statistically in the same way as the SI data except that VARIMAX rotated PC scores were used as input variables in the FA data analysis. A combination of GLM and GAM was used to examine sex effect (46 females, 44 males) and trends over the study period (years) and among seasons (Julian days), whereas a hierarchical cluster analysis was used to examine groupings among fin whales (Appendix 5). Here again, 10% of the individuals (n = 10 individuals) were excluded to avoid distorting cluster centroids (Hair *et al.*, 1995).

FA profiles of fin whale potential prey were also examined using VARIMAX rotated PCA analysis. The rotated PC scores of prey that were too similar to be discriminated based on stable isotopes alone, were compared using MANOVAs to determine if they differed based on sets of FAs (PCs). Abundance of FAs with the highest loadings were compared qualitatively between whales and prey to determine whether some inferences could be made about the prey most likely contributing to fin whale diet.

All statistical analyzes were performed using various packages developed using the R programming language (R core development team 2013, version 3.0.1).

Results

3.1. Stable isotopes

3.1.1. Fin whale isotopic composition

Individual isotopic signatures of fin whales sampled in the St. Lawrence Estuary between June and November ranged from -21.1 to -16.95‰ for $\delta^{13}C$ and from 9.3 to 14.64‰ for $\delta^{15}N$ (for mean values per year see Table 1). Male (n = 47) and female (n = 54) fin whales exhibited similar isotopic signatures when controlling for sampling year ($\delta^{13}C$: $F = 1.78$, $df = 1$, $p = 0.19$; $\delta^{15}N$: $F = 2.70$, $df = 1$, $p = 0.10$; Table 1). Consequently, the two sexes were pooled to examine year and seasonal effects.

Table 1: Mean (± SD) $\delta^{13}C$ and $\delta^{15}N$ values (‰) for male and female fin whales (corrections for DMSO treatment and lipid extraction have been applied). Sample sizes are indicated in brackets

	$\delta^{13}C$						$\delta^{15}N$					
Year	**Females**			**Males**			**Females**			**Males**		
1998	-17.6	±0.3	(6)	-17.3	±0.2	(5)	10.9	±0.7	(6)	11.4	±1.3	(5)
1999	-17.6	±0.4	(12)	-17.5	±0.3	(16)	11.7	±1.3	(12)	12.1	±1.5	(16)
2000	-17.6	±0.3	(6)	-17.8	±0.3	(6)	11.1	±0.7	(6)	11.2	±1.2	(6)
2001	-17.3		(1)			(0)	11.5		(1)			(0)
2002	-18.5	±0.4	(5)	-18.4		(1)	11.4	±1.1	(5)	11.4		(1)
2003	-18.2	±0.2	(2)	-19.1	±1.8	(3)	11.4	±0.4	(2)	11.6	±1.0	(3)
2004	-18.2	±0.3	(6)	-18.1	±0.1	(3)	11.7	±1.2	(6)	11.7	±0.7	(3)
2005			(0)	-18.2	±0.2	(3)			(0)	12.7	±0.6	(3)
2006	-18.4	±0.3	(16)	-18.3	±0.3	(10)	12.0	±1.0	(16)	12.4	±1.1	(10)
Average	-17.9	±0.3	(54)	-18.1	±0.5	(47)	11.5	±0.9	(54)	11.8	±1.1	(47)

Seven groups were identified among the 90 remaining whales (Dunn index = 1.149; Fig. 2). No clear grouping patterns were observed for the sexes, sampling years or seasons

(Appendix 1). The discriminant analysis identified one significant function (p-value < 0.0001), which explained 88.2% of the total variance. Nitrogen contributed more to the discrimination between groups (b = 4.057) than carbon (b = -0.489) for that first dimension. This was confirmed using pairwise t-tests, which identified significant differences among groups based on nitrogen values only, for all but groups 3 and 4, which were differentiated based on their carbon signatures ($\delta^{13}C$: $t = 8.99$, $df = 25.93$, $p < 0.001$; $\delta^{15}N$: $t = 0.40$, $df = 14.75$, $p = 0.70$). The classification error rate obtained by cross-validation was 6%, with 5 of 90 individuals being misclassified.

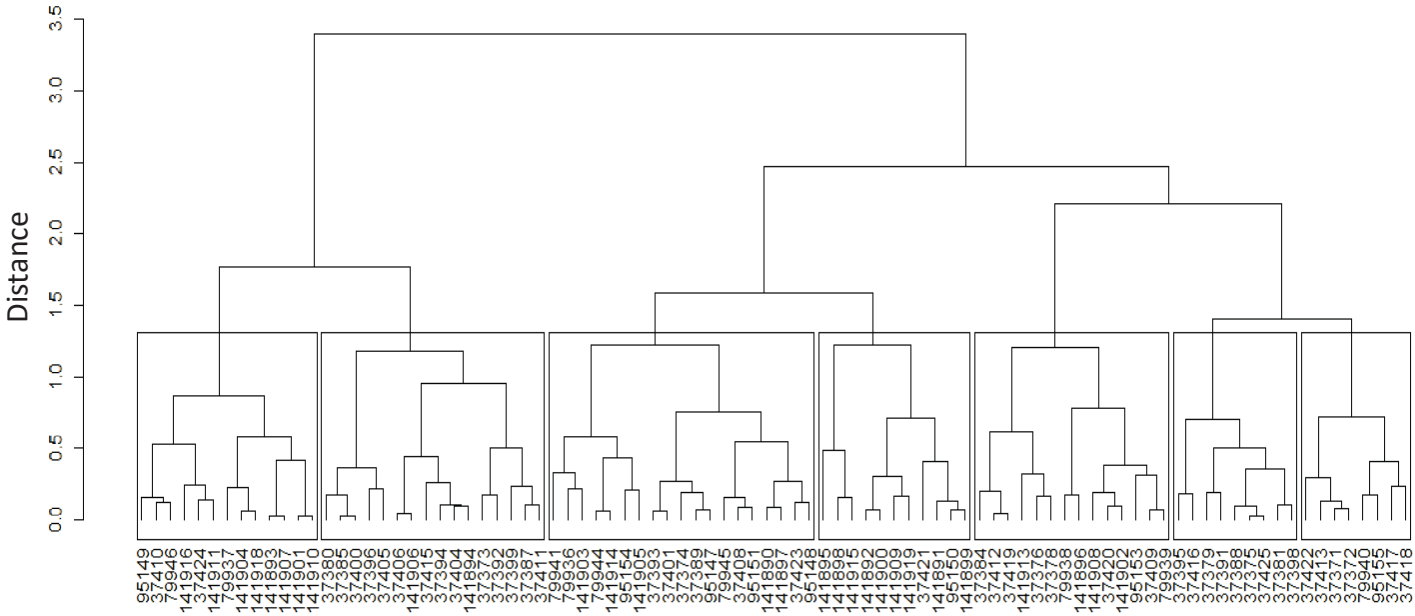


Fig. 2: Connectivity tree from the hierarchical cluster analysis based on the isotopic signatures of fin whales sampled in the St. Lawrence Estuary over the period 1998 to 2006. Boxes indicate groups of whales

3.1.2. Annual and seasonal trends

There was a significant trend over the study period (1998-2006) toward an overall depletion for ^{13}C (Fig. 3A; GAM $edf = 3.67$, $F = 31.96$, $p < 0.001$) and a slight enrichment in ^{15}N (Fig. 3B; GLM $F_{(2,87)} = 3.15$, $p_{year} = 0.14$). There was a significant non-linear seasonal trend in carbon isotope values (Fig. 4A; GAM $edf = 3.56$, $p < 0.001$) toward a

depletion in ^{13}C for animals sampled in September and later months (Julian days 246-324; n = 49) compared to those sampled in June through August (Julian days 100 to 238; n = 52). No linear nor non-linear seasonal trend were identified in $\delta^{15}N$ values (Fig. 4B; GAM *edf* = 2.78; $p = 0.38$). For carbon there was a significant non-linear effect of seasons when years were compared and inversely of years when seasons were compared. This led to think there might be a cross effect between years and seasons for carbon signatures, effect which could be explained by a potential sampling bias. Visually, when adding group assignment on yearly or seasonal trends, groups 2 and 4 were mainly or exclusively composed of individuals sampled prior to 2002 (respectively 88% and 100%; Fig. 3) and prior to September (respectively 88% and 100%; Fig. 4), whereas groups 6 and 7 consisted predominantly in whales sampled between 2002 and 2006 (85% and 91%, respectively; Fig. 3,) and between September and November (92% and 82%, respectively; Fig. 4). Whales in groups 3 and 5 were sampled more evenly across years and seasons (Figs. 3-4). To investigate the effect of this potential sampling bias toward earlier dates in earlier years and later dates in more recent years, the trend in isotopic values over the study period was examined separately for whales sampled prior to and after 1st September, and for whales sampled prior to and after 2002. While the non-linear decline in $\delta^{13}C$ values over the study period remained significant when considering the two seasons separately (Fig. 5; prior to September 1st: GAM *edf* = 2.63, $F = 11.18$, $p < 0.001$; after September 1st: GAM e*df* = 3.50, $F = 2.65$, $p = 0.05$), the increase in $\delta^{15}N$ values over the study period was no longer significant for neither of the two seasons (Fig. 5; prior September 1st: GLM $F_{(2,41)} = 0.95$, $p_{year} = 0.35$; after September 1st: GLM $F_{(2,43)} = 2.56$, $p_{year} = 0.25$). When considering years 1998-2001 separately from years 2002-2006, the decline in carbon isotopic signatures over seasons remained significant only for the period 1998-2001 and not for 2002-2006 (Fig. 6; prior 2002: GAM *edf* = 2.09, $F = 6.92$, $p < 0.001$; after 2002: GAM *edf* = 1.23, $F = 2.16$, $p = 0.13$). The seasonal trend in $\delta^{15}N$ values, which was non-significant with the pooled data, remained non-significant when considering the two blocks of sampling years separately (Fig. 6; prior 2002: GLM $F_{(2,42)} = 1.04$, $p_{season} = 0.33$; after 2002: GLM $F_{(2,42)} = 2.59$, $p_{season} = 0.24$).

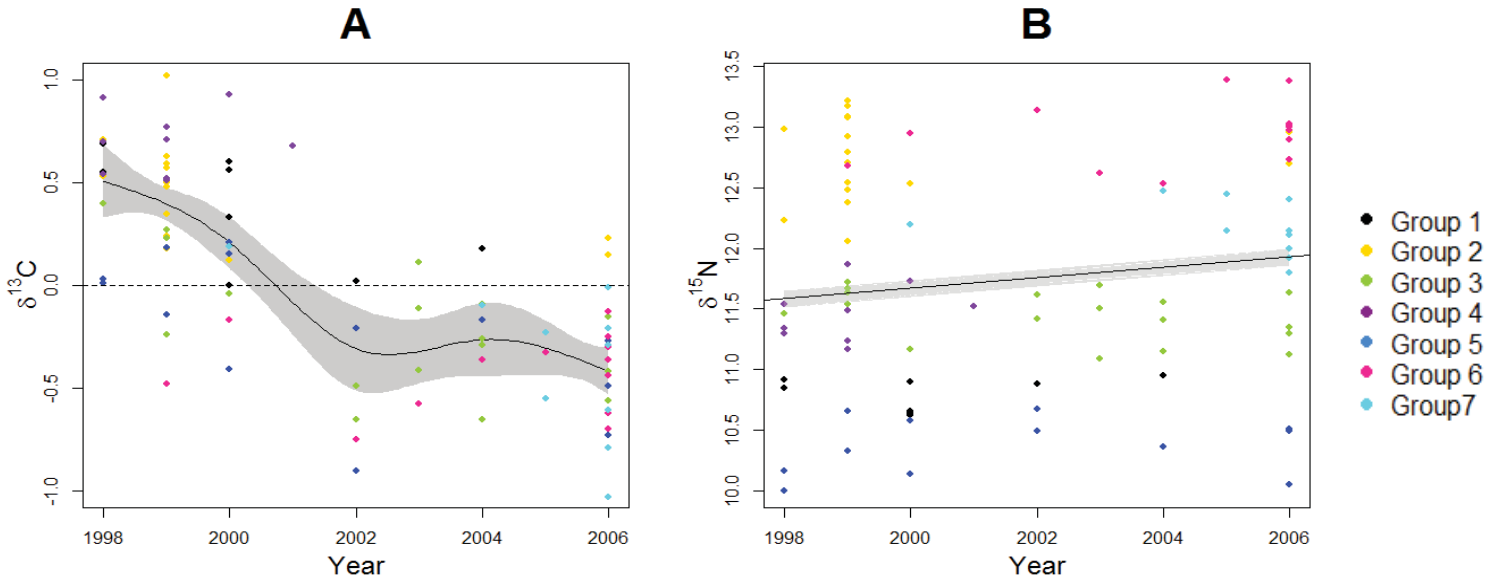


Fig. 3: Annual $\delta^{13}C$ (A) and $\delta^{15}N$ trends (respectively a GAM and a GLM) for fin whales sampled in the St. Lawrence Estuary over the period 1998 to 2006 with group results superposed. The y-axis in A shows deviations from mean isotopic values and the shaded areas in both graphs represent the 95% credibility interval

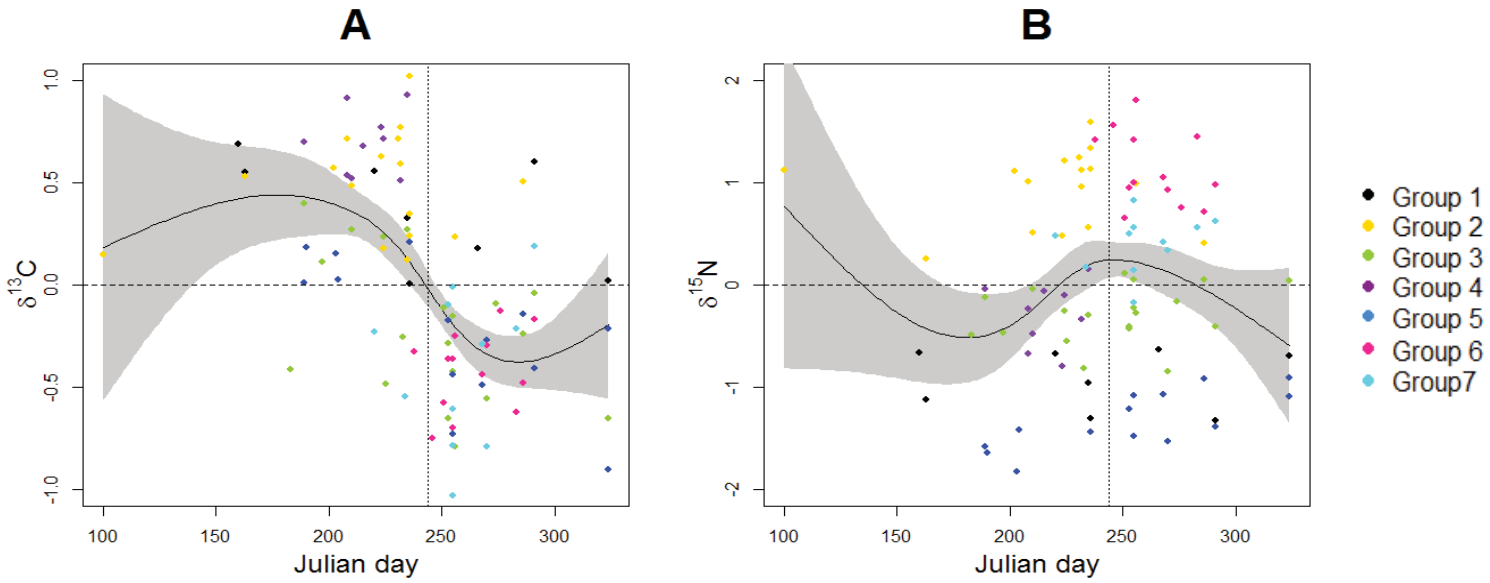


Fig. 4: Seasonal $\delta^{13}C$ (A) and $\delta^{15}N$ (B) trends (GAMs) for fin whales sampled in the St. Lawrence Estuary over the period 1998 to 2006 with group results superimposed. The y-axis shows deviations from mean isotopic values and the shaded area represents the 95% credibility interval. The vertical dotted line represents September 1st

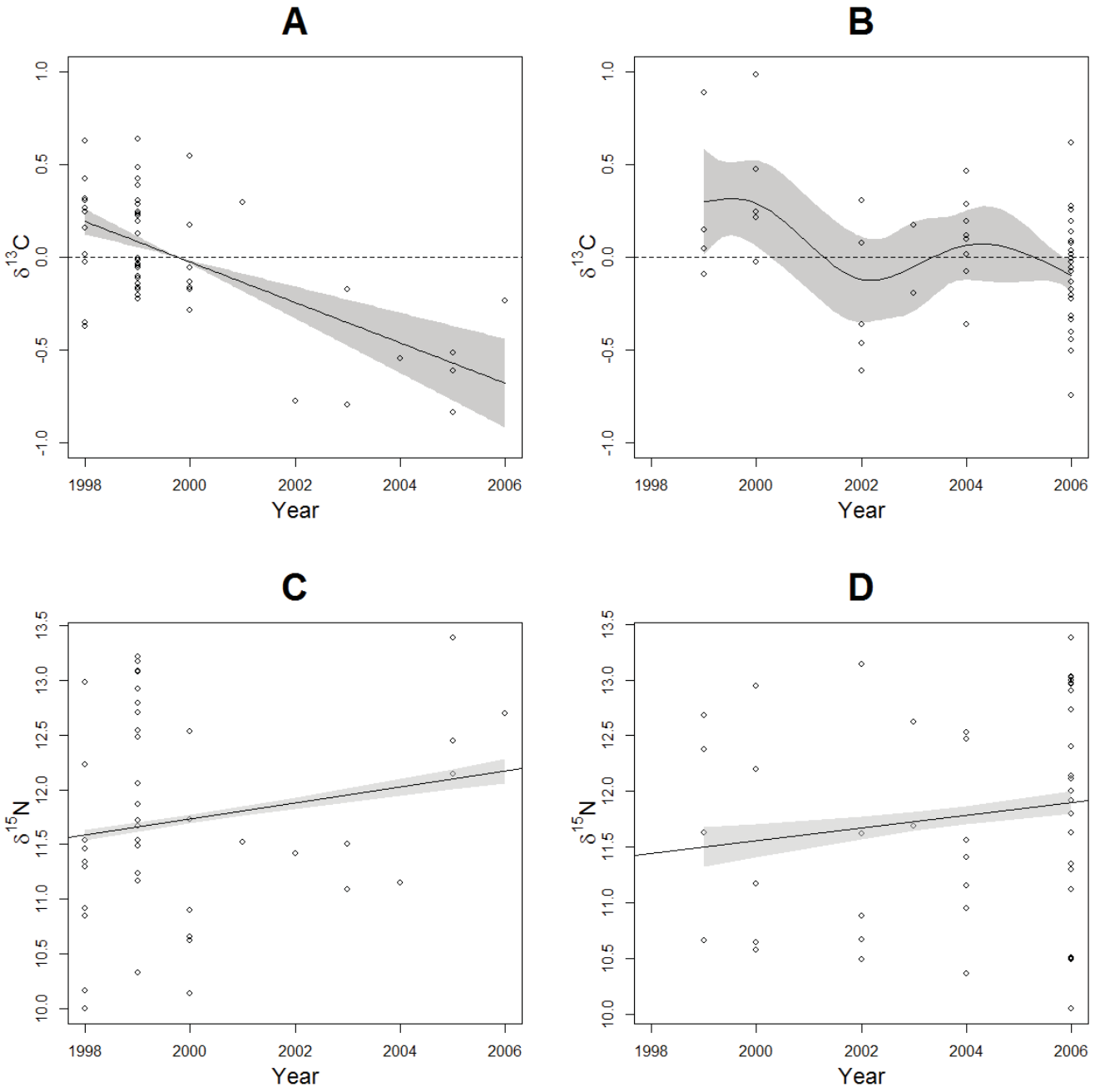


Fig. 25: Interannual $\delta^{13}C$ (GAMs) and $\delta^{15}N$ (GLMs) trends prior (A and C) and after September 1st (B and D) for fin whales sampled in the St. Lawrence Estuary over the period 1998 to 2006. The y-axis in A and B shows deviations from mean isotopic values and the shaded areas across the four graphs represent the 95% credibility interval

