Reconnaissance vocale mère-chiot durant la lactation chez le phoque commun de l’estuaire du St-Laurent

Mémoire

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Résumé

Les pinnipèdes adoptent des stratégies d'allaitement alternatives associées à plusieurs facteurs affectant les capacités du couple mère-petit à rester en contact, notamment la mobilité des jeunes et la fréquence des absences maternelles. Contrairement à la plupart des espèces de phocidés, les femelles phoque commun s'alimentent en mer en cours de lactation et leurs chiots sont très mobiles de la naissance au sevrage. Cette étude visait à caractériser le système de reconnaissance vocale mère-petit chez cette espèce. Les cris des chiots portent un niveau d'individualité intermédiaire comparativement aux valeurs généralement rapportées chez les deux grandes familles de pinnipèdes. Les femelles reconnaissent les cris de leur progéniture, capacité corrélée au niveau d'individualité vocale de leur chiot. Il existe d'importantes différences intra-colonies quant à l'efficacité de propagation des vocalisations. Ces résultats nous renseignent quant à l'influence des contraintes écologiques et environnementales sur l'évolution de la reconnaissance vocale chez le phoque commun.

Abstract

Pinnipeds adopt contrasting maternal strategies, which are associated with ecological factors affecting the difficulties encountered by mother-pup pairs to maintain contact throughout the rearing period. These include offspring mobility and the frequency of maternal absences. As opposed to most phocid species, harbour seal females forage at sea during lactation and their pups are highly mobile from birth to weaning. The objective of this study was to characterize the mother-pup vocal recognition system in this species. Pup calls convey an individual stereotypy level intermediate between that typically found in the two main families of pinnipeds. Females recognize the calls of their pup among others, a capacity that is correlated to the individual stereotypy level of pup voice. The propagation efficiency of pup calls vary considerably among mother-pup reunion sites. These results provide insights as to the influence of ecological and environmental constraints on the evolution of vocal recognition in harbour seals.

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AM: Amplitude modulation (modulation d’amplitude)

DFA: Discriminant function analysis (analyse de fonction discriminante)

f_0 : Fundamental frequency (fréquence fondamentale)

FM: Frequency modulation (modulation de fréquence)

ISL: Individual stereotypy level (niveau d’individualité vocale)

LMM: Linear mixed model (modèle linéaire mixte)

MAC: Mother attraction call (cri d’appel émis pas le chiot)

MPL: Mother protection level (niveau de protection maternelle)

PC: Principal component (composante principale)

PCA: Principal component analysis (analyse en composantes principales)

PIC: Potential for individual coding (potential de codage individual)

REML: Restricted estimator maximum likelihood (estimé restreint du maximum de *likelihood*)

Remerciements

«L'homme n'est rien d'autre que son projet, il n'existe que dans la mesure où il se réalise, il n'est donc rien d'autre que l'ensemble de ses actes, rien d'autre que sa vie.»
L'existentialisme est un humanisme, Jean-Paul Sartre (1945)

Deux années, trois continents, d'incroyables rencontres, des moments privilégiés. Voici ce qui résume mon parcours de maîtrise. Cette aventure a façonné qui je suis scientifiquement, professionnellement et personnellement. Elle fut ponctuée de nombre de moments d'émerveillement et de péripéties, mais celles-ci ne contribuèrent que davantage à mon processus d'apprentissage. Le travail de terrain dans le bas du fleuve me fit voir des scènes d'une beauté indescriptible qui, je l'espère, resteront à jamais ancrées parmi mes plus beaux souvenirs. Je suis d'une extrême reconnaissance à l'endroit des accès uniques à la nature que permet la recherche en biologie. Comme il serait insensé de prétendre que cet ouvrage résulte d'un travail en solo, je noircirai quelques lignes pour faire part de ma gratitude à tous ceux et celles qui m'ont permis de réaliser ce projet.

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Avant-propos

La présente étude porte sur le système de reconnaissance vocale mère-petit chez le phoque commun (*Phoca vitulina*) de l'estuaire du St-Laurent. Elle est constituée de deux chapitres consistant en autant d'articles scientifiques sujets à publication dans des journaux à révision par les pairs. Ainsi, l'article présenté au Chapitre 1 est intitulé *Vocal communication in harbour seal pups: individual identity, call ontogeny and amphibious signals* et a été soumis à *Journal of Mammalogy*. En date du dépôt final, cet article est en révision. Quant au Chapitre 2, il est composé d'un article ayant pour titre *Mother-pup vocal recognition in harbour seals: Call stereotypy and habitat acoustic properties may drive female discrimination abilities*. Cet article est également en révision, pour sa part à *Behavioural Ecology and Sociobiology*.

Je suis première auteure des articles constituant le corps de ce mémoire, qui ont tous deux bénéficié de la contribution des mêmes coauteurs (Tableau I), soit Gwénaël Beauplet, directeur de ce projet à l'Université Laval; Mike O. Hammill, collaborateur affilié à l'Institut Maurice Lamontagne, centre de recherche de Pêches et Océans Canada et Isabelle Charrier, codirectrice de ce projet basée au Centre de Neurosciences Paris-Sud.

Tableau I. Contribution des coauteurs aux articles présentés dans ce mémoire.

	Caroline Sauvé	Gwénaël Beauplet	Mike O. Hammill	Isabelle Charrier
Conception du projet		X		X
Élaboration du projet	X	X		X
Financement		X		
Matériel		X	X	X
Acquisition des données	X	X	X	X
Analyses statistiques	X			
Interprétation des résultats	X			X
Rédaction	X			
Révision		X	X	X

J'ai également présenté le contenu du chapitre 2 au congrès annuel de l'*Animal Behaviour Society* s'étant tenu à l'université de Princeton (NJ) en août 2014 sous la forme d'une présentation orale intitulée *Vocal recognition of pup by harbour seal mothers: discrimination abilities and female personality*.

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Océans Canada et l’équipe bioacoustique du Centre de neurosciences Paris-Sud ont contribué à fournir les ressources humaines et matérielles nécessaires aux expériences et à l’analyse des données.

Introduction

«The formation of different languages and of distinct species, and the proof that both have been developed through a gradual process, are curiously the same. […] Languages, like organic beings, can be classed either naturally according to descent, or artificially by other characters. Dominant languages and dialects spread widely and lead to gradual extinction of other tongues»
The descent of man, and selection in relation to sex, Darwin (1871)

Au-delà de ses impacts en linguistique (voir Ruhlen 1994), cette citation de Darwin suggère que les systèmes de communication évoluent par sélection naturelle. Ce principe orienta les études en communication animale, domaine foisonnant de l'écologie évolutive et comportementale ainsi que des neurosciences. Cet engouement pour l'étude de la communication animale découle de l'omniprésence des systèmes de communication dans l'ensemble du règne, ceux-ci étant nécessaires à l'établissement des interactions sociales (e.g., résolution de conflits, défense du territoire ou du partenaire sexuel, coordination des activités chez les espèces sociales).

Étudier la communication animale est intéressant d'un point de vue évolutif car cela permet de comprendre les relations entre les systèmes de communication et les contraintes écologiques et environnementales. En effet, les systèmes de communication sont susceptibles d'évoluer chez les espèces ou populations où les individus qui y participent en tirent des bénéfices nets en termes de valeur adaptative (*i.e.*, bénéfices > coûts; Bradbury et al. 1998). Or, les coûts et bénéfices associés aux divers contextes de la communication dépendent de plusieurs facteurs écologiques et environnementaux. Par exemple, chez le cyprin américain à nageoires rouges (*Cyprinella lutrensis*), l'intensité de la coloration des mâles, signal sélectionné par les femelles lors des parades nuptiales, est corrélée positivement à la turbidité de l'habitat (Dugas et Franssen 2011). Cela permettrait aux variations interindividuelles de coloration d'être perçues par les femelles sans attirer outre mesure les prédateurs étant donné la visibilité réduite dans les eaux plus turbides.

Les études comparatives en communication animale permettent donc de révéler l'effet de diverses contraintes environnementales, écologiques, démographiques et phylogénétiques sur l'évolution des systèmes de communication. La caractérisation d'un système de communication permet également d'identifier les signaux essentiels pour le maintien des interactions sociales chez une espèce donnée, dont il est nécessaire de tenir compte lors d'études d'impacts des activités anthropiques sur l'écologie faunique. Finalement, la découverte des signaux utilisés par les animaux pour se reconnaître entre eux peut permettre d'exploiter lesdits signaux pour recenser les individus dans un habitat. Par exemple, les hiboux grands-ducs (*Bubo bubo*) et les loups de l'est (*Canis lupus lycaon*) peuvent être identifiés par leurs cris individualisés, permettant de réaliser des suivis bioacoustiques de distribution spatiale (Grava et al. 2008, Root-Gutteridge et al. 2014).