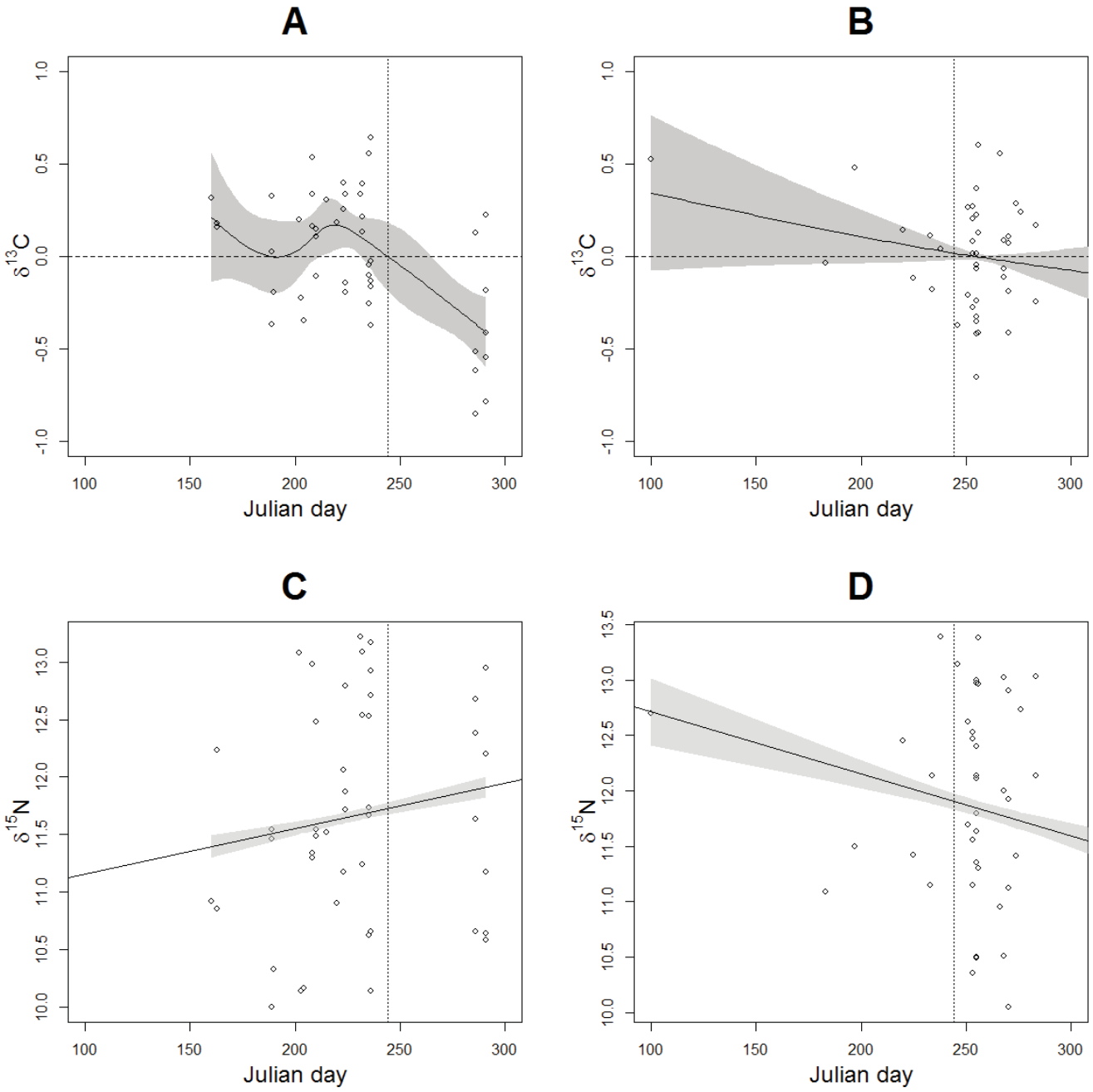


Fig. 6: Seasonal $\delta^{13}C$ (GAMs) and $\delta^{15}N$ (GLMs) trends prior (A and C) and after 2002 (B and D) for fin whales sampled in the St. Lawrence Estuary. The y-axis in A and B shows deviations from mean isotopic values and the shaded areas across the four graphs represent the 95% credibility interval. The vertical dotted line represents September 1st

3.1.3. Prey selection

Based on literature, and on prey distribution and relative abundance in the Estuary, 10 species were considered as potential prey when estimating fin whale diet using isotope mixing models: copepods *Calanus finmarchicus, C. glacialis, C. hyperboreus*, capelin *Mallotus villosus,* Atlantic herring *Clupea harengus,* American sandlance *Ammodytes* sp.*,* northern krill *Meganyctiphanes norvegica,* amphipod *Themisto libellula* and Arctic krill *Thysanoessa raschii* (Table 2).

Table 2: Mean (± SD) $\delta^{13}C$ and $\delta^{15}N$ values (‰) for selected prey according to their sampling site. Sample sizes are indicated in brackets

English name	Latin name	Sampling site	$\delta^{13}C$	$\delta^{15}N$
***Calanoid* copepods**	*Calanus finmarchicus*	Estuary (15)	-19.2 ±0.7	9.1 ±0.5
	Calanus hyperboreus	Estuary (18)	-17.3 ±0.2	9.4 ±0.2
	Calanus sp.	Estuary (12)	-18.8 ±0.2	9.3 ±0.2
	Calanus glacialis	Estuary (2)	-18.9 ±0.1	10.1 ±0.1
Capelin	*Mallotus villosus*	Estuary (96)	-18.4 ±1.0	12.8 ±1.0
		Gulf (10)	-19.5 ±0.2	12.1 ±0.4
		Saguenay (34)	-18.8 ±0.2	12.3 ±0.3
Atlantic herring	*Clupea harengus*	Estuary (46)	-18.0 ±0.9	12.6 ±0.7
		Gulf (12)	-19.8 ±0.8	12.2 ±0.5
American sandlance	*Ammodytes* sp.	Estuary (8)	-18.8 ±0.5	10.8 ±0.3
		Gulf (18)	-18.7 ±0.6	10.9 ±0.5
Northern Krill	*Meganyctiphanes*	Estuary (117)	-19.5 ±0.6	10.8 ±0.4
	norvegica	Gulf (15)	-19.4 ±0.6	10.4 ±0.5
Arctic krill	*Thysanoessa raschii*	Estuary (35)	-18.7 ±0.4	9.5 ±0.7
Amphipod	*Themisto libellula*	Estuary (42)	-19.2 ±0.5	11.8 ±0.6

Prey were pooled across years and locations given the highly uneven sampling scheme over the study area and period. *Calanoid* copepods were entered into the model as a single source. Capelin and herring were isotopically similar (Fig. 7), and thus were grouped *a posteriori*. Diagnostic plots indicated highly negatively correlated diet contributions from

arctic krill and *Calanoid* copepods. These two sources were also pooled, leading to a final isotopic model solution with five dietary sources and two isotopes.

3.1.4. Diet composition

While diet composition varied between fin whale groups, copepods and arctic krill as a combined dietary source was the dominant prey for all groups, and comprised on average between 36 and 72% of fin whale diet (Figs. 8 and 9). Capelin/herring was the second most important prey source for all groups except one (Group 6: 17%), and contributed between 11 and 22% of fin whale diet (Figs.8 and 9). While individuals in group 3 had the highest contribution in copepods/arctic krill (72%) and the lowest in capelin/herring (11%), group 7 showed the exact opposite pattern (copepods/arctic krill: 36%; capelin/herring: 22%). Groups 2, 4 and 6 also had relatively high contributions of capelin/herring (respectively 17, 18 and 17%).

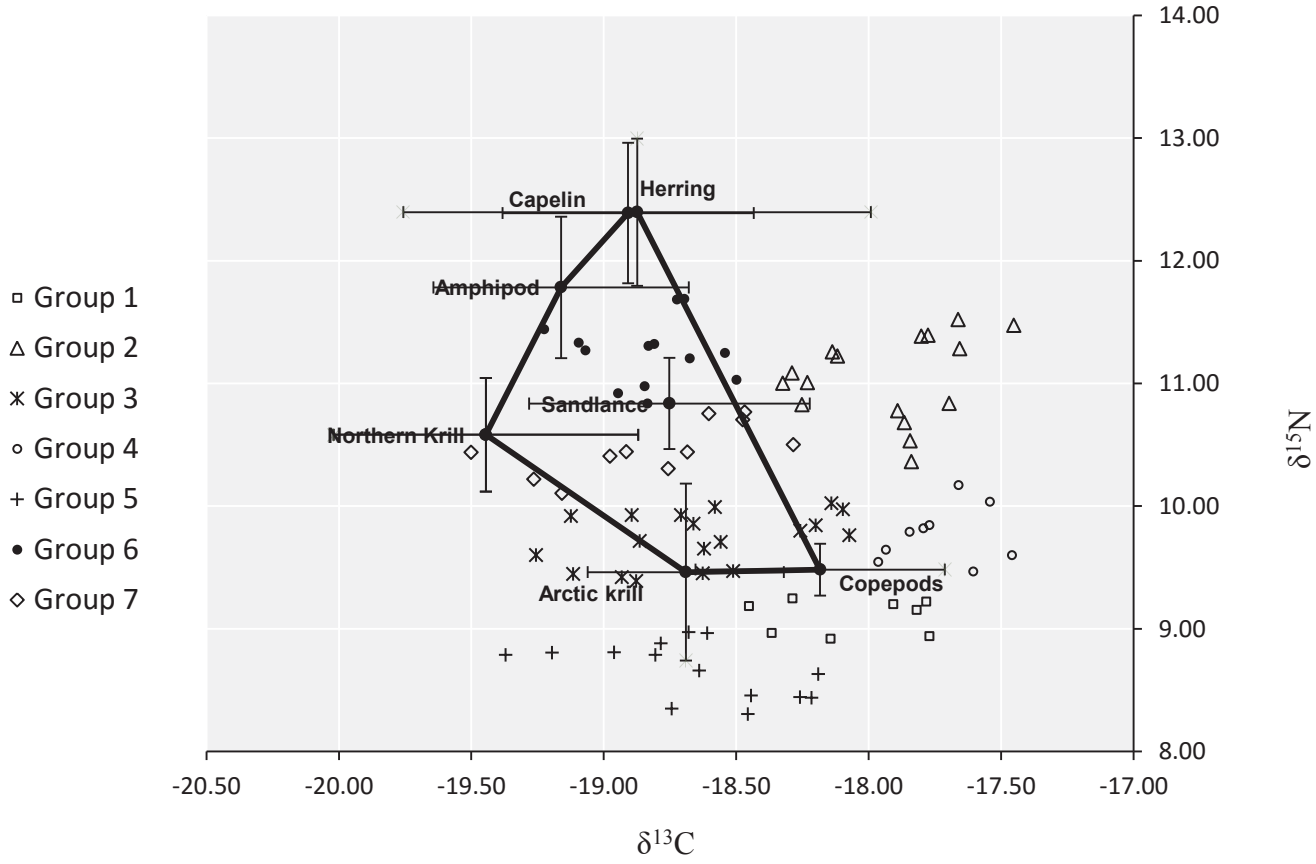


Fig. 7: $\delta^{13}C$ and $\delta^{15}N$ values of St. Lawrence Estuary fin whales *Balaenoptera physalus* and six potential prey sources (copepods *Calanus sp.*, capelin *Mallotus villosus*, Atlantic herring *Clupea harengus*, American sandlance *Ammodytes americanus*, northern krill *Meganyctiphanes norvegica*, amphipod *Themisto libellula* and Arctic krill *Thysanoessa raschii*) sampled between 1998 and 2006 in the EGSL. Prey isotopic signatures are corrected for trophic discrimination (i.e., 0.5 and 1.7‰ for $\delta^{13}C$ and $\delta 1^{5}N$, respectively, with SD = 0.5). Solid lines show the convex hull defined by sources mean isotopic values while broken lines show the maximum convex hull (higher isotopic values possible for sources, taking into account standard errors). Note that sandlance is not a vertex of the convex polygon created, because its inclusion as vertex would create concave sides

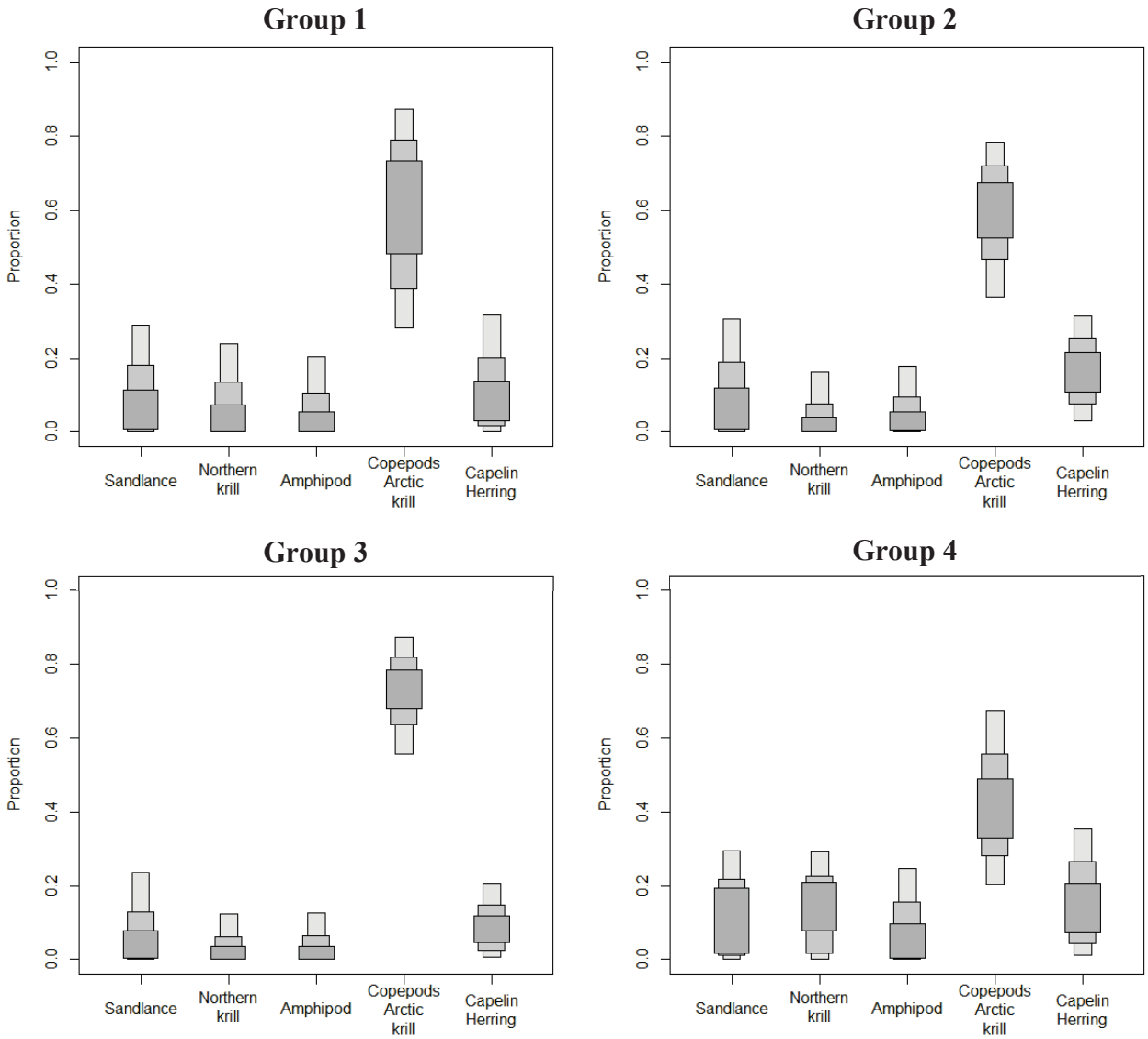


Fig. 8: Overall diet composition estimated for groups 1-4 of fin whales from 1998 to 2006 in the St. Lawrence Estuary. Proportions for each prey source are presented as 50 (inner box), 75, and 95% (outer box) credibility intervals

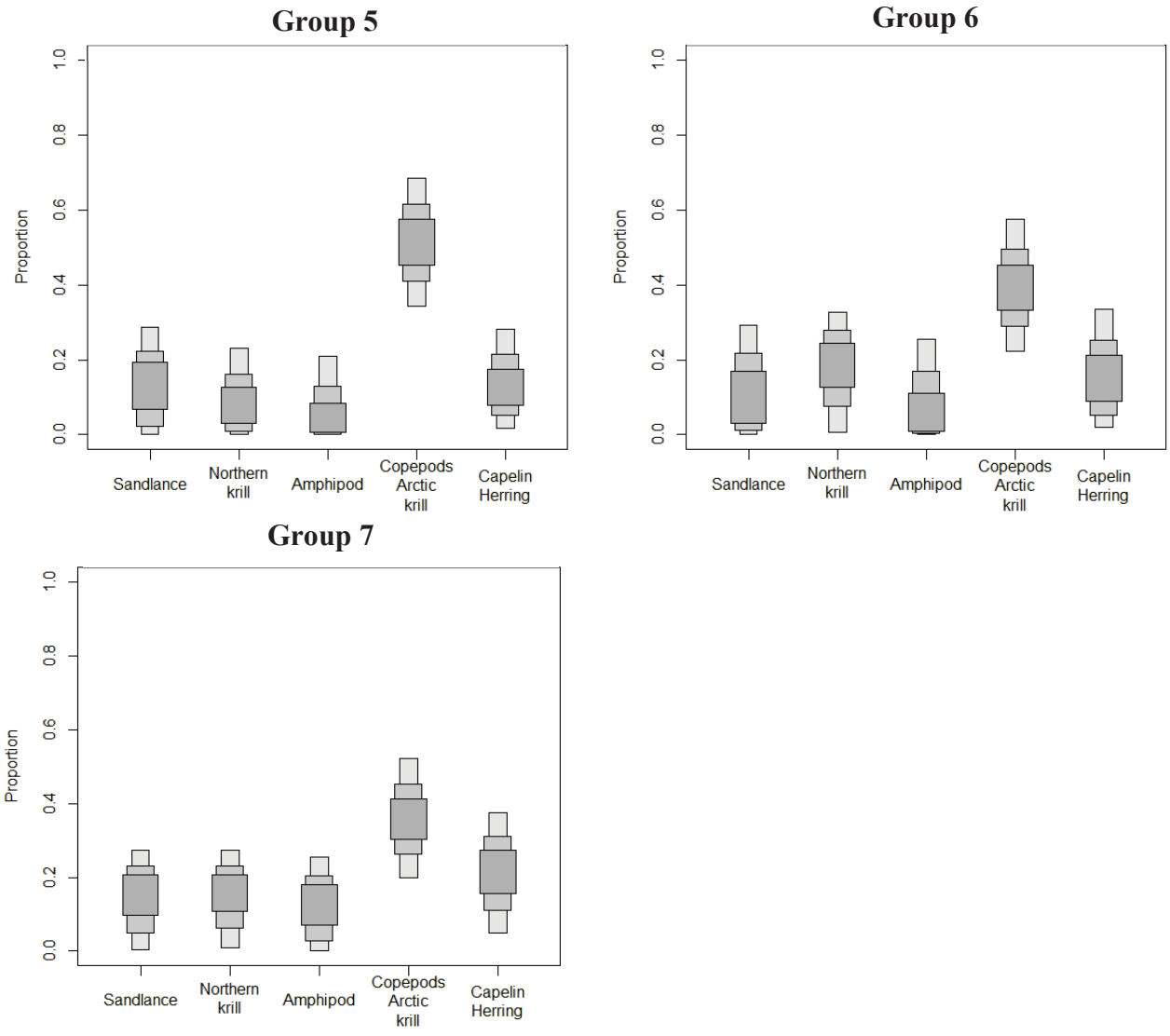


Fig. 9: Overall diet composition estimated for groups 5-7 of fin whales sampled from 1998 to 2006 in the St. Lawrence Estuary. Proportions for each prey source are presented as 50 (inner box), 75, and 95% (outer box) credibility intervals

3.1.5. Trends in the diet composition

The decrease in carbon signature over the study period corresponds to a change from a diet composed almost exclusively of arctic krill/copepod to one that included a greater proportion of fish prey and northern krill (Fig. 10), which is coherent with the

gradual increase in $\delta^{15}N$ over time. Similarly, the seasonal decline in $\delta^{13}C$ values before 2002 corresponded to a progressive increase in the proportion of fish and northern krill in the diet of fin whales (Fig. 11).

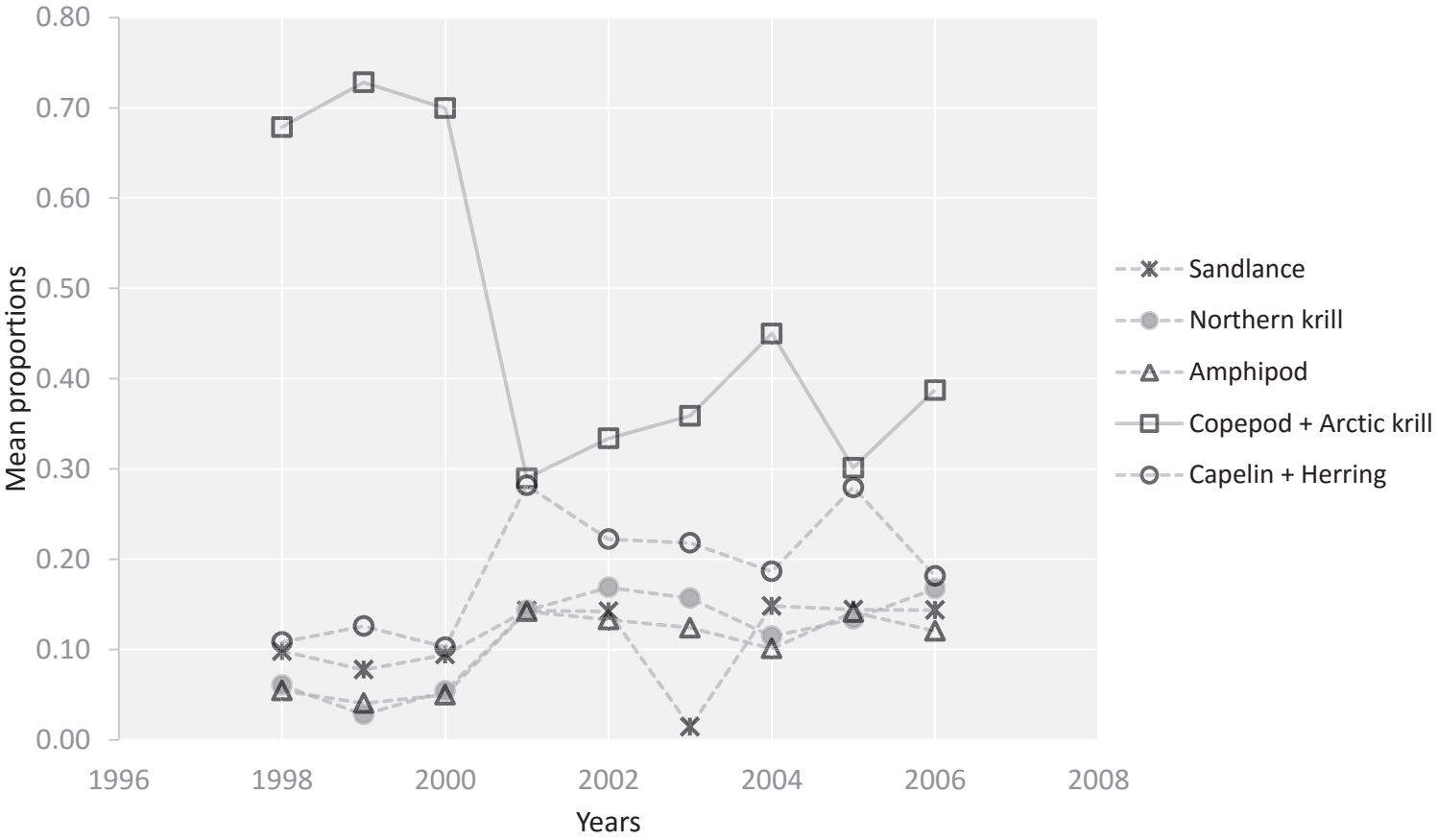


Fig. 10: Diet composition for fin whales sampled from 1998 to 2006 in the St. Lawrence Estuary. The mean proportion of each dietary source is presented for each year and credible intervals have been removed for clarity

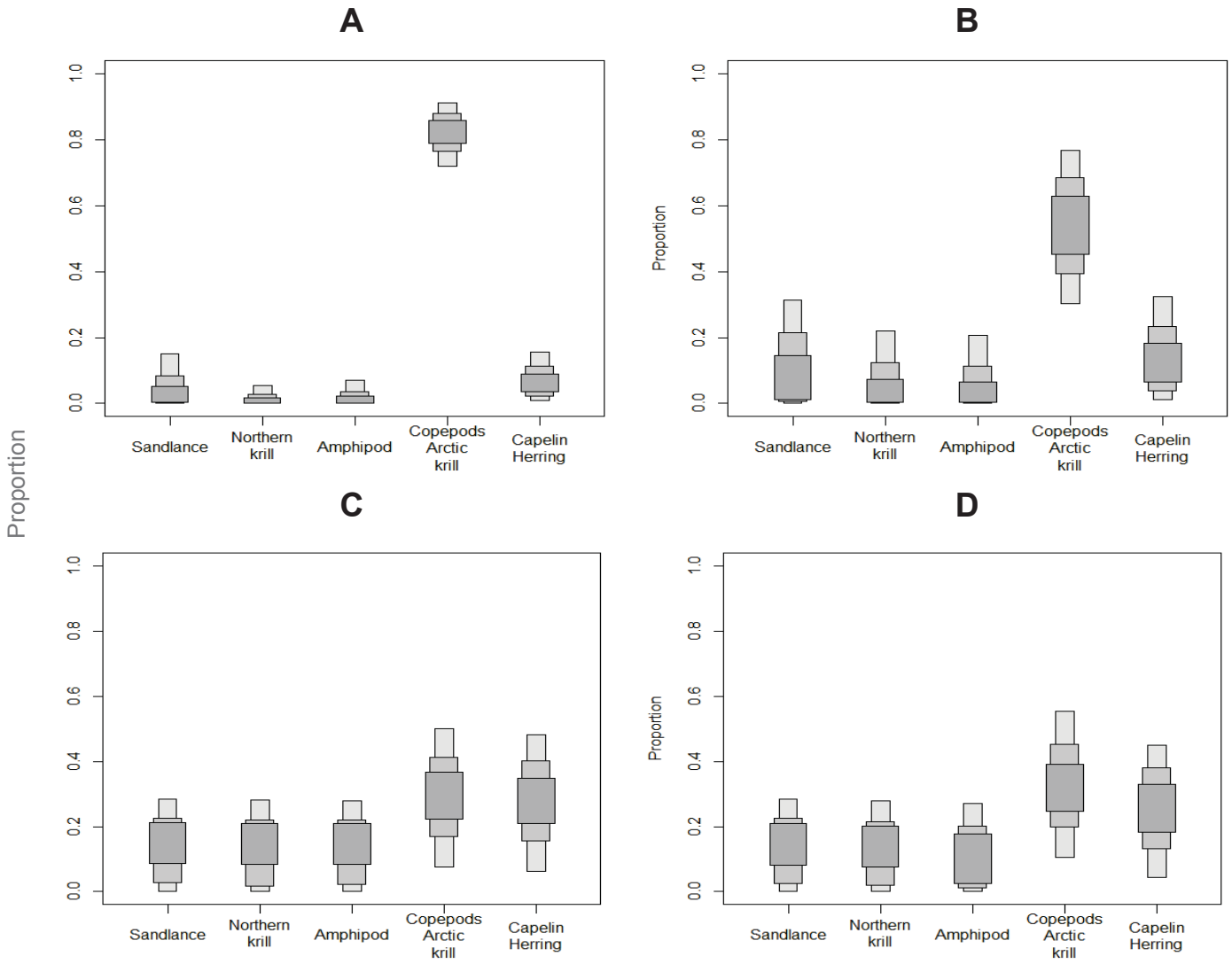


Fig. 11: Overall diet composition estimated for fin whales sampled (A) prior to 1st September and (B) after 1st September of 1998 to 2001 and (C) prior to 1st September and after 1st September of 2002 to 2006 in the St. Lawrence Estuary, estimated using Bayesian isotopic mixing models. Proportions for each prey source are presented as 50 (inner box), 75, and 95% (outer box) credibility intervals

3.2. Fatty acids

3.2.1. Fin whales general FA composition

Fifteen of the 69 fatty acids identified, representing 88.8% of the total FAs, were of dietary origin and contributed > 1% of total FAs (Table 3). The outer layer of fin whale blubber was dominated by monounsaturated fatty acids (MUFAs) with an average of 70.5 ±16.7% of total FA content, the most abundant MUFAs being c18:1n-9, c16:n-7 and c20:1n-9 (Table 3). Saturated fatty acids (SFAs) comprised 18.3 ± 4.0% of the total FA content and were dominated by c16:0, while polyunsaturated fatty acids (PUFAs) contributed the least with an average of 11.1 ± 5.1% (Table 3). These patterns in FA composition were consistent among male and female fin whales (Table 4).

Table 3: FA composition (mass %) of blubber from fin whales sampled in the St. Lawrence Estuary from 1998 to 2006 (n=100). * Designates the 16 FAs retained for analyzes. SFAs = saturated fatty acids, MUFAs = monounsaturated fatty acids and PUFAs

SFAs			MUFAs			PUFAs		
	Average			Average			Average	
c8:0	0.01	±0.01	**c14:1n-9**	0.08	±0.03	**c16:2n-6**	0.05	±0.02
c10:0	0.04	±0.02	**c14:1n-7**	0.06	±0.02	**c16:2n-4**	0.10	±0.04
c12:0	0.11	±0.06	**c14:1n-5**	0.83	±0.32	**c16:3n-6**	0.43	±0.12
c13:0	0.04	±0.01	**c15:1n-8**	0.02	±0.01	**c16:3n-4**	0.14	±0.07
iso14:0	0.04	±0.01	**c15:1n-6**	0.05	±0.02	**c16:3n-1**	0.00	±0.00
c14:0*	4.39	±0.37	**c16:1n-11**	0.52	±0.25	**c16:4n-3**	0.13	±0.05
iso15:0	0.08	±0.02	**c16:1n-9**	0.25	±0.09	**c16:4n-1**	0.13	±0.04
anti15:0	0.18	±0.08	**c16:1n-7***	12.97	±2.52	**c18:2d(5,11)**	0.09	±0.03
c15:0	0.34	±0.13	**c16:1n-5**	0.04	±0.02	**c18:2n-7**	0.08	±0.02
iso16:0	0.09	±0.04	**c17:1**	0.44	±0.14	**c18:2n-6***	1.17	±0.30
c16:0*	10.36	±2.60	**c18:1n-13**	0.36	±0.10	**c18:2n-4**	0.16	±0.04
c7Me16:0	0.28	±0.06	**c18:1n-11***	1.23	±0.42	**c18:3n-6**	0.08	±0.04
iso17:0	0.08	±0.02	**c18:1n-9***	23.17	±2.40	**c18:3n-4**	0.28	±0.05
c17:0	0.23	±0.07	**c18:1n-7***	6.70	±1.07	**c18:3n-3**	0.62	±0.21
c18:0*	1.85	±0.49	**c18:1n-5**	0.49	±0.12	**c18:3n-1**	0.10	±0.03
c20:0	0.15	±0.05	**c20:1n-11***	1.49	±0.59	**c18:4n-3**	0.31	±0.13
			c20:1n-9*	10.57	±3.20	**c18:4n-1**	0.25	±0.09
			c20:1n-7*	1.51	±0.80	**c20:2n-9**	0.20	±0.07
			c22:1n-11*	6.35	±3.20	**c20:2n-6**	0.22	±0.06
			c22:1n-9*	2.36	±0.83	**c20:3n-6**	0.12	±0.04
			c22:1n-7	0.76	±0.44	**c20:4n-6**	0.23	±0.10
			c24:1n-9	0.33	±0.10	**c20:3n-3**	0.17	±0.06
						c20:4n-3	0.51	±0.18
						c20:5n-3*	1.58	±0.90
						c22:2n-6	0.10	±0.06
						c21:5n-3	0.20	±0.09
						c22:4n-6	0.19	±0.10
						c22:5n-6	0.20	±0.11
						c22:4n-3	0.21	±0.11
						c22:5n-3*	1.45	±0.76
						c22:6n-3*	1.64	±1.19
Subtotal	**18.27**	**±4.05**		**70.60**	**±16.66**		**11.14**	**±5.11**
Total							**100.00**	**±25.82**

Table 4: Contribution of the 16 selected FAs (mass % of lipids) in male and female fin whales sampled in the St. Lawrence Estuary from 1998 to 2006 (n = 100)

	Males		Females	
SFAs				
c14:0	4.37	±0.34	4.41	±0.41
c16:0	10.25	±2.78	10.48	±2.43
c18:0	1.80	±0.53	1.89	±0.45
MUFAs				
c16:1n-7	13.24	±2.81	12.70	±2.17
c18:1n-11	1.28	±0.47	1.17	±0.35
c18:1n-9	23.05	±2.41	23.29	±2.40
c18:1n-7	6.60	±1.15	6.80	±0.98
c20:1n-11	1.53	±0.60	1.45	±0.59
c20:1n-9	10.66	±3.67	10.48	±2.67
c20:1n-7	1.48	±0.86	1.54	±0.74
c22:1n-11	6.35	±3.44	6.34	±2.97
c22:1n-9	2.35	±0.94	2.38	±0.72
PUFAs				
c18:2n-6	1.17	±0.32	1.17	±0.29
c20:5n-3	1.54	±1.01	1.62	±0.79
c22:5n-3	1.41	±0.89	1.49	±0.59
c22:6n-3	1.68	±1.37	1.59	±0.97
SFAs	16.42	±3.64	16.78	±3.30
MUFAs	66.54	±16.35	66.15	±13.58
PUFAs	5.81	±3.59	5.86	±2.64
Total	**88.78**	**±23.58**	**88.79**	**±19.51**

As expected, there was collinearity between some of the FAs, especially between the following pairs: c22:1n-11 and c20:1n-9, c22:5n-3 and c20:5n-3, c22:5n-3 and c22:6n-3 as well as between c22.6n-3 and c20:5n-3 (Table 5).

Table 5: Correlations (Pearson) among the 16 selected FAs, where ' ' denotes a correlation of 0.6 or less and '1' perfect correlation. Correlations > 0.6 and < 1 are indicated by figures: triangles for positive ones and circles for negatives. A filled figure indicates a high correlation (0.8 and more)

	c14.0	c16.0	c16.1n7	c18.0	c18.1n11	c18.1n9	c18.1n7	c18.2n6	c20.1n11	c20.1n9	c20.1n7	c20.5n3	c22.1n11	c22.1n9	c22.5n3	c22.6n3
c14.0	1															
c16.0		1														
c16.1n7			1													
c18.0		▲		1												
c18.1n11					1											
c18.1n9						1										
c18.1n7							1									
c18.2n6								1								
c20.1n11					△				1							
c20.1n9					△				△	1						
c20.1n7											1					
c20.5n3	○				○				○	○		1				
c22.1n11									△	▲		○	1			
c22.1n9										△		○		1		
c22.5n3	○								○	○		▲	○	○	1	
c22.6n3					○					○		▲	○	○	▲	1

The 16 FAs were summarized using five principal components (PC) that retained 88% of the total variance (Table 6). PC1 was strongly negatively correlated with three of the four PUFAs and positively correlated with some of the c20 and c22 MUFAs as well as with c18:1n-11. PC2 reflected the positive correlations among the three SFAs, while PC3 was negatively correlated with two MUFAs. PC4 was highly positive for shorter MUFAs, whereas PC5 was strongly positively correlated with c18:2n-6 (Table 6).