Reconnaissance individuelle

Il y a reconnaissance individuelle lorsqu'un animal traite de façon différentielle un individu en fonction d'indices distinctifs, et non uniquement selon le contexte (Waldman 1987, Pfennig et Sherman 1995). La reconnaissance individuelle implique deux parties: 1) un émetteur, qui produit un signal porteur d'une signature individuelle et 2) un receveur, qui perçoit le signal, le compare à un gabarit gardé en mémoire, et valide l'identité de l'émetteur (Beecher 1982). La variation interindividuelle du signal ainsi que la capacité du receveur à percevoir les subtilités de cette variabilité représentent donc deux conditions essentielles pour l'évolution des systèmes de reconnaissance individuelle.

Comme toute autre forme de communication, la reconnaissance individuelle est susceptible d'évoluer chez les espèces ou populations où elle confère des bénéfices nets tant à l'émetteur qu'au receveur (Tibbetts et Dale 2007). Ces avantages peuvent être associés à la valeur adaptative directe ou inclusive (Hamilton 1964). En effet, la discrimination des individus à différents niveaux de résolution[1] (e.g., espèce, statut hiérarchique, sexe, classe d'âge, individu) constitue une condition nécessaire pour la plupart des interactions sociales (choix du partenaire sexuel, direction des soins parentaux et des comportements altruistes, etc.). Chez les espèces ou populations où la reconnaissance individuelle confère un avantage, les traits distinctifs (signaux d'identité; e.g.; voix, coloration, odeur) sont sous sélection négative dépendante de la fréquence (Dale et al. 2001). En effet, les individus ayant un phénotype rare pour un trait d'identité sont plus distinctifs, moins sujets à être confondus avec d'autres et donc favorisés par la sélection naturelle. Il en résulte que les traits d'identité sont généralement fortement héréditaires et variables entre individus. Ainsi, chez le travailleur à bec rouge (*Quelea quelea*) et le combattant varié (*Philomachus pugnax*) où la reconnaissance visuelle diminuerait les interactions agressives entre mâles défendant leur territoire (Crook 1960, Dale 2000, Van Rhijn 1991), le patron de coloration est polymodal, alors qu'il est unimodal chez le roselin familier (*Carpodacus mexicanus*) qui n'est pas territorial (Dale et al. 2001).

La reconnaissance parent-jeune représente un contexte particulier de reconnaissance individuelle pouvant être favorable aux deux parties. Elle permet en effet aux parents d'allouer des soins exclusivement à leurs jeunes,

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[1] Plusieurs auteurs ont remis en question la définition de la «vraie» reconnaissance individuelle (*True individual recognition*), notamment en suggérant que le terme devrait être limité aux cas où le receveur associe le signal à un individu précis, et non à une classe d'individus (Beecher, M. D. 1989. Signaling systems for individual recognition - An information-theory approach. Animal Behaviour 38: 248-261; e.g., progéniture *vs* autres jeunes, dominant *vs* dominé). Cependant, comme cette distinction réfère généralement au processus cognitif impliqué sans affecter le résultat des interactions entre les individus, le terme reconnaissance individuelle est ici utilisé sans distinction.

ce qui augmente leur succès reproducteur en favorisant la survie de leur progéniture (Clutton-Brock 1991, Royle et al. 2012). La reconnaissance parent-jeune permet également aux petits d'éviter les risques de blessures associés aux interactions avec des adultes non apparentés et potentiellement agressifs (e.g., Boonstra 1984, Troisi et al. 1988, Silk 1990, Harcourt 1992). La période de soins parentaux achevée, la reconnaissance parent-jeune peut permettre d'éviter les accouplements consanguins (Bateson 1978, 1983) et d'augmenter la valeur adaptative inclusive (Hamilton 1964) des individus en favorisant l'altruisme entre parents et progéniture.

Les modalités sensorielles associées à la reconnaissance parent-jeune résultent des forces de sélection propres au contexte dans lequel évoluent les espèces ou populations, notamment en termes de complexité du signal et de distance effective (Bradbury et al. 1998). Ainsi, la reconnaissance visuelle des œufs par leur forme et/ou patron de couleur est répandue chez les espèces d'oiseaux sujettes au parasitisme au nid (e.g., Paruline rouge, *Cardellina rubra*: Marchetti 2000; grive musicienne, *Turdus philomelos*: Honza et al. 2007; coucou gris, *Cuculus canorus*: Aviles et al. 2010; caille du Japon, *Coturnix japonica*: Pike 2011). Chez les fourmis, l'olfaction est utilisée pour ce même processus (Helantera et al. 2014). L'olfaction permet également la reconnaissance parent-jeune à très faible distance (< 0.25 m), et est largement utilisée chez les mammifères pour confirmer l'identité du jeune préalablement à l'allaitement (e.g.: Alexander 1978, Pitcher et al. 2011). La reconnaissance vocale est répandue dans de nombreux taxons chez lesquels des forces de sélection favorisent un mode de reconnaissance efficace sur de longues distances (e.g.: pinnipèdes: Insley et al. 2003a; chauves-souris: Balcombe 1990, Knornschild et al. 2013; ongulés: Torriani et al. 2006, Briefer et McElligott 2011; oiseaux coloniaux: Falls 1982). Finalement, certaines espèces disposent de systèmes de reconnaissance parent-jeune multimodale (e.g.: Alexander et Shillito 1977, Keller et al. 2003, Pitcher 2010).

Les systèmes de reconnaissance parent-jeune des différents taxons ou espèces reflètent généralement les difficultés rencontrées par les deux parties à rester en contact et à se retrouver pendant la période de soins parentaux. Ainsi, les systèmes de reconnaissance parent-jeune diffèrent grandement entre deux espèces d'hirondelles étroitement apparentées (Beecher et al. 1986). Chez l'hirondelle à front blanc (*Petrochelidon pyrrhonata*), caractérisée par un mode de vie colonial, une reproduction synchronisée entre les individus et la formation de crèches lorsque les adultes partent s'alimenter, les parents reconnaissent les cris individualisés de leurs poussins. En revanche, l'adulte hirondelle rustique (*Hirundo rustica*), espèce solitaire aux naissances asynchrones, ne démontre aucune reconnaissance des cris faiblement individualisés des jeunes. Également, les poussins des espèces de manchots sans nid (*Aptenodytes patagonius* et *A. fosteri*) se basent sur une signature acoustique plus complexe que les espèces à nid (*Pygoscelis adaliae* et *P. papua*) pour discriminer les cris de leurs parents (Jouventin et al. 1999, Jouventin et Aubin 2002). De même, il y a reconnaissance vocale mutuelle père-petit et absence de reconnaissance mère-petit chez le petit pingouin (*Alca torda*; Insley et al. 2003b). Chez cette espèce, les deux sexes prodiguent des soins parentaux lorsque les jeunes sont au nid, mais seul le mâle continue d'aider ses petits en mer durant une période de transition vers l'indépendance nutritionnelle. Enfin, le niveau d'individualité des cris des chiots est inférieur chez l'éléphant de mer septentrional (*Mirounga angustirostris*) que chez l'otarie à fourrure du Nord (*Callorhinus ursinus*; Insley 1992). En effet, chez l'éléphant de mer, femelles et jeunes ne se quittent pas au cours de la lactation alors que chez l'otarie à fourrure, les chiots sont séparés de leur mère lorsqu'elle part chasser en mer au cours de la lactation. À travers ces exemples, il apparaît que la densité de la population au site de reproduction, la mobilité des jeunes et la fréquence des absences parentales sont des forces de sélection qui modulent les systèmes de reconnaissance parent-jeune. Celles-ci pourraient également agir sur les capacités de reconnaissance parent-jeune entre populations d'une même espèce (McCulloch et al. 1999, McCulloch et Boness 2000).