Table 6: Loadings for each varimax-rotated PCs of PCA run on fin whales FA profiles. The highest loading for each FA is bolded

	PC1	PC2	PC3	PC4	PC5
SFAs					
c14:0	0.57	**0.59**	0.15	0.28	-0.02
c16:0	-0.24	**0.89**	0.11	0.28	-0.02
c18:0	-0.17	**0.94**	0.09	0.01	0.10
MUFAs					
c16:1n-7	0.07	-0.04	0.17	**0.91**	-0.14
c18:1n-11	**0.63**	-0.29	0.23	0.26	-0.43
c18:1n-9	0.28	0.27	0.02	**0.70**	0.43
c18:1n-7	0.00	0.31	-0.27	**0.79**	-0.01
c20:1n-11	**0.75**	-0.17	0.49	-0.01	-0.19
c20:1n-9	**0.89**	-0.34	-0.01	-0.16	-0.08
c20:1n-7	0.01	-0.17	**-0.92**	0.04	-0.13
c22:1n-11	**0.84**	-0.25	0.07	-0.35	-0.01
c22:1n-9	**0.62**	-0.16	**-0.65**	-0.07	-0.11
PUFAs					
c18:2n-6	-0.17	-0.01	0.17	0.01	**0.93**
c20:5n-3	**-0.92**	-0.06	0.16	-0.28	0.03
c22:5n-3	**-0.95**	-0.08	0.16	-0.16	0.02
c22:6n-3	**-0.90**	0.00	0.17	-0.30	0.08
Variance explained	37%	16%	16%	11%	8%

When controlling for sampling year, FAs loading heavily on each of the PCs were similarly abundant in male and female fin whales, except for those loading high on PC3 (PC3: $F = 4.31$, $df = 1$, $p = 0.04$). Given that sex difference was marginally significant, males and females were pooled when examining year and seasonal effects. Natural groupings of fin whales according to their FA profiles (using VARIMAX scores) were also examined and results are shown in Appendix 5.

3.2.2. Annual and seasonal trends

Both the annual and seasonal trends were tested using 84 whales instead of 90, given that sampling date was not available for some of the whales. There was a significant trend over the study period (1998-2006) toward an overall reduction in mean scores for FAs loading on each of the PCs except the single FA loading high on PC5 (Fig.12; PC1: GAM $edf = 2.49$, $F = 9.85$, $p < 0.001$; PC2: GAM $edf = 2.09$, $F = 7.79$, $p < 0.001$; PC3: GAM $edf = 3.46$, $F = 13.18$, $p < 0.001$; PC4: GAM $edf = 3.71$, $F = 4.18$, $p < 0.001$; PC5: GLM $F_{(2,81)} = 0.80$, $edf = 1$, $F = 1.54$, $p = 0.22$). Inversely, the seasonal trend was significant for none of the PCs (Fig.13; PC1: GLM $F_{(2,81)} = 2.21$, $p_{season} = 0.05$; PC2: GLM $F_{(2,81)} = 2.59$, $p_{season} = 0.03$; PC3: GAM $edf = 3.36$, $F = 1.70$, $p = 0.16$; PC5: GLM $F_{(2,81)} = 0.06$, $p_{season} = 0.80$) except for PC4 which showed a weak but significant decrease in shorter MUFAs from spring through fall (Fig. 13; PC4: GLM $F_{(2,81)} = 4.98$, $p_{season} = 0.005$).

Given the sign of the correlations with each of the PCs, these seasonal and yearly trends in mean scores corresponded to an overall increase in the MUFAs loading strongly on PC3 and PUFAs loading high on PC1, and a decrease in the one PUFA loading on PC 5, the SFAs correlated with PC2, the MUFAs correlated with PC4 and PC1 (Figs. 12 and 13, Table 6). Overall, an increase was observed over time in c20 and c22 PUFAs and in both c20:1n-7 and c22:1n-9, while a decrease was observed in all the other FAs (i.e., all SFAs and almost all MUFAs).

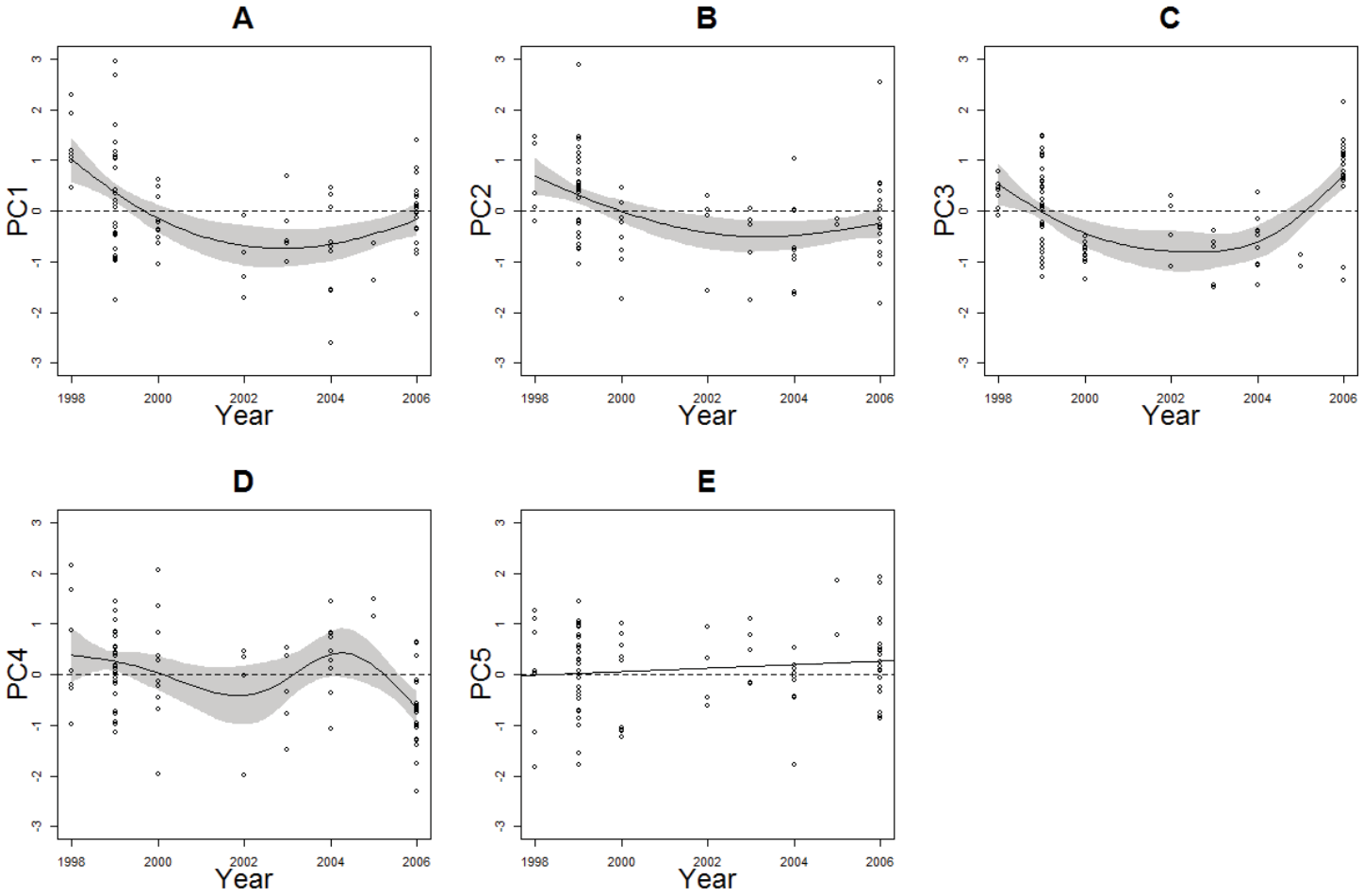


Fig. 12: Annual trends in FA abundance in fin whales sampled in the St. Lawrence Estuary over the period 1998 to 2006, synthesized into 5 rotated PCs (GAMs for graphs A to D; GLM for graph E). The y axis in A to D shows deviations from mean score for a given PC and the shaded areas represent the 95% credibility interval

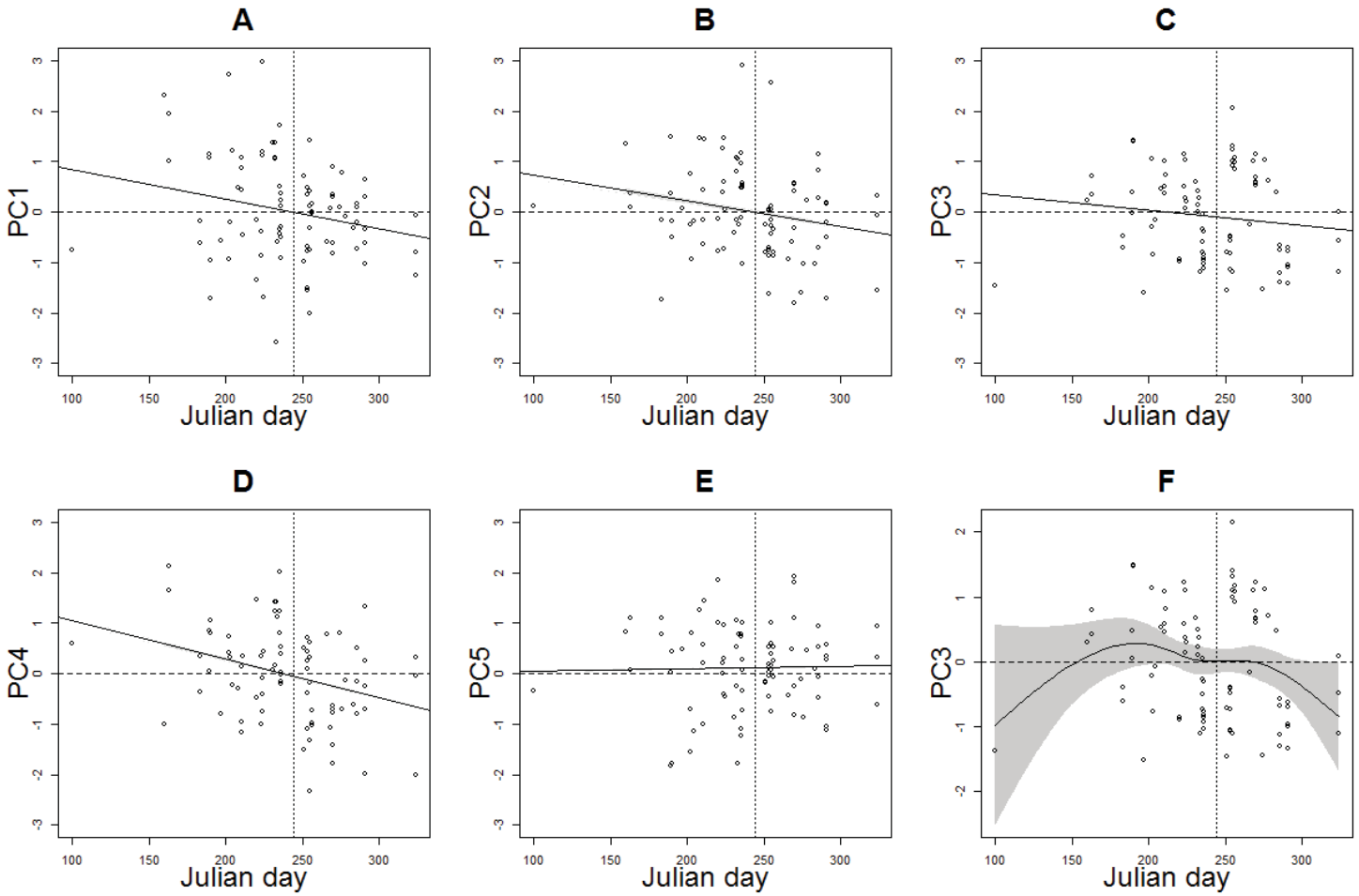


Fig. 13: Seasonal trends (GLMs) in FA abundance in fin whales sampled in the St. Lawrence Estuary over the period 1998 to 2006, synthesized into 5 rotated PC factors (A to E). The vertical dotted line represents September 1st. Graph F represents the only PC (PC3) with a significant non-linear effect (GAM) and its y-axis shows deviations from mean score for a given factor and the shaded area represents the 95% credibility interval

3.2.3. Prey general FA composition

The FA composition of fin whale potential prey is shown in Table 7**.** Overall, MUFAs were the most abundant FAs for all prey. SFAs and PUFAs were generally similarly abundant in all prey, except sandlance and capelin for which PUFAs were more abundant than SFAs. Among MUFAs, c20:1n-9 and c22:1n-11 were generally the most

abundant FAs; SFAs and PUFAs were dominated by c16:0 and c20:5n-3, respectively (Table 7, Fig. 14, Appendix 6-7-8-9).

Table 7: FA composition of selected FAs (mass %) of potential prey of fin whales

	Sandlance (n = 42)	**Copepod** (n = 12)	**Herring** (n = 126)	**Capelin** (n = 101)	**Northern krill** (n = 33)	**Amphipod** (n = 16)	**Arctic krill** (n = 5)
SFAs							
c14.0	4.0 ±1.2	3.4 ±1.9	4.8 ±1.0	4.1 ±1.6	4.3 ±0.6	4.5 ±0.6	4.8 ±0.2
c16.0	14.7 ±3.8	4.9 ±0.7	12.2 ±2.7	15.4 ±3.2	13.0 ±1.5	10.1 ±2.4	15.3 ±0.6
c18.0	2.7 ±1.2	0.3 ±0.1	1.3 ±0.5	1.9 ±0.7	1.2 ±0.2	0.8 ±0.3	2.3 ±0.1
MUFAs							
c16.1n7	6.8 ±2.0	8.8 ±0.4	6.6 ±1.7	6.6 ±3.2	8.7 ±0.8	7.9 ±1.1	9.8 ±0.4
c18.1n11	0.4 ±0.2	0.1 ±0.1	0.6 ±0.3	0.6 ±0.3	0.1 ±0.0	0.4 ±0.1	0.1 ±0.0
c18.1n9	6.9 ±2.4	1.9 ±1.2	7.2 ±3.1	9.3 ±3.9	8.2 ±0.8	10.2 ±2.5	8.8 ±0.3
c18.1n7	3.6 ±1.5	1.4 ±0.1	2.9 ±1.0	4.0 ±1.4	4.2 ±0.4	3.3 ±1.0	4.9 ±0.4
c20.1n11	0.4 ±0.2	0.6 ±0.4	1.1 ±0.7	0.5 ±0.3	0.6 ±0.1	3.9 ±1.5	0.4 ±0.1
c20.1n9	8.4 ±4.9	21.6 ±1.8	14.0 ±4.0	8.3 ±5.4	12.5 ±2.8	15.9 ±4.6	7.8 ±0.8
c20.1n7	0.6 ±0.3	2.6 ±0.5	0.9 ±0.3	0.7 ±0.4	0.9 ±0.2	1.1 ±0.2	0.8 ±0.1
c22.1n11	9.5 ±5.7	29.1 ±1.4	20.3 ±5.7	8.8 ±6.4	15.5 ±2.9	15.6 ±5.7	6.4 ±1.1
c22.1n9	1.1 ±0.7	3.4 ±0.7	1.8 ±0.7	0.9 ±0.6	1.5 ±0.3	1.8 ±0.5	1.0 ±0.1
PUFAs							
c18.2n6	0.9 ±0.3	0.2 ±0.1	0.6 ±0.2	0.7 ±0.2	0.8 ±0.2	0.8 ±0.1	0.6 ±0.0
c20.5n3	12.7 ±2.1	7.3 ±1.0	7.0 ±2.4	11.9 ±3.1	10.1 ±1.6	8.2 ±2.3	14.6 ±0.5
c22.5n3	0.9 ±0.3	0.6 ±0.1	0.7 ±0.2	1.1 ±0.4	0.4 ±0.0	0.4 ±0.1	0.5 ±0.0
c22.6n3	14.7 ±5.9	2.8 ±0.6	9.5 ±4.1	15.9 ±8.4	8.9 ±1.8	7.0 ±1.3	6.0 ±0.3
Total							
SFAs	21.4 ±6.2	8.6 ±2.7	18.2 ±4.1	21.5 ±5.6	18.5 ±2.4	15.3 ±3.2	22.4 ±1.0
MUFAs	37.7 ±17.9	69.5 ±6.7	55.4 ±17.5	39.8 ±21.9	52.1 ±8.4	60.2 ±17.2	39.9 ±3.2
PUFAs	29.1 ±8.6	10.8 ±1.7	17.8 ±6.8	29.6 ±12.2	20.2 ±3.6	16.4 ±3.8	21.6 ±0.9
Total	88.1 ±32.7	88.9 ±11.1	91.4 ±28.4	90.9 ±39.7	90.8 ±14.4	91.9 ±24.2	83.8 ±5.1

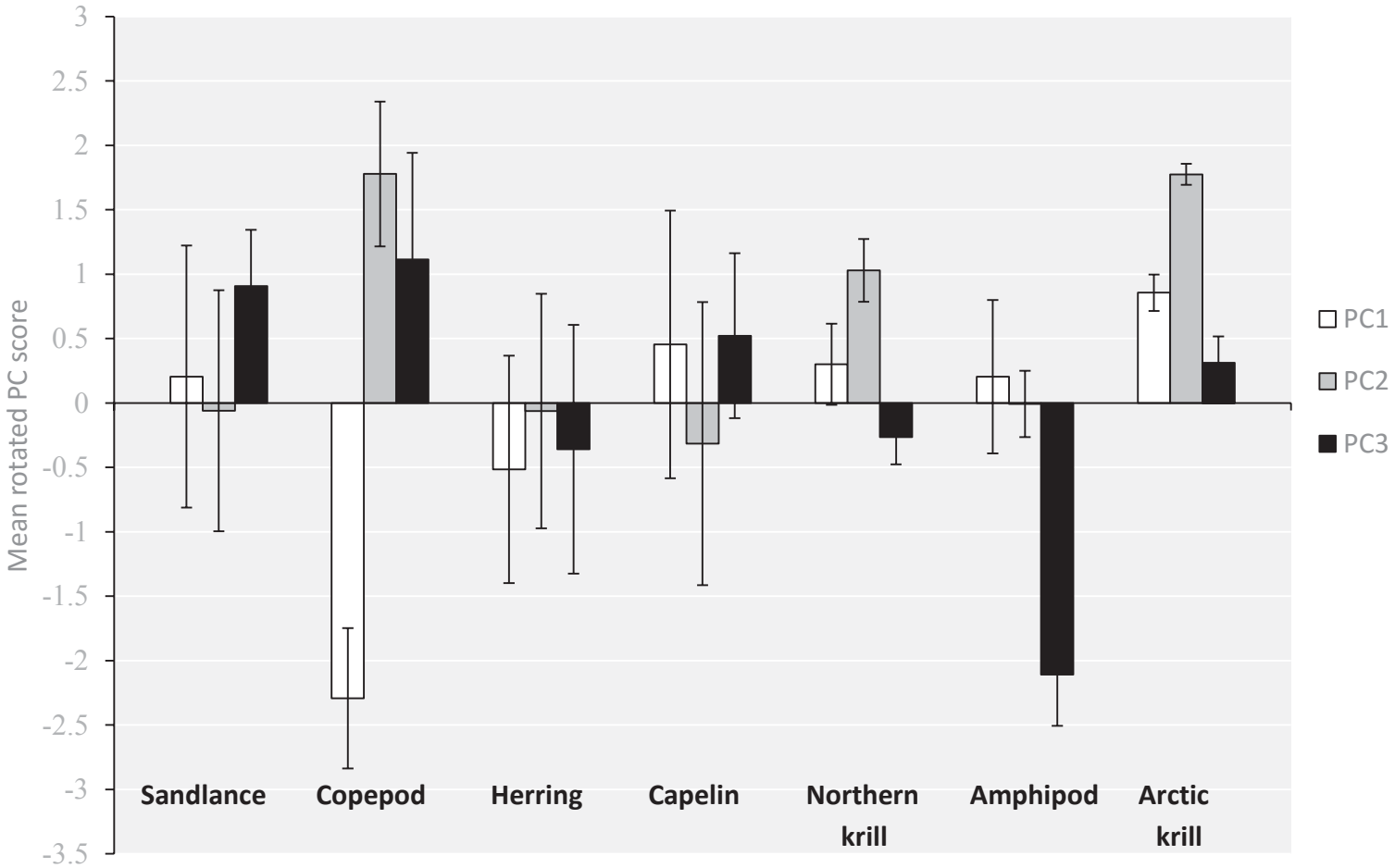


Fig. 14: Mean rotated PC scores and standard deviation for each selected prey

Correlations among prey FA profiles were also summarized using PCA, with three PCs being retained and explaining 82% of total variance (Table 8). PC1 was strongly correlated with several MUFAs, some positively (c18) others negatively (c20 and c22). PC2 was positively correlated with both c16:1n-7 and c14:0 and negatively correlated with c18:1n11 and c22:6n-3. Finally, PC3 was positively correlated with two PUFAs and negatively with 20:1n-11 (Table 8).