Les différences inter- et intra- spécifiques observées quant aux capacités de reconnaissance parent-jeune peuvent être attribuables aux deux parties impliquées dans le processus. D'une part, les études bioacoustiques comparatives ont démontré que la quantité d'information relative à l'identité de l'émetteur (*i.e.*, nombre de paramètres acoustiques individualisés et potentiel de codage individuel[2] (PIC) de ces paramètres) encodée dans ses vocalisations est fortement variable entre les espèces (e.g., Lengagne et al. 1997, Mathevon et al. 2003). Les PICs sont supérieurs chez les espèces pour lesquelles les facteurs associés à la stratégie reproductive (e.g., forte mobilité des jeunes et densité d'individus) complexifient la reconnaissance des parents par les jeunes. L'intensité des forces de sélection agissant sur le système de reconnaissance parent-jeune affecte donc le niveau d'individualité vocale des émetteurs. D'autre part, l'efficacité de la reconnaissance parent-jeune dépend des capacités de perception sensorielle et d'analyse du signal du receveur (Beecher 1991). Chez les espèces où le système de reconnaissance vocale parent-jeune est sous forte pression de sélection, les receveurs se fient à un plus grand nombre de paramètres acoustiques individualisés pour la reconnaissance de l'émetteur (Charrier et al. 2001a, 2002, 2003, 2009, Aubin et Jouventin 2002, Searby et Jouventin 2003). En effet, la redondance de l'information encodée dans un signal optimise les chances du receveur de percevoir correctement le message (Shannon et Weaver 1949).

Individualité des signaux vocaux

Chez les mammifères, la production vocale comporte deux étapes impliquant des structures anatomiques distinctes. Ainsi, des vibrations de l'air sont générées par une «source» (*i.e.*, larynx et structures laryngales et sous-laryngales) puis modifiées par un «filtre» (tractus vocal reliant le larynx à la bouche et aux

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[2] Un paramètre acoustique est considéré comme individualisé lorsque son potentiel de codage individuel (PIC, *pontential for individual coding*), défini comme le rapport de la variabilité interindividuelle et la variabilité intra-individuelle moyenne est supérieur à 1 (i.e., lorsque PIC = $CV_{\mathrm{int}\,er-individu}/\overline{CV}_{\mathrm{int}\,ra-individu} > 1$; Robinson, P., Aubin, T. et Bremond, J.-C. 1993. Individuality in the voice of emperor penguin Aptenodytes forsteri: adaptation to a noisy environment. Ethology 94: 279-290).

narines; source-filter theory of voice production; Fant 1960, Singh et Singh 1976, Titze 1994). L'équivalent a été caractérisé chez les oiseaux (Beckers et al. 2003, 2004, Fletcher et al. 2004, Elemans et al. 2008), toutefois seul le cas des mammifères sera présenté ici afin d'alléger le texte.

La glotte est formée des plis vocaux (cordes vocales chez l'humain; Bradbury et al. 1998) et de l'espace qui sépare ces derniers. Lorsque la glotte est fermée, l'air expulsé des poumons force les plis vocaux à se séparer. Ceux-ci se referment aussitôt par l'action de forces biomécaniques (Taylor et Reby, 2010). La répétition de ce processus génère une variation cyclique de la pression d'air à la sortie du larynx. C'est cette vibration de l'air qui constitue les sons bruts qui se propageront à travers le tractus vocal, puis à l'extérieur du corps de l'animal. Le rythme d'ouverture-fermeture de la glotte détermine la fréquence fondamentale (f_0), alors que le flux et la pression de l'air poussé par l'expiration, influencés par les capacités respiratoires de l'animal, établissent la durée, le tempo et l'amplitude des vocalisations (Titze 1994, Fitch 1997). Ces paramètres acoustiques sont associés à la source de la production vocale. La f_0 des vocalisations est influencée par l'état de motivation (Morton 1977) et corrélée négativement avec la longueur et l'épaisseur des plis vocaux (Titze 1994, Fitch 1997) de l'animal. Or, les plis vocaux et le larynx sont constitués de tissus mous dont l'anatomie n'est pas contrainte par des structures squelettiques (Fitch 1997, 2000a). Ainsi, les paramètres acoustiques associés à la source présentent des variations interindividuelles indépendantes de la taille corporelle (Masataka 1994, Fitch 1997, Reby et McComb 2003, Rendall et al. 2005). Ces paramètres sont plutôt influencés par les niveaux sanguins de testostérone (Charlton et al. 2011, Galeotti et al. 1997, Evans 2008), puisque ceux-ci régulent le développement du larynx (e.g., Fischer et al. 1995).

Le tractus vocal agit comme un résonateur, amplifiant et atténuant différentes fréquences du signal émis par la source. Il détermine donc la composition spectrale des vocalisations. Cet effet dépend des propriétés physiques du filtre, qui sont le résultat de la position de la langue dans la cavité buccale, du degré d'ouverture de la bouche et des narines, des mouvements de la mâchoire inférieure, etc. (Fant 1960, Titze 1994). Toutefois, lors de la vocalisation, ces structures permettent peu de flexibilité chez la plupart des espèces animales. Il en résulte que les caractéristiques spectrales d'un même individu sont généralement constantes d'une vocalisation à l'autre (Fitch 1994, 2000a, 2000b). Néanmoins, puisque les structures anatomiques impliquées croissent en concomitance avec le reste du corps, les paramètres acoustiques associés au filtre sont étroitement corrélés à la taille corporelle (Fitch 1997, Riede et Fitch 1999, Reby et McComb 2003, Taylor et al. 2008, Charlton et al. 2009).

La dépendance des paramètres acoustiques à l'anatomie de l'appareil vocal est à la base d'une signature individuelle encodée dans les vocalisations. Il a ainsi été démontré que divers paramètres acoustiques peuvent contribuer à la signature vocale individuelle. Chez les mammifères, la f_0 et la modulation de fréquence

(FM, *frequency modulation*) constituent les plus importants paramètres porteurs de l'identité individuelle associés à la source (*e.g.*, Owren et al. 1997, Janik 2000, Charrier et Harcourt 2006, Torriani et al. 2006, Palacios et al. 2007). À cela s'ajoutent la durée, le tempo, la modulation d'amplitude et la présence de subharmoniques (Rendall et al. 1998, Reby et al. 1999, Yin 2002, Charrier et al. 2003a, Rendall 2003, Khan et al. 2006). Le filtre permet également d'encoder de l'information relative à l'individu émetteur, notamment via les fréquences amplifiées (harmoniques ou formants; Rendall 2003, Briefer et McElligott 2011). La composition spectrale permet d'ailleurs la conservation de l'individualité vocale entre divers types de cris (e.g. roucoulement, grognement, cris) émis par un même animal (Rendall et al. 1998, Reby et al. 2006).

Malgré la quantité de paramètres acoustiques porteurs d'information sur l'identité de l'émetteur, l'influence de l'anatomie sur ceux-ci constitue une contrainte dans le contexte de la reconnaissance vocale de la progéniture par les parents. En effet, au cours de la période des soins parentaux, les jeunes sont en pleine croissance, et leur système hormonal se met en place. Or, les paramètres acoustiques liés au filtre seront susceptibles de subir des modifications allométriques pendant la croissance corporelle des jeunes alors que les paramètres liés à la source changeront en fonction de la maturation des structures laryngales associées aux niveaux hormonaux. La redondance du codage de l'identité du jeune dans les vocalisations apparaît donc particulièrement importante pour la reconnaissance vocale parent-jeune. Elle permettrait en effet la reconnaissance continue du jeune par ses parents malgré la modification de certains paramètres acoustiques au cours de la période de soins parentaux.

Reconnaissance vocale parent-jeune chez les pinnipèdes

Étant donné l'étroite relation entre les systèmes de reconnaissance vocale parent-jeune et les contraintes écologiques propres aux espèces animales, les études comparatives sont d'un intérêt particulier dans ce domaine. Les taxons utilisés comme modèles pour l'étude de la reconnaissance parent-jeune sont caractérisés par la diversité, au sein d'espèces apparentées, du niveau de difficulté ou de contraintes pour les parents et leur progéniture à rester en contact durant la période de soins parentaux. Ainsi, les chiroptères, oiseaux marins, ongulés grégaires et pinnipèdes sont de bons modèles d'études en raison de la variabilité de la taille des groupes et des stratégies de reproduction rencontrées dans ces taxons (e.g.: Lengagne et al. 1997, Insley et al. 2003a, Torriani et al. 2006, Knornschild et Von Helversen 2008)).