Table 8: Loadings for each rotated PCs of PCA run on prey FA profiles. Higher loadings are bolded

	PC1	PC2	PC3
SFAs			
c14:0	-0.23	**0.67**	-0.15
c16:0	**0.87**	0.06	0.40
c18:0	**0.78**	-0.27	0.45
MUFAs			
c16:1n-7	-0.02	**0.93**	0.03
c18:1n-11	-0.07	**-0.81**	-0.16
c18:1n-9	**0.94**	0.05	-0.23
c18:1n-7	**0.91**	0.26	0.18
c20:1n-11	-0.18	-0.35	**-0.76**
c20:1n-9	**-0.90**	0.21	-0.32
c20:1n-7	**-0.70**	0.50	-0.21
c22:1n-11	**-0.84**	0.24	-0.40
c22:1n-9	**-0.84**	0.33	-0.35
PUFAs			
c18:2n-6	0.44	-0.18	0.32
c20:5n-3	0.54	0.10	**0.74**
c22:5n-3	0.15	-0.50	**0.77**
c22:6n-3	0.54	**-0.60**	0.53
Variance explained	42%	21%	19%

3.2.4. Comparison among isotopically similar prey

In order to determine the added value of FAs over SIs in separating arctic krill from copepods, or capelin from herring as dietary sources for fin whales, their FA composition was examined in greater details.

Copepods were represented by three species in the stable isotope analysis (*C. hyperboreus*, *C. finmarchicus*, *C. glacialis*), and only one species (*Calanus hyperboreus*) in the FA analysis. FA profiles of copepods in our study were dominated by c22:1n-11 and c20:1n-9 while those of arctic krill showed high contributions of c16:0, c16:1n-7. c18:1n-9

and c20.5n-3 (Table 7; Appendix 6-7-8-9). A MANOVA on rotated PC scores indicated that copepod and arctic krill differed in the FAs loading high on PC1 only (PC1: F =156.64, $p < 0.001$; $p > 0.05$ for the other two). The FAs positively correlated with this PC1 (i.e. c18:0 and c16:0 SFAs and c18 MUFAs) represented 8.5% and 31.3% of total FAs in copepod and arctic krill respectively while those negatively correlated with the PC1 (i.e. c20 and c22 MUFAs) showed the opposite pattern, contributing respectively to 56.7% and 16% of the total FAs (Table 7). Like arctic krill, fin whales tended to have higher amounts of c18:0 and c16:0 SFAs and c18 MUFAs and lower amounts of c20 and c22 MUFAs: 42.1% compared to 20.8% (Table 3).

FA profiles of herring in our study were dominated by c22:1n-11 while capelin had c22:6n-3 and c16:0 as major contributors to their FA profiles (Table 7; Appendix 6-7-8-9). A second MANOVA on rotated PC scores indicated that herring and capelin differed significantly for FAs loading strongly on PC1 and PC3 (PC1: $F = 48.369$, $p < 0.001$; PC2: $F = 0.423$, $p = 0.516$; PC3: $F = 100.420$, $p < 0.001$). The FAs which had strong and positive loadings on PC1 (i.e. c18:0 and c16:0 SFAs and c18 MUFAs) accounted for 30.6% and 23.6% of total FAs for capelin and herring respectively while those that were negative (i.e. c20 and c22 MUFAs) accounted for 18.7% and 37% of their total FAs (Table 7). A similar scheme was observed for FA loading strongly on PC3, those being positively correlated (i.e. c20:5n-3 and c22:5n-3) accounting more for capelin then herring total FAs (13% compared to 7.7%; Table 7) and those being negatively correlated (i.e. i.e. c20:1n-11) accounting less for capelin than herring total FAs (8.8% compared to 20.3%; Table 7). Like capelin, fin whales tended to have higher amounts of c18:0 and c16:0 SFAs and of c18 MUFAs, and lower amounts of c20 and c22 MUFAs: 42.1% compared to 20.8% (Table 3). As did capelin, they also tended to have higher contributions of c20:5n-3 and c22:5n-3 than of c20:1n-11: 3.0% compared to 1.5% (Table 3).

Discussion

The combination of quantitative analyses of stable isotopes with qualitative analyses of FA profiles revealed inter-annual, seasonal, and inter-individual variability in diet composition of fin whales.

4.1. Diet Composition

Stable isotope analyses showed that Arctic krill/copepods are the predominant prey of fin whales using the St. Lawrence Estuary as a feeding area, but could not discriminate between the two dietary sources. FA analyses suggested that Arctic krill, but not copepods, might be the prey contributing more to the diet of fin whales in this area. Fin whales exhibited greater proportions of c18 MUFAs, and c18 and c16 SFAs, relative to c20 and c22 MUFAs. MUFAs of the types c20 and c22 are synthesized *de novo* and are known to be more abundant in calanoid copepods than in Arctic krill (Kattner et Hagen, 1995; Falk-Petersen *et al.*, 2000; Lee *et al.*, 2006). MUFAs such as c18:1n-9 (oleic acid), which are strongly associated with carnivory (Falk-Petersen *et al.*, 2000; Lee *et al.*, 2006), and c18:1n-7, which is probably derived from the elongation of c16:1n-7, a very abundant FA in phytoplankton (Falk-Petersen *et al.*, 2000), are more abundant in omnivorous species such as Arctic krill than in copepods (Falk-Petersen *et al.*, 2000). SFA c16 is also known to be particularly abundant in Arctic krill (Falk-Petersen *et al.*, 1982; Falk-Petersen *et al.*, 2000), even though in this study this FA was also present in northern krill (*M. norvegica*) and in fish species. Copepods were represented by three species in the stable isotope analysis (*C. hyperboreus*, *C. finmarchicus*, *C. glacialis*) but by only one (*Calanus hyperboreus*) in the FA analysis. One could ask if the FA profile of *C. hyperboreus* is representative of the three species and therefore if conclusions drawn from its FA composition could be applied to all of them. Better adapted to polar climates, *C. hyperboreus* is slightly different in term of FA composition from *C. finmarchicus* and *C. glacialis,* which show particularly similar FA profiles. *C. hyperboreus* synthetizes more wax ester (based on c20:1n-9 and c22:1n-11) than the other two (Kattner et Hagen, 1995). However, because this characteristic is also present in the other two species and because the

St. Lawrence is a less harsh environment than its polar counterpart, it could be assumed that the FA profiles of the three copepods species should be similar enough to conclude on the three species.

The higher contribution of Arctic krill to the diet of fin whales, compared to that of copepods, concur with earlier findings based on quantitative stable isotope analyses alone but for fin whales sampled in the Gulf of St. Lawrence. Earlier findings which indicated a diet constituted on average of > 50% Arctic krill, the remainder prey being essentially northern krill and sandlance (Gavrilchuck *et al.*, 2014). In our study, northern krill occupied only a small fraction of the diet, although it increased in importance in fin whale diet after 2000.

Our stable isotope data showed that capelin/herring could be more important in the diet of fin whales from the Estuary than in that of fin whales sampled in the Gulf where their contribution was close to nil (Gavrilchuck *et al.*, 2014). Both adult capelin and herring migrate into the Estuary to spawn during spring and overlap in distribution with fin whales (El-Sabh et Silverberg, 1990), with capelin arriving sooner than herring (November-December compare to April-May) (Sergeant, 1973; Bailey *et al.*, 1977). Adult capelin that survive reproduction is thought to migrate back to their summer-feeding areas in the western Gulf in late June and July (Bailey *et al.*, 1977), while one and two year juvenile capelin remain in the Estuary year-round (Ménard, 1998). Herring also goes back to the Gulf after spawning in the spring, but some individuals might spawn in the Estuary during summer and/or fall and could form dense groups (Rivière *et al.*, 1985; Fortier et Gagné, 1990). Since both species use the Estuary over substantially the same period, their availability may remain high to fin whales over the spring to fall.

Our study failed to decipher among capelin and herring in their relative contribution to the diet, even by using a combination of SI and FA analysis. These two species were isotopically similar and only slightly different in their FA composition. Capelin and herring have a similar diet, i.e. based on plankton, with an ontogenic shift toward larger plankton and small fish as they grow in size (Scott et Scott, 1988; Gerasimova, 1994). Their shared diet might explain the similarity of their fatty acid signatures (Budge *et al.*, 2002; Iverson *et*

al., 2002; Huynh et Kitts, 2009). Iverson *et al.* (2002) highlighted considerable within-species variability, especially between age classes of herring in Alaska. Budge *et al.* (2002) found a less marked, but still significant effect of age on both capelin and herring on the Scotian Shelf, Georges Bank, and Southern Gulf of St. Lawrence.

FA profiles of herring in our study were dominated by c22:1n-11, as were those of Budge *et al.* (2002). Capelin had c22:6n-3 and c16:0 as major contributors to their FA profile whereas in Budge *et al.* (2002), c22:1n-11 was the prevailing FA. Though, c18 MUFAs, and c18 and c16 SFAs were more abundant in capelin than herring whereas for MUFAS of type c20 and c22, it was the opposite. The greater proportions of c18 MUFAs, and c18 and c16 SFAs, relative to c20 and c22 MUFAs in fin whale tissue lean towards a greater intake of capelin. However, the metabolic alteration that some FA undergo before deposition in predator tissues, and uncertainties associated with this process, make direct inferences of predator diets based on similarities in abundance of FA with potential prey highly problematic (Budge *et al.*, 2006).

Based on stable isotope analyses, sandlance does not appear to be an important prey of fin whales in the St. Lawrence Estuary. FAs were of no help in clarifying its contribution. This result contrasts with findings from the Gulf, and should be interpreted with caution given the relative placement of dietary sources and isotopic signatures of fin whales (Fig. 7). In general, the consumer isotopic values must fall within the range of food sources isotopic values (i.e. the mixing-space) for them to be the solution to its diet composition (Phillips *et al.*, 2014) and prey that lie within the convex polygon formed by the isotopic values of all dietary sources, like sandlance here (Fig. 7), could contribute, or not, to the diet (Phillips et Gregg, 2003). The geometry of the mixing space, i.e. where the consumer falls within the range of its food sources and how different those food sources are from each other, affects greatly the precision of the contribution estimates of dietary sources (Phillips *et al.*, 2014). All potential prey must be included; otherwise, the validity of the results will be compromised. However, the number of sources included in the model also affects the precision of the diet estimates, as usually, the more sources there are, the

less accurate these estimates will be. This effect can also be magnified by that of the mixing-space geometry. Combining food sources based on their isotopic similarity and according to their biological proximity is a desirable approach to reduce the total number of sources while keeping all potential prey and may lead to more constrained, less diffuse results (Phillips *et al.*, 2014). Variations in isotopic composition of sources and consumers, as well as uncertainties associated with TDFs, may affect diet composition estimates (Phillips *et al.*, 2014). Temporal and spatial variations might also occur in the consumer diet within the time frame over which diet is integrated to his tissues (turnover) as the isotopic signatures of sources may vary over time, between locations and within the same geographic and temporally sampled population (Phillips *et al.*, 2014). Spatial variations may be important for highly mobile consumers like fin whales, which may visit isotopically distinct systems. The sampling of dietary sources must then be designed to capture these variations in time and location. In our study, this potential bias in diet estimation has been accounted for by including prey sampled both in the Estuary and Gulf of St. Lawrence.

4.2. Within-species variability

Diet varied among individuals, seasons and years, and confirmed the generalist nature of fin whale, and what seems to be a preference for krill over fish prey, although the relative importance of the two groups was more balanced in the 2000s. The stable isotope analysis also revealed individual variability in niche breadth (or width) with some individuals being largely specialist feeders on Arctic krill (e.g., group 3), and others having a highly varied diet among the various invertebrate and fish prey (e.g., group 7).

Niche width of a consumer is usually assessed through his diet diversity (Bearhop *et al.*, 2004) and is affected over time by the physical environment, the availability of resources and the presence/absence of competitors (Feinsinger *et al.*, 1981). It is not a fixed concept as both species and environment may change over time (Polechová et Storch, 2010). Wide niches are usually attributed to generalist species, i.e. consuming sources available, while narrow niches are generally more typical of specialist species, i.e. concentrating their foraging effort on some specific sources while bypassing the others

(Feinsinger *et al.*, 1981). Specifically, considering the isotopic space, when a species presents a narrow niche, it means that it is composed of individuals with particularly similar isotopic signatures. That is, individuals consume essentially the same prey, and in the same proportions. Thus, a generalist species could have a narrower isotopic niche than a specialist one in the event that little variability is observed between the diets of each individual. Moreover, if all the prey of a consumer have similar diets, those consumers will tend to have similar isotopic signatures which in the end will lead to a reduction of the variation in their isotopic ratios and therefore to a decrease of their niche width. For example, the humpback whale is a generalist in the Gulf of St. Lawrence (i.e. eating capelin, herring, sandlance and northern krill, all carnivorous species), but presents a narrower isotopic niche than blue whale, which is clearly a specialist (Gavrilchuck *et al.*, 2014). Blue whales feed either on Arctic krill or northern krill, or on a mix of the two. The fact that these two euphausiids are isotopically different, the first being essentially herbivorous and the second carnivorous (Saether *et al.*, 1986), explains the greater variation in the isotopic niche width of blue whales.

Niche breadth is also strongly affected by the isotopic composition of the sources (Matthews et Mazumder, 2004) and by the isotopic distance between those sources (Newsome *et al.*, 2007). The $\delta^{13}C$ of food sources may vary among regions, enabling consumers to have different carbon signatures while consuming the same sources (Dunton *et al.*, 1989; Lesage *et al.*, 2001). Similarly, differences in $\delta^{15}N$ among consumers could arise from regional differences at the base of the food web (Post, 2002) since variations in primary production, both spatial and temporal, are strongly influenced by factors such as light availability and intensity, nutrients availability and uptake or temperature (Valiela, 1995; Dufour et Ouellet, 2007; Cloern *et al.*, 2014). Those factors are influenced by physical processes (e.g. horizontal and vertical mixing, advection, tidal oscillations, wind stress, fresh, salt water and sediments inputs) and may therefore vary between regions (Cloern, 1996; Dufour et Ouellet, 2007; Cloern *et al.*, 2014). With highly mobile species having a relatively long turnover, like fin whales (probably more than 75 days, see methodology), the effect of possible regional differences on isotopic signatures is difficult

to discern as their isotopic ratios represent the average of all intakes and diet switches that may have occurred during this period (Phillips *et al.*, 2014).

In the present case, group 7 are interpreted as having a wider niche than group 3, not only because of its generalist diet, but probably because both carnivorous (sandlance, northern krill, capelin, and herring; 52%) and herbivorous species (amphipods, copepods and Arctic krill; 49%) represent a similar proportion of its diet. On the contrary, group 3 present a much narrower niche as its diet is almost entirely composed of Arctic krill (72%).

The absence of differences between males and females fin whales isotopic signatures and FA profiles is consistent with their weak sexual dimorphism (Richard et Prescott, 2005; NOAA Fisheries, 2015). Similar results were obtained for other whales with mild or no sexual dimorphism (Todd *et al.*, 1997; Lowry *et al.*, 2004; Budge *et al.*, 2008; Whiteveen *et al.*, 2012). However, when including FA data, fin whales grouped to some extent according to sex, although this pattern was not statistically significant (except for one PC for which sex was mildly significant). The study conducted in the Gulf of St. Lawrence found a significant difference in isotopic signature between males and females fin whales, with males feeding at a slightly higher trophic level than females (Gavrilchuck *et al.*, 2014). They thought this to reflect social preferences or strong competitive pressure among individuals.

Two other factors that may affect the isotopic signature and FA profiles of consumers were not considered in this study: differences in age (e.g. body size, diving capabilities, food handling) and in reproductive status (e.g. Kleiber, 1961; Scholander *et al.*, 1982; Peters, 1983; Werner et Gilliam, 1984; Sprules et Bowerman, 1988; Aguilar et Borrell, 1990; Budge *et al.*, 2006; Budge *et al.*, 2008; Lesage, 2014). Their effect on diet composition could also be confused with that of gender since they could be intimately linked.

4.3. Trends over the study period

There was an overall decrease in fin whale $\delta^{13}C$ values over the study period, and this trend was revealed both when considering samples collected early or late in the season (before and after September 1st) separately. Over essentially the same period, a similar decline in mean $\delta^{13}C$ values was observed in the same species but sampled in the Gulf, along with three other baleen whales (blue, humpback and minke whales) (Gavrilchuck *et al.*, 2014), as well as in beluga whales from the St. Lawrence Estuary (Lesage, 2014). In baleen whales from the Gulf, this decrease was concomitant to an overall increase in $\delta^{15}N$ values (Gavrilchuck *et al.*, 2014); such a parallel change in $\delta^{15}N$ values was not observed in our study.