Depuis les trois dernières décennies, les pinnipèdes constituent un groupe cible pour les études comparatives portant sur la reconnaissance vocale parent-jeune (Insley et al. 2003a). En effet, la phylogénie des différentes familles et espèces de pinnipèdes ainsi que les stratégies de reproduction qui leur sont propres sont relativement bien établies (Bowen 1991, Boness et Bowen 1996, Berta et Churchill 2012), permettant d'établir des liens entre les systèmes de reconnaissance, les contraintes écologiques et l'histoire évolutive des espèces.

Le sous-ordre des pinnipèdes comprend trois familles: les otariidés (otaries à fourrures et lions de mer, 13 espèces actuelles), les phocidés (phoques, 19 espèces actuelles) et les odobenidés (une seule espèce actuelle: le morse, *Odobenus rosmarus;* Berta et Churchill 2012). À l'exception du morse, les pinnipèdes mettent bas et allaitent leurs jeunes en milieu terrestre (terre ferme, récif ou banquise) alors qu'ils dépendent du milieu marin pour leur alimentation (Bonner 1984, Oftedal et al. 1987). Cette séparation spatio-temporelle des activités de reproduction et de prospection alimentaire complique d'autant plus l'acquisition de l'énergie nécessaire à la production du lait maternel qu'aucun soin parental n'est prodigué par les mâles pinnipèdes (Le Boeuf 1991). Pour faire face à ces contraintes, les femelles pinnipèdes produisent un seul chiot par portée (Bowen 1991) et adoptent différentes stratégies d'allaitement pendant la période de lactation.

Les otariidés sont des reproducteurs sur revenu. Après un jeûne *post-partum* de 7 à 11 d pendant lequel elles allaitent leur chiot, les femelles alternent épisodes d'alimentation en mer et d'allaitement sur la terre ferme tout au long de la période de lactation qui s'étend généralement sur 4 à 18 mois (Boness et Bowen 1996, Schulz et Bowen 2004). Au cours des absences maternelles, qui durent de 2 d à 3 semaines, les chiots otariidés se regroupent en crèches (Bowen 1991, Boness et Bowen 1996). Cette stratégie d'allaitement implique donc une importante fréquence de séparations mère-petit et une forte mobilité du chiot durant la période de soins maternels. Ces deux caractéristiques des otariidés, couplées à la très forte densité d'individus aux sites de reproduction chez ces espèces (Boness et al. 2002), constituent des forces de sélection favorisant un système de reconnaissance vocale mère-petit fiable. Les phocidés, quant à eux, sont des reproducteurs sur capital. Ainsi, les femelles accumulent d'importantes réserves énergétiques sous forme de gras corporel avant la mise-bas. Elles dépendront alors de ces réserves pour la production du lait maternel et jeûneront tout au long de la courte période de lactation (4-60 d; Schulz et Bowen 2004) afin de rester auprès de leur chiot. Quelques espèces font toutefois exception à cette règle: les femelles phoques du Groenland (*Pagophilus groenlandicus*; Hammill et al. 1991)), annelé (*Pusa hispida*; Lydersen et Kovacs 1993), commun (*Phoca vitulina*; Boness et al. 1994) et de Weddell (*Leptonychotes weddellii*; Wheatley et al. 2008) s'alimentent pendant la période de lactation. Hormis les phoques barbus (*Erignathus barbatus*), communs et de Weddell, les chiots phocidés sont relativement sédentaires, accumulant passivement l'énergie transférée via le lait maternel afin d'optimiser leur taux de croissance pendant la brève période de soins maternels (Bowen 1991, Lydersen et al. 1994). Par conséquent, la stratégie d'allaitement des phocidés est associée à de rares et brèves séparations mère-petit, ainsi qu'à une faible mobilité des jeunes. De plus, les densités de population dans les colonies de phocidés sont nettement inférieures à celles des otariidés (Boness et al. 2002), sauf dans les cas des phoques gris et des éléphants de mer. Les forces de sélection agissant sur les systèmes de reconnaissance vocale mère-petit sont donc moins importantes et plus variables entre les espèces de phocidés comparativement aux otariidés.

Les pressions de sélection différentielles ont favorisé l'évolution de divers systèmes de reconnaissance vocale mère-petit parmi les pinnipèdes. Ainsi, tant les mères que les chiots otariidés produisent des cris hautement individualisés, et un système de reconnaissance vocale bidirectionnel (la mère reconnait la voix de son chiot et *vice versa*) a été démontré chez toutes les espèces étudiées à ce jour (Insley et al. 2003a). À l'inverse, les systèmes de reconnaissance vocale mère-petit sont plus variables chez les phocidés. Chez plusieurs espèces, les femelles ne vocalisent que rarement à l'égard de leur chiot. Le niveau d'individualité vocale des chiots est également plus variable et inférieur à celui rencontré chez les otariidés (voir Charrier et Harcourt 2006 pour synthèse). Il en résulte que chez certains phocidés, il y a absence de reconnaissance vocale du chiot par la mère (phoque moine d'Hawaii[3], *Monachus schauinslandi*: Job, Boness et al. 1995; phoque de Weddell: Van Opzeeland et al. 2012; phoque à capuchon[4], *Cystophora cristat:* Ballard et Kovacs 1995). Un système de reconnaissance unidirectionnel, où les femelles reconnaissent la voix de leur chiot, a également été décrit chez l'éléphant de mer septentrional (*Mirounga angustirostris*; Petrinovich 1974). Finalement, la reconnaissance vocale du chiot par la mère a été démontrée chez le phoque gris (*Halichoerus grypus*) de Sable Island (Nouvelle-Écosse; McCulloch et Boness 2000), alors que les femelles de la population de l'Isle of May (Royaume-Unis, McCulloch et al. 1999) ne discriminent pas les cris de leur jeune.

Le phoque commun

Le phoque commun est le plus répandu des phocidés, sa répartition s'étendant le long des côtes septentrionales de l'Atlantique et du Pacifique (Thompson et al. 1997, Burns 2009). Cette espèce utilise une variété d'habitats, et les femelles mettent bas sur divers substrats (sable, récifs rocheux, rochers côtiers, glaciers, etc.) selon les populations (Robillard et al. 2005, Blundell et al. 2011).

La stratégie d'allaitement du phoque commun constitue un cas particulier parmi les phocidés puisqu'après un jeûne post-partum de 2 à 14 d, les femelles effectuent de courts (durée moyenne[5]: 7h) épisodes de chasse en mer pendant la période de lactation, qui dure entre 21 et 42 jours (Riedman 1990, Boness et al. 1994). De plus, le chiot phoque commun est exceptionnellement mobile, commençant à nager dès sa naissance et demeurant hautement actif dans l'eau tout au long de la période de lactation (Bigg 1981). Les chiots accompagnent parfois leur mère lors des voyages d'alimentation en mer (Bowen et al. 1999). Ces caractéristiques associées à la

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[3] Observations seulement, aucune expérience de playback

[4] *Idem*

[5] Observée à la colonie de l'île de Sable, Nouvelle-Écosse, Canada. Susceptible de varier considérablement entre les colonies et populations.

stratégie d'allaitement suggèrent de plus sérieuses difficultés pour le couple mère-petit à rester en contact pendant la période de lactation comparativement à la majorité des phocidés. Les pressions de sélection favorisant l'évolution du système de reconnaissance vocale mère-petit sont donc susceptibles d'être plus importantes chez cette espèce. En outre, les importants gradients topographiques et d'exposition aux activités anthropiques et aux éléments (*i.e.*, vents, courants, marées) caractérisant les sites utilisés par le phoque commun (Burns 2009, Robillard et al. 2005, Thompson et al. 1997) sont susceptibles d'être associés à des différences d'efficacité de propagation acoustique. Les propriétés physiques du site de réunion mère-petit pourraient ainsi avoir un impact sur le processus de reconnaissance vocale mère-petit. L'ensemble de ces particularités fait du phoque commun une espèce fortement intéressante pour les études comparatives intra- et interspécifiques. La caractérisation de son système de reconnaissance vocale mère-chiot permettrait de discriminer le rôle des contraintes écologiques et de la phylogénie sur l'évolution des systèmes de communication chez les pinnipèdes. En effet, un système de reconnaissance vocale semblable à celui des otariidés indiquerait que celui-ci a été façonné par les contraintes écologiques partagées par cette famille de pinnipèdes et le phoque commun. Un système de reconnaissance vocale plutôt typique des autres phocidés permettrait pour sa part de conclure à l'influence de la phylogénie dans l'évolution de ce système de communication.