In the early 1990s, the EGSL has suffered a major collapse of groundfish, mainly Atlantic cod, *Gadus morhua* (Myers *et al.*, 1997; Savenkoff *et al.*, 2007; Bundy *et al.*, 2009; Morissette *et al.*, 2009; Plourde *et al.*, 2013). As a result of that collapse, other species such as small pelagic fishes, crustaceans, and plankton should have been favored (Worm et Myers, 2003; Frank *et al.*, 2005; Savenkoff *et al.*, 2007; Plourde *et al.*, 2013). Even though sampling of this study occurred well post-collapse, the effect of the decrease in Atlantic cod biomass is still being felt as its population in the EGSL is still significantly smaller than before the collapse. Increased predation pressure on cod eggs and larvae, due to the larger stocks of pelagic fishes like capelin, herring, spat and sandlance (Swain et Sinclair, 2000; Walters et Kitchell, 2001; Worm et Myers, 2003; Bundy et Fanning, 2005), competition for food in early life history cod with highly abundant competitors (Swain et Sinclair, 2000; Walters et Kitchell, 2001; Bundy et Fanning, 2005), an increase in water temperature (Worm et Myers, 2003; Bundy et Fanning, 2005) and a possible changes in abundance, size and species diversity of copepods, the favored prey of newly hatched larval cod (Bundy et Fanning, 2005) are hypothesis that have been most often retained to explain the non-recovery of the Atlantic cod in the EGSL system. Taking that into account, an enrichment over the years in both $\delta^{15}N$ and $\delta^{13}C$ values was expected as whales should consume more small fishes and less krill than before which was not the case here.

It is difficult to tell if the $\delta^{13}C$ trend is due to a change in the diet of fin whales or to other factors since there is no isotopic baseline record spanning the entire study period. It is possible that the isotopic change observed in fin whales resulted from a change in the diet and isotopic signature of their prey. If this was the case, then a necessary corollary would be that prey that underwent a change in isotopic signature is common to the rorquals and the beluga and has changed diet both in the Estuary and GSL. There is currently no data to examine this hypothesis further. The depletion in $\delta^{13}C$ values could also be explained by a change at the base of the food web, e.g. primary production. While there is currently little data available to fully examine this hypothesis, two studies conducted 15 years apart and using the same collection methodology and sampling station indicate no clear shift in isotopic signatures for the few species examined (Lesage, 2014). Given the observed attenuation of isotopic variation with trophic position (Gavrilchuck *et al.*, 2014), it is unlikely that changes in the isotopic signature of primary producers or consumers can be the main cause for the approximately 1‰ depletion of $\delta^{13}C$ values in fin whales.

The reduced contribution of the combined prey group copepods/Artic krill and the increase in northern krill and fish in the diet of fin whales could also explain the isotope signature trends over the years. If the C trend was due to a decrease in trophic position, a corresponding decrease would also be observed for nitrogen as the $\delta^{15}N$-enrichment with trophic position is normally higher than that of carbon; however, this is not the case here. Considering that the change observed in the isotopic values of carbon in fin whales is a consequence of a change in their diet and not in that of their prey, the $\delta^{13}C$ trend observed means that they continued to feed essentially on the same trophic level while changing the contributions of prey having different carbon source (Lesage, 2014). The decrease in carbon signatures could then indicate a reduced consumption of ^{13}C-enriched prey or an increase in the contribution of marine species or catadromous/anadromous, but of similar trophic levels.

A phenomenon known as the Suess effect could also be responsible for the decline of carbon isotope signature in fin whales over the years. This effect consists in a change in the ratio of atmospheric concentrations of heavy carbon isotopes (^{13}C and ^{14}C) and is

caused by the burning of large amount of fossil-fuels, which are ^{13}C-depleted. This leads to a rise in atmospheric CO_2 and cause a decrease in $\delta^{13}C$ values of atmospheric CO_2 and a subsequent decline in $\delta^{13}C$ values of oceanic dissolved inorganic carbon (DIC) pool (Friedli *et al.*, 1986; Keeling *et al.*, 1996). Assuming the ^{13}C decline in DIC observed in the North Atlantic Ocean (~0.03‰ per year) reported by (Sonnerup *et al.*, 1999; Körtzinger *et al.*, 2003) is also valid for the EGSL, this rate would still be insufficient to explain the decline observed in the fin whales. Thus, it is likely that a combination of several, or all of these factors, have led to the isotopic trends observed in the fin whales of St. Lawrence.

The long term trend observed through FA data is consistent with that established using stable isotopes. The FA analysis showed an increase in c20 and c22 PUFAs over the study period. These FAs are highly present in fish (Budge *et al.*, 2002; Iverson *et al.*, 2002; Copeman et Parrish, 2004; Huynh et Kitts, 2009). An increase over time was also observed in two long-chain MUFAs which, as previously mentioned, are typical of *calanoid* copepods. However, those MUFAs are also found in significant proportions in fish species eating copepods, like herring and capelin (Budge *et al.*, 2002; Copeman et Parrish, 2004; Huynh et Kitts, 2009). Huynh and Kitts (2009) reported that MUFAs contribute to approximately 50% of all FAs in both Atlantic capelin and herring. This trend could thus also be associated with an increased contribution of fish to fin whale diet.

4.4. Inter-annual variability

Despite the presence of a clear trend towards a depletion of $\delta^{13}C$ in fin whale over the study period, little inter-annual variation was observed between consecutive years. However, it seems a more drastic change in carbon isotope ratios occurred in the ecosystem between 2001 and 2003 (Fig. 3).

Plourde *et al.* (2013) documented important changes within the Gulf of St. Lawrence during this period, including a decrease in cold water shelf copepod species (*Calanus glacialis* and *Metridia longa*) and a concomitant increase in large bodied species (*Calanus hyperboreus*). At the same period, a decrease in mackerel and herring and an increase in capelin were also documented. Around 2000, Plourde *et al.* (2013) found some

evidences of a shift in the EGSL toward warmer conditions. Considering that the Artic krill is better adapted to colder waters than northern krill (Saether *et al.*, 1986), we speculate that the warming environment should favor northern krill over Arctic krill. Unfortunately, there is currently no reliable, free of bias, time series to document this. Assuming that Arctic krill is the favorite prey of fin whales in the EGSL, its decrease in biomass over the years (due to warming conditions) leave the fin whales with two choices: (1) stay and switch diet toward more available prey, i.e. northern krill and fishes, or (2) change foraging site to continue feeding preferentially on Arctic krill. Unpublished data indicate that movement patterns of fin whales in the St. Lawrence Estuary has changed over the past 15 years, with some period influxes of individuals, but what appears to be shorter residency time during summer (R. Michaud, GREMM, Tadoussac, Québec, pers. comm., 2015). These observations suggest that fin whales visiting the St. Lawrence Estuary in the 1990s may be exploiting alternative foraging sites, possibly providing them with higher biomasses or densities of the prey prevalent in the diet in the 1990s.

4.5. Seasonal variability

Stable isotope analysis also revealed a significant seasonal effect for carbon but not for nitrogen. Whales sampled throughout the summer (June to August) had higher $\delta^{13}C$ values than those sampled during fall (September to December), but only before 2002. Considering the long turnover of skin tissues of baleen whales (probably more than 75 days, see methodology), individuals sampled in the summer should have isotope values reflecting their spring or early summer diet. At that time of year, animals are either in less productive, more oceanic areas, or may be taking advantage of spawning species such as capelin and herring. Both of these patterns would result in isotopically lighter signatures, but the reverse was observed in our study. Our results are coherent with the progressive decline in the contribution of Arctic krill, which before September 1st represented 82% of the diet of fin whales and only 54% after, and a progressive increase in northern krill and fish (2 to 8%, and 8 to 16%, respectively). FA data showed a seasonal trend in some FAs that are abundant in fish (i.e., c20 and c22 PUFAs and two long-chain MUFAs), thus

supporting the conclusions drawn from the stable isotope analysis of a decreasing contribution of Arctic krill compared to northern krill and fish. Our results also suggest that spawning fish (e.g., capelin and herring) may not be an important prey in the spring or early summer for fin whales sampled in the St. Lawrence Estuary. In contrast with our study, no seasonal trend was found in the isotopic signature of fin whales sampled in the Gulf of St. Lawrence as part of another study (Gavrilchuck *et al.*, 2014). These findings suggest that fin whales occupying adjacent regions may have access to different resources over the feeding period (Gavrilchuck *et al.*, 2014).

After 2002, the stable isotopes indicated a decrease in the consumption of Arctic krill combined with an increase in the consumption of northern krill and fish. Thus, less discrepancy is expected to be observed between the isotopic signatures of prey consumed as their diets are more similar (mostly carnivorous) than before 2002 (both herbivorous and carnivorous). This could explain the non-significant seasonal trend after 2002, from a strictly statistical point of view. Moreover, McQuinn *et al.* (2015) documented a strong inter-seasonal variability in stratum-specific density estimates for Arctic krill in 2008-2009, while for the same period northern krill was less dense and exhibited less inter-seasonal variability.

In conclusion, fin whales are generalist feeders in the EGSL system, exploiting krill but also fish prey. Within-species variability in diet composition was documented, with some groups showing a higher degree of specialisation than others. Fin whales were shown to vary their diet seasonally and between years. What seems to be a progressive change in diet toward species other than Arctic krill, their main prey, raises a number of questions regarding the potential influence of climate variability on the distribution, body condition and fitness of this species. The ability of fin whales to switch prey represents an asset relative to more specialized cetaceans, such as blue whales (Gavrilchuck *et al.*, 2014). Given the documented changes in the trophic structure and environmental conditions in the

EGSL over the past decades (Savenkoff *et al.*, 2007; Plourde *et al.*, 2013), further changes might be expected in their feeding ecology. Continued monitoring will help understand the relative vulnerability of this and similar species to climate variability.

CONCLUSION GÉNÉRALE

Il est essentiel de connaître le régime alimentaire des espèces pour mieux comprendre leur écologie et définir avec précision leur rôle de consommateur (Knox, 1994; Pauly *et al.*, 1998b; Hooker *et al.*, 2001; Santos *et al.*, 2001; Best *et al.*, 2003). Une meilleure connaissance de la diète d'une espèce donnée permet aussi de mieux évaluer l'impact des changements écosystémiques sur ses populations (Best *et al.*, 2003), connaissance d'autant plus importante pour les espèces en péril ou ayant un statut précaire, comme c'est le cas pour les rorquals communs séjournant dans le Saint-Laurent (COSEWIC, 2011).

Au cours des dernières décennies, l'Estuaire et le Golfe du Saint-Laurent (EGSL) ont été le théâtre de nombreux changements, dont les plus flagrants sont l'effondrement des stocks de poissons démersaux, l'augmentation concomitante des petits poissons pélagiques ainsi que la hausse des températures de surface (Myers *et al.*, 1997; Worm et Myers, 2003; Frank *et al.*, 2005; Savenkoff *et al.*, 2007; Bundy *et al.*, 2009; Morissette *et al.*, 2009; Plourde *et al.*, 2013). Les répercussions de tels changements sur la structure trophique et l'alimentation des grands prédateurs comme le rorqual commun demeurent incertaines. Hormis celle-ci, une seule autre étude a examiné la diète du rorqual commun dans le Saint-Laurent et n'avait pas permis de déterminer avec certitude si cette espèce y consomme à la fois du krill et des poissons, ou exclusivement des euphausiacés (Gavrilchuck *et al.*, 2014). Notre étude comble par conséquent certaines lacunes importantes dans nos connaissances de l'écologie alimentaire de cette espèce.

Une diète généraliste

Dans l'EGSL, le rorqual commun a une diète clairement généraliste, c'est-à-dire qu'il exploite un éventail de proies. Malgré la variation interindividuelle importante, des groupes de baleines ayant des régimes alimentaires similaires ont pu être révélés. Alors que certains groupes semblent plus spécialisés que d'autres, une donnée importante peut être

dégagée : le krill arctique (*Thysanoessa rachii*) est la proie contribuant le plus à la diète de l'espèce dans cette région, ce qui est également supporté par l'autre étude sur cette espèce et menée dans le Golfe du Saint-Laurent (Gavrilchuck *et al.*, 2014). Cependant, tandis que Gavrilchuck *et al.* (2014) avaient identifié le krill nordique et le lançon comme proies secondaires à la diète du rorqual commun dans le Golfe, ces deux espèces n'y contribuent que peu dans l'Estuaire. Le capelan et le hareng semblent, quant à eux, avoir une importance plus marquée dans l'alimentation du rorqual commun dans l'Estuaire que dans le Golfe.

Aucune différence significative entre les mâles et les femelles n'a été observée, ce qui est cohérent avec leur faible dimorphisme sexuel (Richard et Prescott, 2005; NOAA Fisheries, 2015). Toutefois, la seule autre étude réalisée dans le même secteur a indiqué une différence significative entre les signatures isotopiques des mâles et des femelles, mais n'a pas été en mesure d'identifier la source de cette différence (Gavrilchuck *et al.*, 2014).

De la variabilité interannuelle et saisonnière ont été documentées. La tendance annuelle générale de diminution du $\delta^{13}C$ serait due à la combinaison de plusieurs ou de tous les facteurs suivants : distribution différente des baleines (Dunton *et al.*, 1989; Lesage *et al.*, 2001), changement dans l'habitat ou à la base de la chaîne alimentaire, modification de la composition de la diète de l'espèce, altération anthropogénique (effet de Suess) du taux de fractionnement du carbone chez le phytoplancton (Friedli *et al.*, 1986; Keeling *et al.*, 1996). Un changement dans la composition de la diète du rorqual commun, débutant en 2000, vers une baisse générale de l'importance du krill arctique et une augmentation générale de celle du krill nordique (*Meganyctiphanes norvegica*) et des poissons (capelan et hareng) a été montré par les isotopes stables et dans une certaine mesure par les AG. Aucune tendance saisonnière n'a été observée pour l'azote alors que pour le carbone, les baleines échantillonnées en été (Juin à Août) avaient des valeurs en $\delta^{13}C$ plus élevées que celles échantillonnées pendant l'automne (Septembre à Décembre), mais seulement avant 2002. Cette diminution fait écho à la tendance annuelle puisqu'elle reflète une diminution de la contribution du krill arctique et une augmentation progressive de celle du krill nordique et des poissons (capelan et hareng).

Effets sur cette population

Les variations interannuelles du régime alimentaire du rorqual commun indiquent un certain degré d'adaptabilité chez cette espèce. Sa capacité à changer de proie pourrait favoriser le rorqual commun en cas de changement majeur dans son habitat, en particulier comparativement aux cétacés, comme le rorqual bleu, qui ont une alimentation plus spécialisée, comme le rorqual bleu (Gavrilchuck *et al.*, 2014). Cependant, la diète du rorqual commun étant principalement composée de krill, cette baleine est tout de même sensible aux changements climatiques puisque la composition et l'abondance de la communauté zooplanctonique sont étroitement couplées avec les caractéristiques des masses d'eau, donc très influencées par les changements de température et de salinité de l'eau (Hagen et Auel, 2001; Beaugrand *et al.*, 2002; Fetzer *et al.*, 2002).

Considérant que le krill arctique est mieux adapté aux eaux plus froides que le krill nordique (Saether *et al.*, 1986), le réchauffement de son habitat (Plourde *et al.*, 2013) devrait le défavoriser. En supposant que le krill arctique est la proie de prédilection du rorqual commun dans l'EGSL, une biomasse réduite de celui-ci avec les années (en raison du réchauffement) laisse les rorquals communs avec deux choix : (1) rester et modifier leur diète vers des proies plus disponibles, c'est-à-dire le krill nordique et les poissons ou (2) changer de site d'alimentation pour continuer à se nourrir préférentiellement de krill arctique. Avec les années, les grands groupes de rorquals communs sont de moins en moins présents dans l'Estuaire et peu d'entre eux y restent tout l'été (GREMM, comm. pers., 2015). Il semblerait donc que la majorité des rorquals communs aillent ailleurs alors que ceux qui reviennent se tournent vers une alimentation comportant majoritairement du krill nordique et des poissons.

Finalement, il est difficile d'affirmer si les variations interannuelles observées dans la diète du rorqual commun sont le reflet, direct ou indirect, de changements écosystémiques survenus lors de la décennie 90. Lors de cette période, les stocks de poissons démersaux se sont effondrés (Myers *et al.*, 1997; Bundy *et al.*, 2009; Morissette *et al.*, 2009; Plourde *et al.*, 2013) favorisant du coup certaines espèces de poissons pélagiques

tels que le capelan et le hareng (Myers et Worm, 2003; Frank *et al.*, 2005). Le rorqual commun semble avoir profité de cette disponibilité accrue puisqu'avec les années la contribution de celles-ci à sa diète tend à augmenter légèrement. Néanmoins, cette augmentation n'est pas très marquée ni dénuée d'incertitudes, ce qui porterait à croire que les processus dynamiques des populations de proies ne sont pas encore bien compris.

Avantages et limites des outils d'étude

Les conclusions tirées ici sont issues des analyses de deux traceurs biochimiques de plus en plus utilisés en écologie alimentaire : les isotopes stables et les acides gras. Le principal avantage de ces analyses est de documenter la diète sur une longue période de temps (diète assimilée vs ingérée) (Jobling, 1987; Hobson *et al.*, 1996; Iverson *et al.*, 1997; Iverson *et al.*, 2004; Dalerum et Angerbjörn, 2005; Newsome *et al.*, 2010; Smith *et al.*, 2011). Étant indirectes, ces méthodes sont beaucoup mieux adaptées que les méthodes traditionnelles (études des contenus stomacaux et fécaux, observation de comportement d'alimentation, etc.) pour l'étude d'espèces cryptiques vivant dans un milieu difficile d'accès, comme c'est le cas pour la plupart des cétacés. D'ailleurs, l'utilisation combinée des ISs et des AGs est relativement récente et offre une avenue prometteuse. Dans le cas présent, les acides gras ont permis de détailler les conclusions tirées des isotopes stables et ont fourni une solution à la proximité isotopique de certaines proies.

Malgré tout, il est important de noter que ces méthodes présentent aussi des inconvénients dont il faut tenir compte. Effectivement, les modèles bayésiens comportent des prérequis importants. Le facteur d'enrichissement trophique, aussi appelé facteur de discrimination, doit aussi être adéquat pour le tissu et l'espèce considérée (Phillips et Gregg, 2001). Sa valeur, qui peut être déterminée grâce à des expériences contrôlées en captivité, a une incidence importante sur les résultats du modèle (Tarroux *et al.*, 2010b) et varie selon la composition de la diète et le tissu utilisé ainsi qu'entre les groupes taxonomiques (Caut *et al.*, 2011). Malheureusement, cette valeur n'est pas disponible pour le rorqual commun et doit donc être déduite à partir d'autres études. De plus, toutes les

proies susceptibles de contribuer de manière significative à la diète du prédateur doivent être incluses dans le modèle et être « isotopiquement » distinctes entre elles, sans quoi il sera difficile, voire impossible de déterminer laquelle contribue à la diète (Phillips, 2001). Malheureusement, plusieurs des proies du rorqual commun montrent un chevauchement important de leur signature isotopique, limitant les conclusions que l'on peut en tirer.

L'utilisation des profils d'AGs a permis de résoudre en partie ce problème, permettant de conclure que le rorqual commun consomme probablement plus de krill arctique que de copépodes. Toutefois, les analyses d'AGs ont elles aussi leurs limites. De nombreuses études ont mis en évidence une stratification verticale des AGs dans la graisse des mammifères marins (Ackman *et al.*, 1965; Ackman *et al.*, 1975; Koopman *et al.*, 1996; Hooker *et al.*, 2001; Best *et al.*, 2003; Koopman, 2003; Thiemann *et al.*, 2004; Koopman, 2007; Strandberg *et al.*, 2008; Thiemann *et al.*, 2008), la couche de graisse interne étant la plus métaboliquement active et donc la plus indicative de l'alimentation (Budge *et al.*, 2008) puisque c'est là que le dépôt et le retrait des lipides sont les plus actifs (Lockyer *et al.*, 1984; Koopman *et al.*, 1996; Hooker *et al.*, 2001). D'autres facteurs peuvent aussi influencer cette stratification : l'âge (Koopman *et al.*, 1996; Koopman, 2003), le statut reproducteur (Stull *et al.*, 1967; West *et al.*, 1979b), la condition physique (Koopman, 2003), le sexe (West *et al.*, 1979a) ainsi que le site d'échantillonnage le long du corps de l'animal (Ackman et Lamothe, 1989; Koopman *et al.*, 1996). Il serait donc préférable d'échantillonner toute l'épaisseur de la couche graisseuse ce qui est difficile, voire impossible avec les techniques de biopsie actuellement utilisée pour les grands rorquals.

En bref, les analyses d'ISs et des AGs sont d'une grande utilité afin d'établir les bases de la niche trophique d'une espèce, mais leur utilisation exige une bonne compréhension et intégration de leurs limites, comme pour tout autre outil écologique.

Perspectives de recherche

Aucune référence isotopique couvrant la période entière de l'étude n'étant disponible, il est difficile de déterminer si les tendances annuelles observées dans les signatures

isotopiques du rorqual commun sont réelles ou simplement un artéfact de changements isotopiques chez les proies. Dans cette optique, il serait intéressant d'établir une surveillance des tendances isotopiques chez les consommateurs primaires et secondaires (base de la chaîne alimentaire) puisque des variations en leur sein ont nécessairement un impact sur les signatures isotopiques des prédateurs supérieurs. D'ailleurs, les consommateurs primaires et secondaires pourraient agir comme des indicateurs écosystémiques efficaces, étant donné leur réponse rapide aux changements environnementaux tels que la disponibilité des nutriments (Cabana et Rasmussen, 1996).

Conjointement, établir une base annuelle documentant l'abondance et la distribution des proies des baleines permettrait une meilleure inférence quant à leur régime alimentaire et conséquemment un meilleur suivi du statut de leur population. Un projet visant cet objectif spécifique a déjà été mis en route par le Ministère des Pêches et Océans Canada, ce projet réalisant des relevés hydroacoustiques systématiques visant à quantifier et localiser la biomasse de zooplancton et les stocks de poissons. Une meilleure compréhension de l'impact des fluctuations dans l'abondance, la distribution et la disponibilité des ressources en lien avec les changements naturels et anthropogéniques devrait aussi être une priorité dans le futur.

Finalement, comme le rorqual commun partage son habitat avec trois autres espèces de *Balaenopteridae* (petit rorqual, rorqual bleu et rorqual à bosse), il serait important d'évaluer les impacts d'une telle coexistence. En effet, selon le principe de Gause, deux espèces ne peuvent occuper une même niche écologique de manière viable puisqu'il en résulte inévitablement de la compétition (Gause, 1934). Les lois de la sélection naturelle tendent à favoriser l'espèce la mieux adaptée, ou ayant le meilleur *fitness,* et éventuellement à exclure l'autre (Hardin, 1960; Tilman, 1982; Chesson, 2000). Cependant, l'action conjointe de mécanismes de stabilisation et d'égalisation peut mener à une coexistence stable entre deux espèces, les premiers permettant de compenser pour les inégalités de *fitness* alors que les seconds réduisent l'amplitude de cette différence (Chesson, 2000). La survie d'une espèce sera donc déterminée par sa capacité à exploiter des ressources malgré la présence de compétiteurs potentiels (Schoener, 1974). Le nombre

d’espèces cohabitant dans une même et unique communauté sera ainsi défini par leur capacité à se répartir les ressources disponibles dans le temps et l’espace (MacArthur et Levins, 1967). Gavrilchuck et ses collègues (2014)se sont penchés sur cette question de coexistence des grands rorquals dans le Saint-Laurent et ont conclu que l’espèce la plus à risque serait la baleine bleue étant donné son régime alimentaire largement spécialiste. Doniol-Valcroze *et al.* (2007) ont quant à eux investigué l’aspect spatial de ce chevauchement en lien avec la distribution des fronts thermiques. Ils ont démontré que les distributions de trois des quatre espèces de rorquals (rorqual bleu, commun et à bosse) sont significativement corrélées avec celle des fronts thermiques. Dans l'ensemble, leurs observations suggèrent un degré plus fin de partitionnement de l'habitat chez les espèces de rorquals dans leurs aires d'alimentation que ce qui était suspecté.

En conclusion, la présente étude a permis de mieux comprendre l’écologie alimentaire du rorqual commun dans l’EGSL. Elle souligne aussi l’importance de prendre en compte les fluctuations dans l’abondance et la disponibilité des proies de même que les impacts potentiels des perturbations anthropogéniques sur celles-ci.

APPENDIX

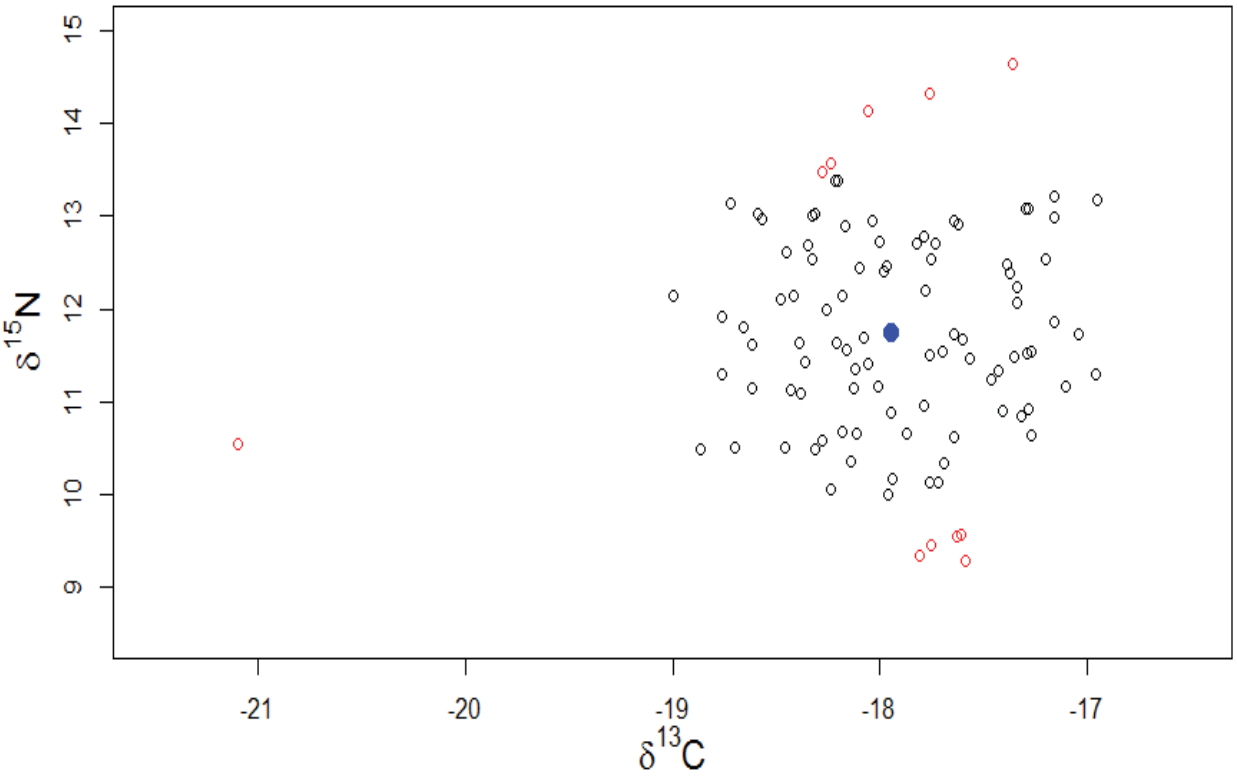
Appendix 1: Distribution of fin whales sampled in the St. Lawrence Estuary according to year, sex, season and Julian days

Year	Sex	Season	Julian Day
1998	F	Spring	160
		Summer	189
			189
			189
			204
			208
	M	Spring	163
			163
		Summer	208
			208
			215
1999	F	Summer	210
			223
			224
			232
			232
			236
			236
			236
			236
			236
		Fall	286
			286
	M	Summer	190
			190
			202
			202
			210
			210
			211
			223
			224
			224
			231
			232
			235
			235
		Fall	286
			286

Year	Sex	Season	Julian Day
2000	F	Summer	220
			235
			235
			236
		Fall	291
			291
	M	Summer	203
			235
			236
		Fall	291
			291
			291
2001	F	Summer	215
2002	F	Summer	246
		Fall	324
			324
			324
			324
	M	Summer	225
2003	F	Summer	183
			251
	M	Summer	197
			251
			183
2004	F	Summer	253
			253
			253
			253
			266
		Fall	274
	M	Summer	233
			253
			253
2005	M	Summer	220
			234
			238

Year	Sex	Season	Julian Day
2006	F	Spring	100
		Summer	255
			255
			255
			255
			255
			255
			256
			256
		Fall	268
			268
			270
			270
			278
			283
			283
	M	Summer	255
			255
			255
			255
			256
		Fall	268
			270
			270
			270
			276

Appendix 2: Potential $\delta^{13}C$ and $\delta^{15}N$ values of fin whales *Balaenoptera physalus* sampled between 1998 and 2006 in the St. Lawrence Estuary. Individuals excluded from the cluster analysis (outliers) are shown in red while the mean isotopic signature of all the fin whales is shown in blue



Appendix 3: Potential prey species sampled, with sampling location and specifications about their use in the analyses (numbers represents sample size). Potential prey were selected based on local availability, as well as through an exhaustive review of the species diets in other parts of the world (Nemoto, 1959; Nemoto et Kasuya, 1965; Jonsgård, 1966; Mitchell, 1974; Sergeant, 1977; Overholtz et Nicolas, 1979; Kawamura, 1980; Besson *et al.*, 1982; Kawamura, 1982; Gambell, 1985; Viale, 1985; Orsi-Relini et Cappello, 1992; Orsi-Relini et Giordano, 1992; Tershy *et al.*, 1993; Orsi-Relini *et al.*, 1994; Clapham *et al.*, 1997; Pauly *et al.*, 1998b; Aguilar, 2002; Flinn *et al.*, 2002; Notarbartolo-Di-Sciara *et al.*, 2003; Borrell *et al.*, 2012)

Group	Species		Location			Analyzes	
	English name	Latin name	Estuary	Gulf	Saguenay	Used	Not Used
Amphipod		*Themisto libellula*	56	5		X	
Copepod	*Calanoid copepod*	*Calanus finmarchicus*	16			X	
	Calanoid copepod	*Calanus glacialis*	5			X	
	Calanoid copepod	*Calanus hyperboreus*	38			X	
	Calanoid copepod	*Calanus sp.*		16			X
		Euchaeta norvegica	19				X
		Metridia longa	31				X
Decapod		*Argis dentata*		16			X
		Crangon septemspinosa	16				X
		Eualus macilentus	18				X
		Pandalus montagui	16				X
		Sclerocrangon boreas		8			X
Euphausiacea	*Krill*	*Meganyctiphanes norvegica*	170	15		X	
	Krill	*Thysanoessa raschii.*	35	6		X	
Fish	*Alose*	*Alosa sp*	2				X
	American sandlance	*Ammodytes spp.*	8	19		X	
	Arctic cod	*Boreogadus saida*		6	2		X
	Atlantic herring	*Clupea harengus harengus*	48	13		X	
		Coregonus clupeaformis	7				X
	Lumpfish	*Cyclopterus lumpus*	2				X
	Greenland cod	*Gadus ogac*	4				X
	Daubed shanny	*Leptoclinus maculatus*			1		X
	Snailfish	*Liparis sp*	5				X
	Capelin	*Mallotus villosus*	136	10	34	X	
	Atlantic tomcod	*Microgadus tomcod*	14				X
	Rainbow smelt	*Osmerus mordax*	14	10	2	X	
	Atlantic salmon	*Salmo salar*	6				X
Jellyfish	*Jellyfish*	*Aurelia medusa*	3				X
Mysida		*Boreomysis sp.*	26				X
		Mysis mixta	53	2			X
Mysidacea		*Mysidacea sp*	7				X
Polychaete		*Nereis virens*	7				X

Appendix 4: Potential prey species used in the analyses with sampling year

Species	Sample size	1999	2000	2001	2002	2003	2004	2005
Ammodytes spp.	27	-	-	19	-	-	8	-
Calanus finmarchicus	16	-	-	16	-	-	-	-
Calanus glacialis	5	-	-	5	-	-	-	-
Calanus hyperboreus	38	-	-	38	-	-	-	-
Clupea harengus harengus	61	-	-	35	-	24	2	-
Mallotus villosus	180	-	-	14	-	104	18	44
Meganyctiphanes norvegica	185	-	-	69	44	69	3	-
Osmerus mordax	26	10	-	14	-	-	-	2
Themisto libellula	61	-	-	-	17	31	13	-
Thysanoessa raschii	41	-	-	9	-	18	14	-

Appendix 5: Natural groupings of fin whale according to their FA profiles

Using VARIMAX PC scores (n = 90) as FA input variables in a hierarchical cluster analysis resulted in seven clusters of fin whales (Dunn index =1.141; Table E1). Only group 4 and 5 had a relatively equivalent number of males and females; other groups were dominated by one sex or the other, i.e. females for groups 1 and 3 and males for groups 2, 6 and 7 (Fig. E1). Groups 5 and 6 were mostly composed of whales sampled prior to 2002 (72% and 67%, respectively) while those in groups 3 and 4 were mostly sampled after 2002 (90% and 89%, respectively). Groups 1, 2 and 7 were more evenly distributed over time (Fig. E2).

Table E1: FA composition of selected FAs (mass %) of lipids from groups of fin whales sampled in the St. Lawrence Estuary from 1998 to 2006 (n = 90)

Group	**1** (n = 31)	**2** (n = 7)	**3** (n = 10)	**4** (n = 9)	**5** (n = 18)	**6** (n = 6)	**7** (n = 9)
SFAs							
c14.0	4.41 ±0.40	4.38 ±0.28	4.38 ±0.28	4.34 ±0.30	4.55 ±0.45	4.47 ±0.29	4.19 ±0.34
c16.0	10.40 ±2.44	9.12 ±1.78	10.57 ±2.11	10.63 ±3.09	10.36 ±3.36	10.15 ±2.40	11.03 ±3.27
c18.0	1.89 ±0.49	1.63 ±0.29	1.95 ±0.43	1.87 ±0.64	1.85 ±0.58	1.72 ±0.50	1.91 ±0.53
MUFAs							
c16.1n7	12.71 ±2.38	11.86 ±2.99	12.83 ±1.18	12.25 ±2.64	12.80 ±3.31	13.26 ±1.27	14.02 ±2.59
c18.1n11	1.24 ±0.41	1.36 ±0.38	1.02 ±0.20	1.16 ±0.42	1.34 ±0.55	1.22 ±0.42	1.24 ±0.46
c18.1n9	23.78 ±2.20	21.47 ±1.43	23.90 ±2.83	21.94 ±2.20	23.04 ±2.53	21.51 ±2.43	23.54 ±2.75
c18.1n7	6.65 ±1.08	6.45 ±1.05	6.87 ±0.70	6.10 ±0.45	6.76 ±1.12	6.99 ±1.56	6.50 ±1.46
c20.1n11	1.65 ±0.73	1.48 ±0.52	1.41 ±0.60	1.43 ±0.56	1.48 ±0.58	1.42 ±0.39	1.43 ±0.53
c20.1n9	10.51 ±2.73	13.14 ±4.24	9.83 ±2.22	10.69 ±3.44	10.55 ±3.71	11.28 ±4.11	9.73 ±3.56
c20.1n7	1.44 ±0.75	1.97 ±0.94	1.52 ±0.87	1.19 ±0.85	1.64 ±0.81	1.59 ±0.70	1.10 ±0.61
c22.1n11	6.58 ±2.98	7.75 ±3.88	5.95 ±2.60	6.55 ±2.99	6.59 ±3.78	7.40 ±4.64	4.89 ±2.86
c22.1n9	2.34 ±0.63	2.91 ±0.91	2.21 ±1.00	1.98 ±0.87	2.57 ±0.77	2.24 ±0.61	1.88 ±0.90
PUFAs							
c18.2n6	1.17 ±0.31	1.08 ±0.29	1.25 ±0.36	1.21 ±0.20	1.15 ±0.31	1.27 ±0.24	1.21 ±0.25
c20.5n3	1.36 ±0.73	1.54 ±0.87	1.80 ±0.75	2.59 ±1.28	1.33 ±0.74	1.41 ±0.87	2.02 ±1.09
c22.5n3	1.33 ±0.60	1.31 ±0.74	1.59 ±0.46	2.20 ±1.10	1.18 ±0.59	1.26 ±0.95	1.94 ±1.00
c22.6n3	1.39 ±0.99	1.35 ±0.80	1.69 ±0.71	2.90 ±1.99	1.43 ±0.94	1.62 ±1.77	2.30 ±1.24
Total							
SFAs	16.70 ±3.33	15.13 ±2.36	16.90 ±2.82	16.83 ±4.03	16.76 ±4.39	16.33 ±3.19	17.13 ±4.14
MUFAs	66.90 ±13.88	68.39 ±16.33	65.53 ±12.20	63.29 ±14.42	66.77 ±17.16	66.91 ±16.13	64.33 ±15.74
PUFAs	5.25 ±2.63	5.28 ±2.70	6.33 ±2.28	8.91 ±4.57	5.09 ±2.58	5.56 ±3.82	7.47 ±3.58
Total	83.60 ±17.21	83.53 ±18.68	82.42 ±15.03	80.12 ±18.45	83.53 ±21.56	83.24 ±19.32	81.46 ±19.88

Appendix 5: Natural groupings of fin whale according to their FA profiles – suite 1