Durant la période de lactation, le chiot phoque commun vocalise fréquemment, émettant des cris qui disparaissent de son répertoire vocal après le sevrage (Renouf 1984). Cela suggère un rôle primordial des cris dans le maintien des contacts mère-petit au cours de la période de lactation. Les cris du chiot phoque commun sont émis simultanément dans les milieux aérien et sous-marin lorsque celui-ci crie la tête au-dessus de la surface de l'eau (cris amphibies). Lorsqu'il est hors de l'eau ou entièrement submergé, les vocalisations du chiot sont émises uniquement dans l'air ou dans l'eau, selon le cas. La femelle phoque commun ne vocalise pratiquement jamais pour appeler son chiot (*obs. pers.*).

Malgré l'intérêt de cette espèce, la communication vocale a été peu étudiée chez le chiot phoque commun. D'une part, des travaux préliminaires ont suggéré que les cris du chiot phoque commun comptent plusieurs paramètres acoustiques individualisés (Renouf 1984). Cette étude a été réalisée en milieu naturel sur des animaux non marqués, signifiant qu'il n'y avait pas de possibilité d'évaluer les effets de la maturation et de la croissance sur les cris des chiots. Plus tard, une analyse acoustique des cris aériens a été réalisée chez des chiots en captivité, et des effets de l'âge et du sexe ont été révélés pour divers paramètres acoustiques (Khan et al. 2006). Cependant, l'effet de la taille corporelle sur les vocalisations n'a pas été évalué. D'autre part, une expérience a démontré qu'une femelle phoque commun en captivité peut être entraînée à discriminer les cris de deux chiots différents (Renouf 1985). Toutefois, seuls deux cris (un par chiot) ont été diffusés à répétition au cours de l'expérience. Il est donc impossible de déterminer si la femelle discriminait les variations interindividuelles encodées dans les cris ou simplement les différences entre les deux cris présentés (problème de pseudo-réplication; Kroodsma 1989). De plus, la démonstration d'une discrimination via l'apprentissage par récompense alimentaire ne permet pas d'établir si lesdites capacités sont effectivement utilisées dans un contexte donné en milieu naturel (notion de généralisation des résultats scientifiques; McGregor et al. 1992). Ainsi, à notre connaissance, aucune étude n'a testé expérimentalement si les femelles phoques communs reconnaissent vocalement leur jeune au sein de la colonie.

Objectifs

La présente étude avait pour objectif général de caractériser le système de reconnaissance vocale mère-chiot chez le phoque commun en milieu naturel et compte trois objectifs spécifiques. Alors que le premier objectif fait l'objet du Chapitre 1 de ce mémoire, les deuxième et troisième objectifs sont abordés dans le Chapitre 2.

Le premier objectif spécifique était de caractériser les vocalisations émises par le chiot phoque commun dans les milieux aérien et aquatique. Il s'agissait premièrement de quantifier le niveau d'individualité des cris aériens et sous-marins du chiot et d'identifier les paramètres acoustiques les plus susceptibles d'être utilisés par la femelle pour la reconnaissance vocale de son chiot, le cas échéant. Cela permettra également d'inclure le phoque commun dans les études comparatives portant sur la reconnaissance vocale mère-chiot chez les pinnipèdes. Deuxièmement, l'influence des traits individuels (âge, taille corporelle et sexe) sur les vocalisations du chiot a été déterminée et son implication potentielle sur le processus de reconnaissance vocale du chiot par la mère est discutée. Finalement, les composantes aériennes et sous-marines des cris amphibies ont été comparées afin de déterminer si l'émission simultanée dans les deux milieux de propagation génère des signaux différents. Des paramètres acoustiques conservés entre les deux composantes d'un même cri pourraient permettre aux femelles de ne mémoriser qu'une seule version de la voix de leur jeune et de le reconnaître tant sous l'eau qu'hors de l'eau.

Le deuxième objectif spécifique de ce projet était de tester expérimentalement la reconnaissance vocale du chiot par la mère chez le phoque commun. En plus de déterminer si les femelles reconnaissent la voix de leur chiot pendant la période de lactation, ces expériences ont permis d'établir l'influence du niveau d'individualité vocale du chiot sur les capacités de discrimination de la mère.

Finalement, le troisième objectif spécifique était de déterminer l'effet du site sur l'efficacité de propagation des vocalisations émises par le chiot phoque commun afin de mettre en évidence les éventuelles différences intra- et inter-colonies relatives aux propriétés acoustiques du milieu exploité par les couples mère-petits durant la période de lactation. En effet, les propriétés acoustiques établissent les distances maximales auxquelles la reconnaissance vocale mère-petit est susceptible d’être effective dans un milieu donné.

Chapitre 1 – Vocal communication in harbour seal pups: individual identity, call ontogeny and amphibious signals

Résumé

Les pinnipèdes constituent un taxon intéressant pour les études comparatives en reconnaissance individuelle en raison de la variété de stratégies d'allaitement retrouvée au sein de ce groupe. Cette étude visait à caractériser le niveau d'individualité porté par les cris d'appel aériens et sous-marins émis par les chiots phoques communs, à décrire les effets de l'âge et de la taille corporelle sur ces vocalisations et à comparer les composantes aériennes et sous-marines des cris émis simultanément dans les deux milieux. Seize paramètres acoustiques ont été mesurés sur 1072 cris d'appel produits par 88 chiots enregistrés au cours des saisons estivales 2011 à 2013 dans l'Estuaire du St-Laurent. Quatorze paramètres étaient porteurs d'une signature individuelle tant pour les cris aériens que sous-marins, notamment la fréquence fondamentale, la durée du cri, les quartiles d'énergie et la modulation de fréquence. Une analyse de fonction discriminante a réassigné 42,6 et 44,2% des cris aériens et sous-marins, respectivement, aux individus émetteurs. La majorité des paramètres acoustiques les plus individualisés étaient dépendants de l'âge et de la taille corporelle. Ces résultats indiquent que les cris d'appel du phoque commun portent une signature individuelle ayant le potentiel d'être utilisée par les femelles pour la reconnaissance vocale de leur chiot. Dans cette éventualité, les femelles devraient constamment ajuster le gabarit qu'elles gardent en mémoire pour reconnaître la voix changeante de leur jeune. La fréquence fondamentale, la durée du cri et les pentes de modulation de fréquence étaient relativement constantes entre les composantes aérienne et sous-marine des cris amphibies. Cela suggère que les femelles pourraient apprendre une seule version de ces paramètres fortement individualisés et être en mesure d'identifier la voix de leur chiot dans les deux media.

Abstract

Pinnipeds have great potential for comparative studies of mother-pup recognition due to the contrasting maternal strategies adopted by otariids and phocids. Unlike most phocids, harbour seal (*Phoca vitulina*) females forage during the nursing period, which exacerbates the need for effective mother-pup vocal recognition in this species. Individual differences and ontogeny-related changes in airborne and underwater harbour seal pup mother attraction calls were investigated. Acoustic differences between aerial and underwater components of amphibious pup calls (*i.e.,* calls made while the pup's head was partially submerged) were also assessed. Sixteen acoustic parameters were measured on 1072 calls from 88 pups recorded during the 2011-2013 breeding seasons in the St. Lawrence Estuary, Canada. Fourteen parameters, including the fundamental frequency, duration, energy quartiles and frequency modulation slopes, were individually stereotyped for both airborne and underwater calls. Discriminant function analysis correctly assigned 42.6 and 44.2% of airborne and underwater calls, respectively, to individual pups. A majority of highly individualised acoustic parameters were affected by pup age and body length. These results indicated that harbour seal pup calls encode an individual signature that might allow recognition of young by mothers, in which case females must continuously learn their pup's changing voice in the course of the rearing period. The fundamental frequency, total duration and frequency-modulation slopes were relatively constant between aerial and underwater components of amphibious calls. This suggested that females could rely on a single version of these highly individualised acoustic parameters to identify their offspring's call in both media.

Introduction

Parent-offspring recognition can be mutually beneficial (Trivers 1974) in animal species providing parental care by ensuring resources are not invested in non-filial young and avoiding risks of injury associated with young's interactions with unrelated, potentially aggressive (*e.g.*, Troisi et al. 1988, Harcourt 1992) adults. Under these circumstances, parent-offspring recognition favors offspring growth and survival and therefore adult reproductive success, resulting in positive selection pressures for the ability to emit individualised signals and perceive individuality within these signals (Tibbetts and Dale 2007).

Parent-offspring recognition involves two components: 1) the production of a signal conveying individually-stereotyped characteristics by an emitter, and 2) the perception of the information embedded in the signal and its comparison to a memorised template by a receiver that ultimately makes a decision as to the emitter's identity (Beecher 1982). Therefore, inter-individual signal variation, often referred to as an individual signature, is a prerequisite for recognition abilities by the receiver. If the presence of an individual signature within a communication system is not properly assessed, then it would be impossible to distinguish between failures of recognition by receivers attributable to a lack of perceptual discrimination abilities, from those due to insufficient inter-individual variation within signals (Beecher 1982, 1991).

Signals used for parent-offspring recognition can be associated with various sensory systems such as olfaction (*e.g.*, Alexander 1978, Pitcher et al. 2011, Helantera et al. 2014), vision (*e.g.*, Marchetti 2000, Honza et al. 2007, Pike 2011), audition (*e.g.*, Balcombe 1990, Charrier et al. 2009) or a combination of these factors (*e.g.*, Alexander 1978, Keller et al. 2003). Acoustic signals are reliable over long distances in air or water (Bradbury et al. 1998), which explains why parent-offspring vocal recognition is widespread among animals, particularly across birds and mammals (*e.g.*, Falls 1982, Bradbury et al. 1998, Insley et al., 2003).

The source-filter theory (Fant 1960) provides a framework for studying vocal production mechanisms that has been used in mammalian (see Taylor and Reby 2010 for review) and avian (Beckers et al. 2003, 2004, Fletcher et al. 2004, Elemans et al. 2008) bioacoustic research. According to the source-filter theory, animal vocalizations are generated by the 'source' (*i.e.*, larynx, sublaryngeal structures and vocal folds in mammals; syrinx in birds) and subsequently modified in the 'filter' (*i.e.*, supralaryngeal vocal tract in mammals, trachea in birds; Titze 1994). In addition to their contrasting roles in vocal production, components of the vocal apparatus influence different acoustic features of the vocalizations. Source-related acoustic parameters include the fundamental frequency, tempo, duration and amplitude, while filter-related parameters are associated with spectral characteristics of the vocalizations (Titze 1994, Taylor and Reby 2010). These acoustic parameters are influenced by both the size and shape of the vocal apparatus components (Taylor and Reby 2010). The constraints imposed by anatomical structures on acoustic parameters have been shown to result in vocal distinctiveness between individuals in various species (*e.g.*, Charrier et al. 2002, 2009). However, this influence of anatomy also means that some acoustic features are expected to change as individuals grow and mature. Ontogenic modifications of source- and filter-related acoustic parameters generally differ since structural development of the associated vocal structures are mediated by contrasting factors. Indeed, the vocal tract length is directly dependent on body size (*e.g.*, Fitch 1997, Riede and Fitch 1999, Fitch and Reby 2001). In sexually dimorphic species, divergent growth rates can therefore result in differences in filter-related acoustic parameters between the sexes. Conversely, the larynx is not strictly constrained by surrounding bony structures and therefore not directly related to body size (Fitch 1997, 2000b). Moreover, the larynx is a sex steroid target organ (Aufdemorte et al. 1993) whose development is influenced by testosterone levels. Source-related parameters can thus differ between males and females as a result of sex-related hormonal changes. Ontogenic modifications of vocalization features may impact parent-offspring recognition processes. It can be hypothesised that parents would rely more on acoustic parameters that undergo less considerable changes during the rearing period. Otherwise parents would need to constantly adjust their internal template of their offspring's voice to enable recognition as their offspring grow and mature (Hepper 1991), especially in species with extended parental care.

Comparative studies have demonstrated that parent-offspring vocal recognition systems differ among species and taxa according to the strength of selection pressures for this ability (*e.g.*, Beecher 1982, Jouventin 1982, Insley 1992, Jouventin and Aubin 2002, Insley et al. 2003a). The selective pressures acting on parent-offspring recognition systems are related to the risks of separation between parents and offspring and the constraints to find each other in their environment. Parent-offspring vocal recognition abilities are generally positively correlated with population densities at breeding sites (Beecher et al. 1986) and strongly related to mother-young interactions during lactation in mammals. For example, the two main strategies for predation avoidance in ungulates are associated with contrasting mother-offspring recognition systems. In hider species, offspring lie hidden in the vegetation and females emit individualised calls when approaching the area where the calf was left to initiate nursing bouts (Lent 1974, Torriani et al. 2006). Recognition is therefore unidirectional with offspring recognising the mother's calls (Torriani et al. 2006). In follower species, in which offspring join their mother's social group soon after birth (Lent 1974), females need to identify their mobile calf among others and vocal recognition is usually mutual (Sebe et al. 2007). Similarly, maternal reproductive strategies led to divergent mother-offspring recognition systems in pinnipeds. In otariids, females undertake extended foraging trips at sea during the long lactation period (4-24 months) and must relocate their pup upon return to their dense breeding colony (Riedman 1990, Bowen 1991, Boness and Bowen 1996). As a result, high levels of individual stereotypy of both female and pup calls as well as mutual recognition abilities have been detected in all studied otariid species (Insley et al. 2003a, Charrier and Harcourt 2006, Charrier et al. 2009, Pitcher et al. 2010). In contrast, phocid females generally fast alongside their pup throughout their relatively short lactation period (4-53 d; Bowen 1991), although maternal strategies are more variable than initially conceived in this family (Hammill et al. 1991, Lydersen and Kovacs 1993, Boness et al. 1994, Wheatley et al. 2008). Accordingly, individual stereotypy levels in vocalizations and mother-offspring recognition abilities vary across phocid species (Table 5 in Collins et al. 2006). In contrast to otariids and except for highly colonial species (grey (*Halichoerus grypus*) and elephant (*Mirounga* spp.) seals), phocid females vocalize infrequently and their calls are poorly individualized (Insley et al. 2003a).

Harbour seals (*Phoca vitulina*) have an 'otariid-like' maternal strategy, with females undertaking foraging trips at sea beyond the first week of the ≈34 d lactation period (Boness et al. 1994, Thompson et al. 1997, Dubé et al. 2003). Furthermore, harbour seal pups are exceptional among phocids as they are highly mobile in the water from birth (Bigg 1981, Oftedal et al. 1987) and throughout lactation, sometimes accompanying their mother at sea during foraging trips (Bowen et al. 1999). Such early mobility, in addition to frequent maternal absences during lactation, induces strong constraints to ensure mother-pup contact until weaning (Renouf et al. 1983, Renouf and Diemand 1984). A mother-pup recognition system effective over long distances, such as vocal recognition, is thus likely to be selected for in this species. Harbour seal pups frequently emit vocalizations conventionally called mother attraction calls (MAC; Khan et al. 2006) that are withdrawn from their vocal repertoire after weaning, suggesting a role in mother-pup reunion during lactation (Renouf, 1984). Harbour seal pups vocalize both in-air and under water, and calls produced when the pup is at the surface are designated as amphibious calls since they propagate simultaneously in both media (Renouf 1984, Perry and Renouf 1988).

Renouf (1984) suggested that harbour seal pup MACs have the potential to carry individual signatures which has been demonstrated in captive Pacific harbour seal pups (Khan et al. 2006). However, large-scale studies on free-ranging and tagged animals are required to further characterize the individual stereotypy and ontogeny of harbour seal pup vocalizations. Additionally, components of single amphibious calls are likely to be filtered differently by the vocal tract, as the aerial and underwater components are emitted at the animal's mouth and neck, respectively. This could result in contrasting aerial and underwater individual signatures emitted simultaneously. Comparisons between aerial and underwater components of harbour seal amphibious calls might thus provide insights into the roles of amphibious communication in this species' pre-weaning recognition system.

The objectives of the present study are: 1) to characterize the individual stereotypy of both underwater and airborne harbour seal pup MACs from a large sample of free-ranging animals; 2) to investigate the effects of age, body size and sex on these MACs and 3) to assess the differences between aerial and underwater components of amphibious harbour seal pup MACs. This research therefore aims to provide unprecedented information on harbour seal pre-weaning vocal communication and to interpret results in relation to MACs' potential role in mother-pup recognition in this species.