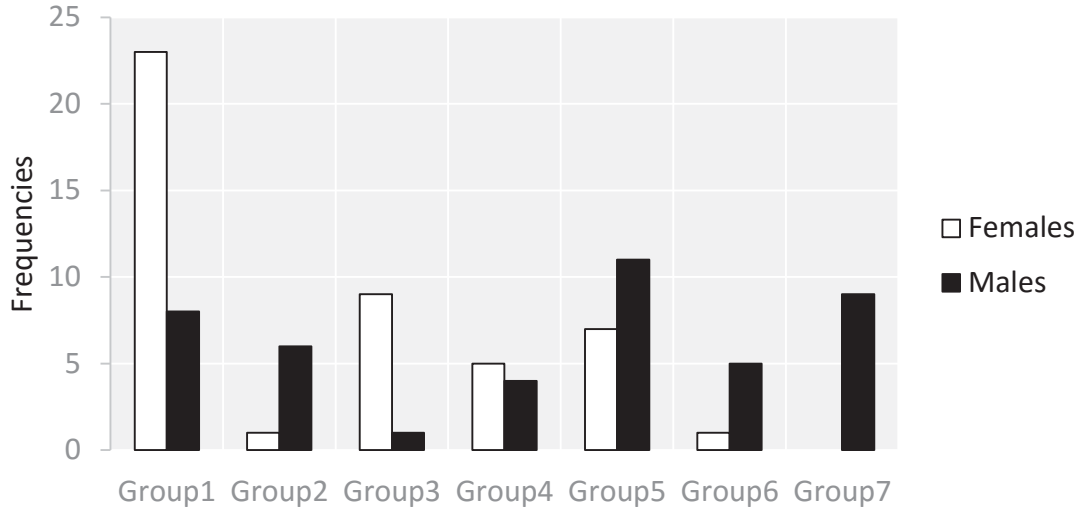


Fig. E1: Distribution of individuals in the seven groups identified by the cluster analysis based on sex

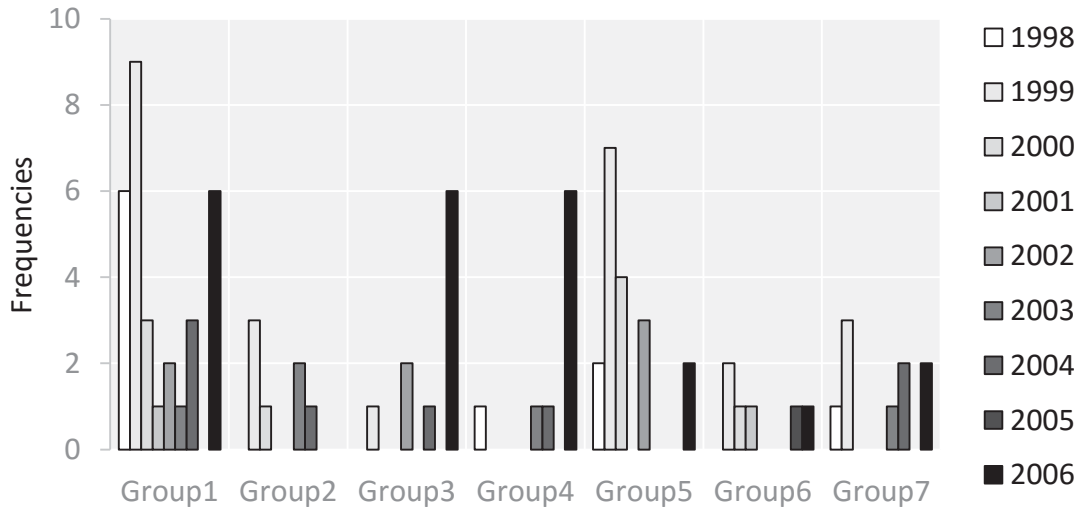
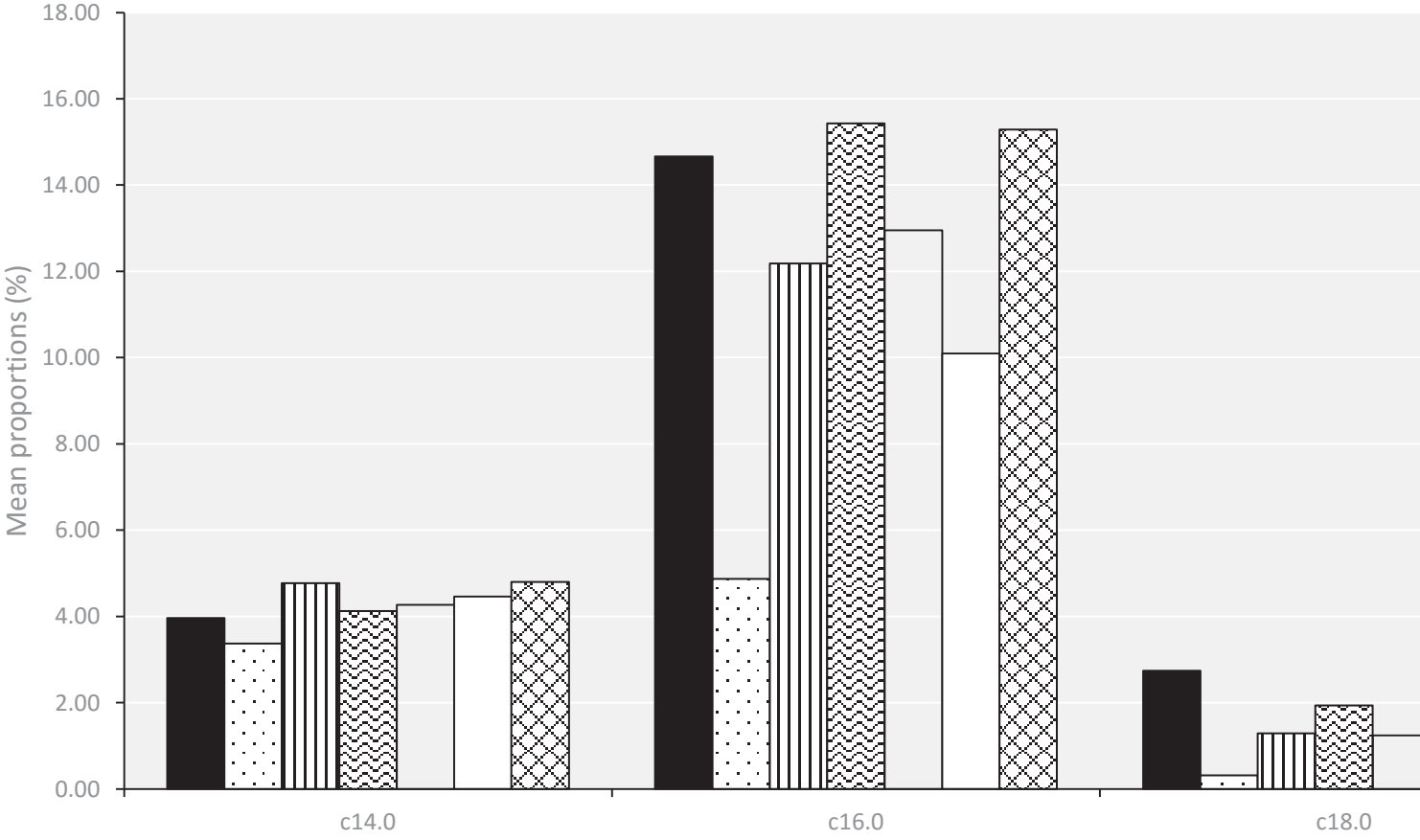


Fig. E2: Distribution of individuals in the seven groups identified by the cluster analysis based on sampling year

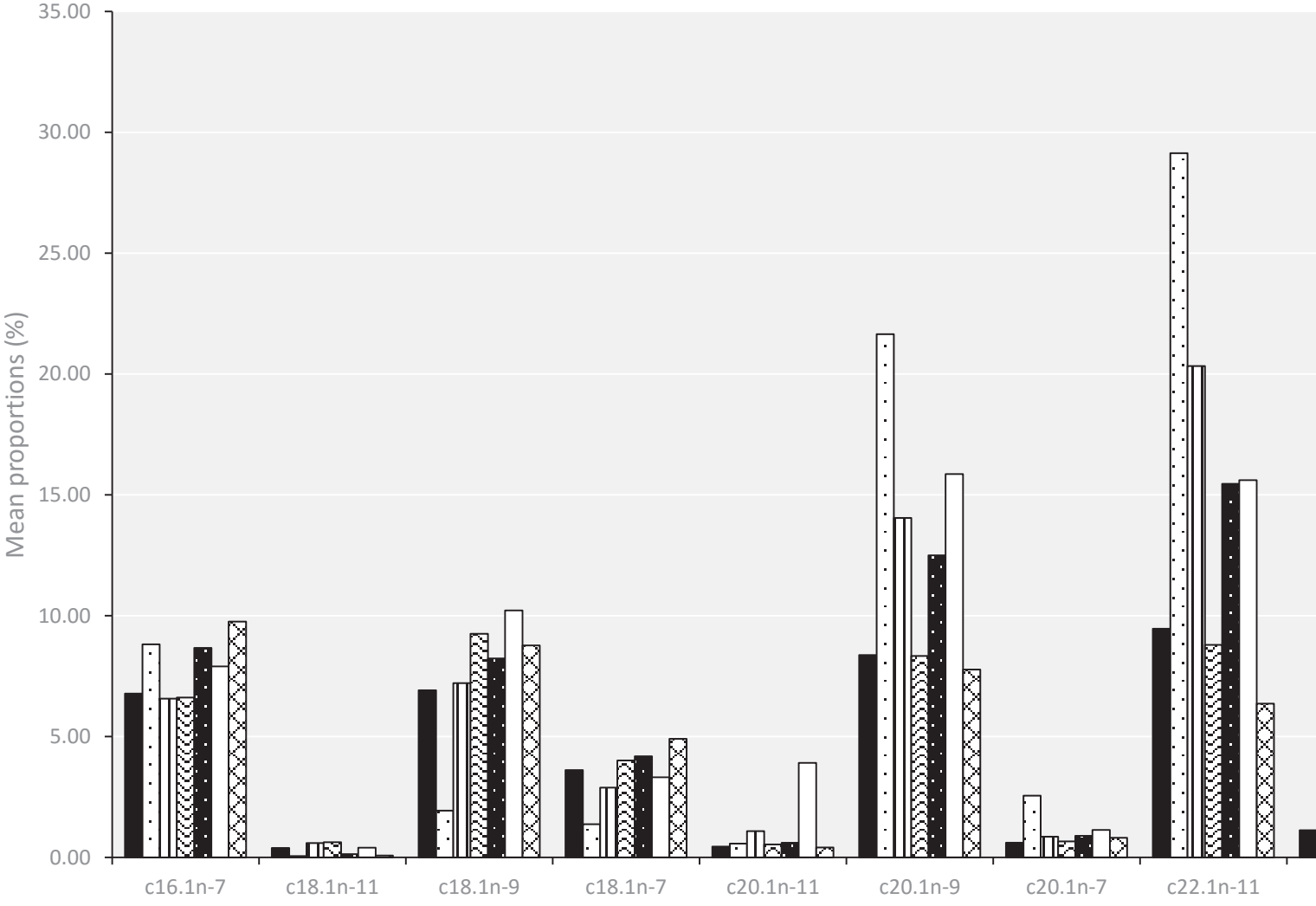
Appendix 5: Natural groupings of fin whale according to their FA profiles – suite 2

The discriminant analysis identified one significant function (*p-value* < 0.0001), which explained 44.1% of the total variance. PC3 seemed to contribute the most to the discrimination between groups (b = -2.069) while PC5 contributed the least (b = 0.162). MANOVA showed all PCs were significantly different between groups except PC5 (F = 0.954, p = 0.3313). The classification error rate obtained by cross-validation was 7%, with six individuals out of 90 being misclassified.

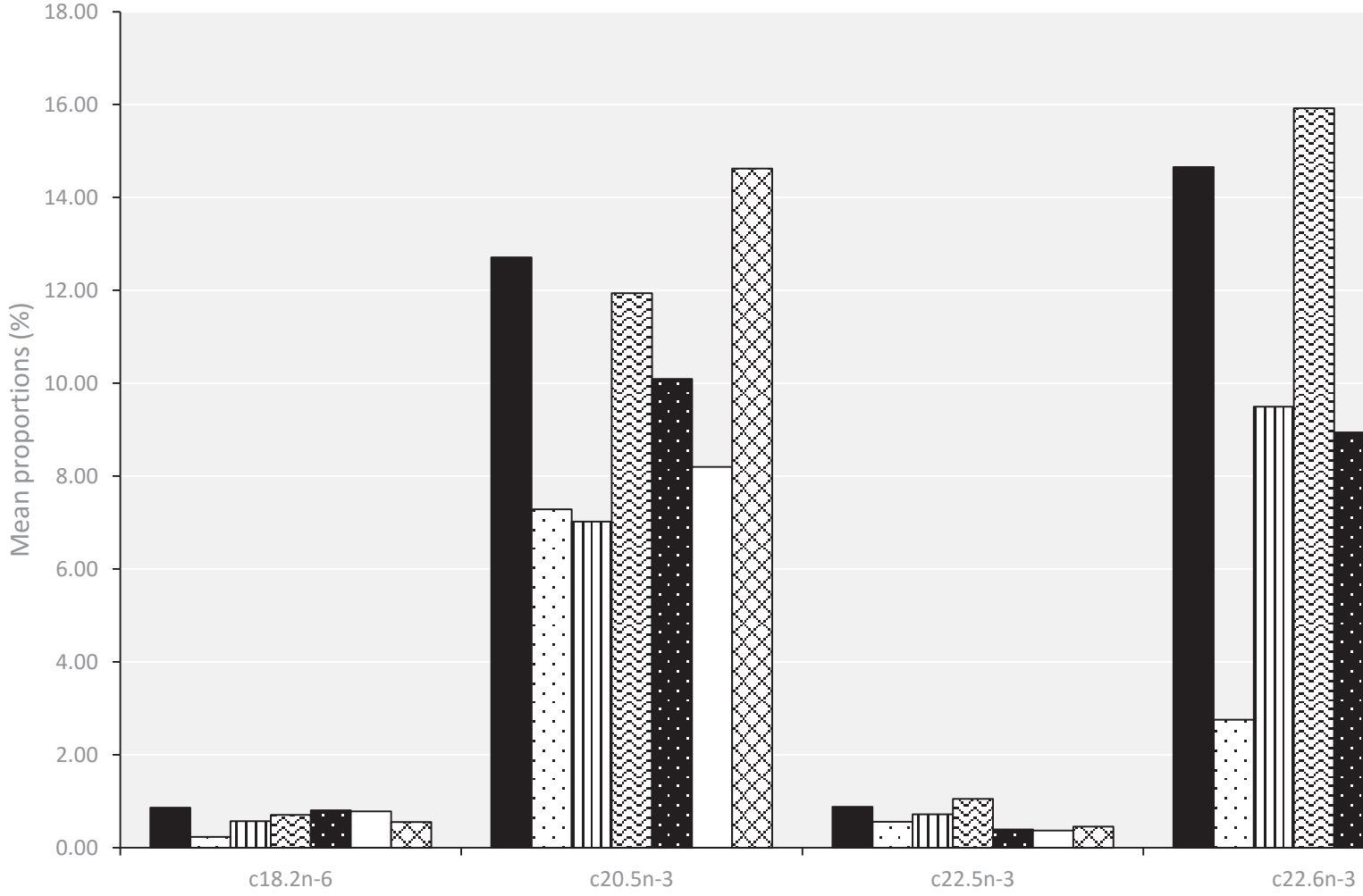
Appendix 6: Mean proportions (%) of SFAs for each prey selected



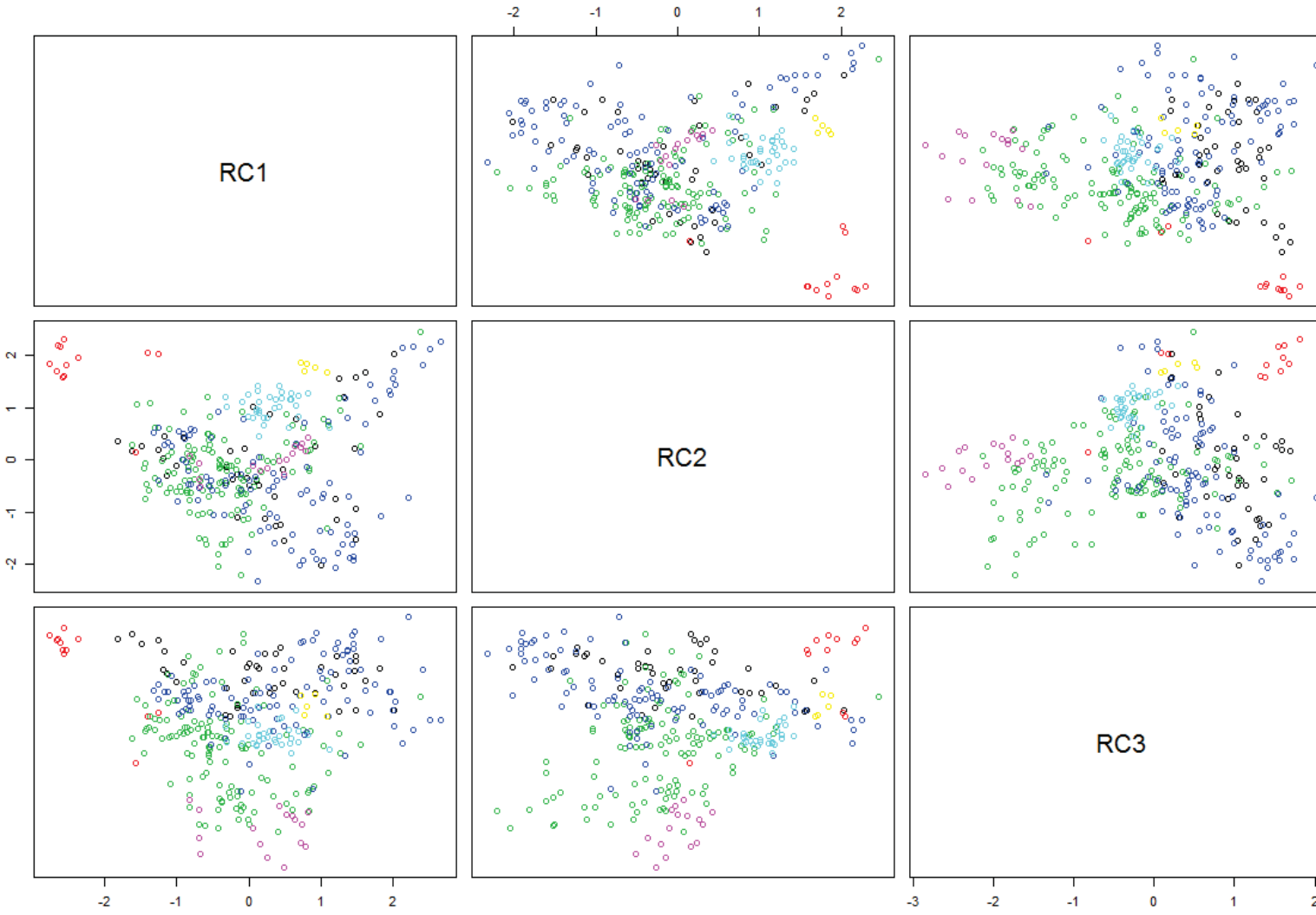
Appendix 7: Mean proportions (%) of MUFAs for each prey selected



Appendix 8: Mean proportions (%) of PUFAs for each prey selected



Appendix 9: Rotated PC scores of selected prey



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