Materials and Methods

Study site and animal handling

This study was conducted at the Bic (48°24’ N, 68°51’ W; N ≈ 100 pups/year; Van de Walle 2013) and Métis (48°41’ N, 68°01’ W; N ≈30 pups/year; Van de Walle 2013) harbour seal colonies located on the South shore of the St. Lawrence Estuary, Canada. These sites were visited (weather permitting) alternately throughout 3 consecutive breeding seasons (2011-2013, from mid-May to mid-July). Harbour seal pups were captured in the water using a dip net and 5 m inflatable boat and then transferred in a 7 m hard-hulled motorboat for handling. At first capture, pup sex was established. To facilitate recaptures, individuals were marked with a coloured and numbered pyramid tag (Seal Hat®, Dalton, England) glued (Loctite #422 cyanoacrylate glue and #7452 Accelerator, Loctite Corp., Mississauga, ON, Canada) on the head and tagged with a uniquely numbered Jumbotag (Dalton, England) in a hind flipper. Upon each capture, pups were weighed (± 0.1 kg; Salter spring scale, West Bromwich, England) and measured to the nearest centimeter (standard length; McLaren 1993). Handling time rarely exceeded 10 min from capture to release. All procedures involving live animals were approved by the Animal Care Commitees of Université Laval and Fisheries and Oceans Canada.

As most pups were not captured immediately after parturition, 2 indirect methods were used to estimate pup age (d). Birthdate of young pups was determined according to umbilicus degeneration when present (Boulva and McLaren 1979, Cottrell et al. 2002, Dubé et al. 2003) and to a back-calculation if the umbilicus had fallen (> 5 d) at first capture (detailed in Van de Walle 2013).

Recording procedures

Most pups called for their mother after being captured. Therefore, MACs produced by pups were recorded for about 1 min following pup transfer to the bigger boat and prior to any handling upon each capture. Aerial calls were recorded using a shotgun microphone (Sennheiser ME 67, Sennheiser, Wedemark, Germany) connected to a digital recorder (Marantz PMD 661, Marantz Europe, Eindhoven, Netherlands). Upon completion of biometric measurements, the pup was held by the hind flippers on the surface of the water for 60 s while MACs were recorded simultaneously in-air and under water using a hydrophone (Cetacean Research C54XRS, Cetacean Research Technology, Seattle, WA) connected to the same digital recorder. Following pup release, recordings were continued until the mother-pup pair reunited or until the pup was out of sight. Airborne and underwater calls were recorded in stereo on two different channels at a 44.1 kHz sampling frequency. Prior to acoustic analysis, airborne and underwater channels of all recordings were separated into two distinct sound files and resampled at 22.05 kHz using Avisoft SAS Lab Pro (R. Specht, version 4.36; Avisoft Bioacoustics, Berlin, Germany) as call maximal frequencies did not exceed 10 kHz.

Acoustical analysis

Recorded vocalizations were divided among three types according to the medium in which they were emitted. Airborne MACs were emitted solely in air while pups were in the boat after capture. When pups were returned to the water they produced simultaneous aerial and underwater MACs, hereafter referred to as amphibious MACs (Perry and Renouf 1988). Finally, some calls (underwater MACs) were emitted solely under water while the pup's head was submerged. To ensure adequate characterisation of intra-individual call variation, only recordings containing at least six vocalizations with a high signal-to-noise ratio were selected for further analysis.

Harbour seal pup vocalizations are tonal and exhibit an inverted 'U' or 'V'-shaped pattern characterized by an ascending FM at the beginning of the call followed by a flat part (plateau) and a descending FM afterwards (Figure 1.1a; Renouf 1984, Khan et al. 2006). Each call from all MAC types (aerial, underwater and amphibious) were characterised by 16 acoustic parameters: total duration of the call (*dt*; ms), fundamental frequency (f_0; Hz), slope of the ascending FM (*AFM*; Hz·s^{-1}) shown at the beginning of the call, slope of descending FM (*DFM*; Hz·s^{-1}) shown at the end of the call, frequency values (f_{max1}, f_{max2}, f_{max3}, f_{max4} and f_{max5}; Hz) at 1st, 2nd, 3rd, 4th and 5th peaks of amplitude (P_1 to P_5 on Figure 1.1c), amplitude ratios between 1st and 2nd, 3rd, 4th and 5th peaks of amplitude (A_2/A_1, A_3/A_1, A_4/A_1 and A_5/A_1, respectively) and the 25%, 50% and 75% energy quartiles (Q_{25}, Q_{50} and Q_{75}; Hz). All 16 variables were measured using Avisoft SAS Lab Pro. The total duration of the call was measured on the oscillogram (cursor precision: 1 ms; Figure 1.1b). To characterize the ascending and descending FMs, four points were defined on the first visible band (FFT window size, 1024 Hz, cursor precision: 20 Hz, 1ms; Figure 1.1a): beginning of the call (t_1; f_1), the 2 inflection points ((t_2; f_2) and (t_3; f_3)) and end of the call (t_4; f_4)). The ascending part of the call is therefore located between t_2 and t_1, the plateau between t_3 and t_2, and the descending part between t_4 and t_3. The *AFM* was calculated using the following equation (see Figure 1.1a): $(f_2 - f_1)/(t_2 - t_1)$, while *DFM* was calculated as: $(f_4 - f_3)/(t_4 - t_3)$. The value of f_0 was calculated as the mean between f_3 and f_2 (Figure 1.1a). Amplitude ratios, frequency peaks and energy quartiles were obtained from the average amplitude spectrum (Hamming window, frequency resolution = 0.336 Hz; Figure 1.1c) measured on the entire duration of the call.

Statistical analysis

All statistical analyses were performed within the R environment (R version 3.1.0; R Development Core Team 2011). When appropriate, normality was tested using Shapiro-Wilk tests and homogeneity of variance using Levene tests on medians (package car; Fox and Weisberg 2011). Results were considered significant at $p < 0.05$ and are presented as means ± standard errors (s.e.), unless stated otherwise.

Vocal stereotypy of pups

Individual differences in calls were characterized by running the analyses described below separately for airborne and underwater MACs. The PIC for each acoustic parameter was assessed by calculating the CV_b/CV_i ratio, where CV_b is the between-individual coefficient of variation and CV_i is the average of all within-individual *CV*s (Robinson et al., 1993). All coefficients of variation were calculated using the correction for small sample sizes: $CV = (\bar{x}/sd) \times (1/4n)$ (Sokal and Rohlf 1995). Parameters for which the PIC value is greater than 1 have the potential to encode individual identity as intra-individual variability is less than inter-individual variability (Robinson et al. 1993). One-way ANOVAs using pup IDs as the group variable were computed for each acoustic parameter to assess inter-individual differences. When required, log-transformations were used to correct for deviations from the normality criterion and Welch's correction for unequal variances was applied when relevant. A sequential Bonferroni adjustment for multiple comparisons was applied to significance levels since the different acoustic parameters tested derived from the same set of calls (Kepel 1991, Quinn and Keough 2002).

Individual stereotypy of MACs was further assessed by performing separate stepwise, cross-validation discriminant function analysis (DFAs, package MASS, Venables and Ripley 2002) on airborne and underwater MACs. In DFAs, the size of the smallest group should be no larger than the number of predictor variables (Bökeoğlu and Büyüköztürk 2008). As the minimal number of calls per pup was set to six in this study, the number of acoustic parameters used as predictors had to be reduced so it did not exceed six. The acoustic parameters with the greatest PIC values were retained as predictors. Pearson's correlation matrices were computed to verify that multicollinearity between predictors was minimal (*i.e.*, $r < 0.5$). Acoustic parameters used as predictors were log transformed when deviating from the normality assumption. The percentage of MACs attributed to the right individual was computed for each pup as well as for the overall set of calls, and compared to the percentage expected by chance. Percent-correct classification scores vary according to sample size (number of individuals and number of calls per individual; Bee et al. 2001). As sample size was notably greater for airborne than underwater MACs, DFA on airborne MACs was performed using a random subsample of 15 individuals and iterated 100 times. The percent-correct classification scores presented for the airborne MACs are the means of all 100 iterations. This procedure allowed further comparison between results from airborne and underwater MACs. Calls from pups recorded at different ages were pooled together in DFAs. In the event that MACs are modified as a function of pup age, this combination of calls is expected to lower the DFAs' classification efficiency. Resulting percent-correct scores are thus highly conservative. Individual percent-correct scores were tested by a Welch two sample *t*-test to determine if pups recorded at different ages obtained lower percent-correct scores than other pups.

Individual traits and acoustic parameters

The effects of age, body size and sex on the MACs acoustic parameters were investigated using linear mixed models (LMMs, package nlme; Pinheiro et al. 2012) fitted with restricted estimator maximum likelihood (REML). Each acoustic parameter was defined as the response variable of a model in which fixed effects were pup sex, age (d), body length (cm) and the age*sex interaction, and pup identity was included as a random effect. Variance inflation factors (*VIF*) were computed for each model to detect eventual collinearity among dependent variables (vif.mer function; Frank 2011). Some parameters were log-transformed to obtain homoscedastic variables. Since transformation of the data did not always correct deviations from the normality of residuals, significance levels of coefficients were calculated by randomisation of the y axis (nb of iterations = 1000; Mazerolle 2013a). This analysis was performed separately for airborne and underwater MACs.

Characterization of amphibious calls

The acoustic parameters measured on aerial components of amphibious calls were plotted against their equivalent measured on the underwater component (1 plot per acoustic parameter) to illustrate the differences and similarities between both components of single MACs. To assess whether acoustic parameters were conserved between aerial and underwater versions of a same call, the hypothesis that the slope between both components is equal to 1 was tested using the function *slope.test* (package smart; Warton et al. 2013) for each acoustic parameter. A robust regression method was used to account for greater influence of some observations. In addition, a significance level of 1% was used for this test otherwise the test would have been more precise than the measurement error on acoustic parameters.

Results

A total of 1737 MACs with high signal-to-noise ratios from 109 harbour seal pups were recorded over the 2011-2013 breeding seasons. Exclusion of recordings with less than six calls of the same type resulted in 1072 vocalizations from 88 pups (39 females and 49 males) including 678 airborne (from 70 individuals), 114 underwater (from 13 individuals) and 280 amphibious (from 55 individuals) MACs. Overall, MACs fundamental frequency (f_0) ranged from 270-620 Hz (Table 1.1; mean= 434 ± 2 Hz) and total duration of the calls varied between 165-1113 ms (mean = 411 ± 4 ms). In some instances (*n*= 37, 16 and 8 for airborne, underwater and amphibious MACs, respectively), MACs did not exhibit any FM and were visibly flat. Thus *AFM* and *DFM* could not be measured on these MACs. For inverted U- and V-shaped calls, FM slopes varied between 73-8485 $\mathrm{Hz \cdot s^{-1}}$ (mean = 800 ± 20 $\mathrm{Hz \cdot s^{-1}}$) and -5692 to -31 $\mathrm{Hz \cdot s^{-1}}$ (mean= -930 ± 20 $\mathrm{Hz \cdot s^{-1}}$) for ascending and descending parts of the calls, respectively. Energy quartiles averages were Q_{25}: 850 ± 10 Hz, Q_{50}: 1250 ± 10 Hz and Q_{75}: 2060 ± 30 Hz.

Vocal stereotypy of pups

Acoustic parameters showing the highest PIC values included spectral (f_0, Q_{25}, Q_{50} and Q_{75}) and FM (*DFM* and *AFM*) features (Figure 1.2), which were therefore retained for DFAs. For both airborne and underwater MACs, correlation matrices indicated coefficients < 0.5 for each pair of these parameters, except for Q_{25}:Q_{50} and Q_{50}:Q_{75} which had correlation coefficients > 0.6. The DFAs were therefore performed using all of the parameters listed above except Q_{50}. As DFAs require a value for each discriminant, linear calls missing *AFM* and *DFM* were excluded from the analysis. Recordings containing less than six MACs of the same type following this exclusion were also removed from the dataset. The DFAs were performed on 596 airborne MACs from 61 individuals (28 females and 33 males) and 95 underwater MACs from 12 individuals (5 females and 7 males). Overall, stepwise cross-validation DFAs classified 42.6 ± 0.5% [32.0-53.4%] of airborne MACs to the right individual, which is greater than expected by chance (8.7%). Similarly, 44.2% of all underwater MACs were correctly assigned, compared to 9.3% as expected by chance. Correct classification rates were greater than expected by chance for 60/61 and 11/12 of the individuals recorded in-air and underwater, respectively (Tables 1.2 and 1.3). Individuals for which recordings collected at different ages were combined in DFAs did not obtain lower correct classification rates than non-repeated individuals for either airborne ($t_{44.73} = 3.67$, $p > 0.99$) and underwater (percent-correct classification for repeated individuals = 66.7%; 95% confidence interval for non-repeated individuals = 19.07-60.74%) MACs.

Individual traits and acoustic parameters

All VIFs were substantially < 10, indicating that collinearity was not an issue when including age and body length as fixed effects in single LMMs (Neter et al. 1990, Chai-Terjee and Price 1991; Tables 1.4 and 1.5). At birth, airborne MACs produced by males generally exhibited a f_0 25.9 Hz higher than females (Table 1.4, Figure 1.3a). This sex difference declined with pup age and body length as f_0 decreased by 2.2 $\text{Hz}\cdot\text{cm}^{-1}$ (coefficient of body length effect) and asymmetrically between sexes, by 0.4 $\text{Hz}\cdot\text{d}^{-1}$ (coefficient for age effect) in females and 1.4 $\text{Hz}\cdot\text{d}^{-1}$ (sum of coefficients for age and age*sex effects) in males. Slopes of both ascending and descending FMs of airborne calls became less steep with age, an effect that was less conspicuous in males than females (*i.e.*, *AFM*: -1.6 vs -11.2 $\text{Hz}\cdot\text{s}^{-1}\cdot\text{d}^{-1}$ and *DFM*: 3.3 and 5.5 $\text{Hz}\cdot\text{s}^{-1}\cdot\text{d}^{-1}$ for males and females, respectively). The first energy quartile (Q_{25}) increased with body length (5.7 $\text{Hz}\cdot\text{d}^{-1}$) for both sexes and age in males (2.0 $\text{Hz}\cdot\text{d}^{-1}$ vs no significant effect in females). The Q_{25} at birth was also 88.7 Hz lower in males than females. The Q_{50} decreased with pup age and the Q_{75} with body size. In males, f_{max3} increased (7.6 $\text{Hz}\cdot\text{d}^{-1}$) while f_{max4} and f_{max5} decreased by 7.3 and 23.2 $\text{Hz}\cdot\text{d}^{-1}$ respectively with age, whereas no significant effect of age on f_{max}s was found in females. Males also emitted shorter calls (Δdt = 55 ms) with greater *DFM* (ΔDFM = -222.8 $\text{Hz}\cdot\text{s}^{-1}$). Pups tended to concentrate their energy spectrum on a single frequency peak as they grew, as all amplitude ratios decreased with body size (non-significant effect for *A2/A1*).

Regarding underwater MACs (Table 1.5), there was also a negative effect of body length on f_0 in males (-3.1 $Hz \cdot cm^{-1}$), and this variable was 27.1 Hz higher at birth for males than females (Figure 1.3b). In females, calls became more frequency modulated with age, while the opposite was found for males that displayed lower *DFM* at birth. Body size also had a strong negative effect on FM slopes (in absolute value). Both Q_{25} and Q_{50} increased with age and decreased with body size, although the effect of age on Q_{25} was less prominent for males. Regarding the energy spectrum, age did not have any significant effect on f_{max1} and f_{max2} in females, whereas f_{max1} decreased and f_{max2} increased, respectively, in males. While f_{max3} and f_{max4} showed age-related increases, f_{max5} decreased with age in both sexes. As pups grew, all peak frequencies became lower, although effects of body length were only significant for f_{max3} and f_{max4}. Furthermore, all amplitude ratios increased with age and decreased with body size.

Characterization of amphibious calls

Total duration and fundamental frequency of calls did not vary between aerial and underwater components of amphibious calls (p= 0.51 and 0.04, respectively; Figures 1.4 and 1.5, Table 1.6). Aerial and underwater components of all other acoustic parameters differed significantly, although Q_{50} and FM slopes (*AFM* and *DFM*) tended to covary (Figure 1.5, Table 1.6). Graphical analysis also revealed that aerial and underwater frequency peaks (f_{max}s) were interchanged between harmonics, and thus amplitude ratios between the 1st and 2nd to 5th peaks of amplitude showed no correlation, indicating that energy distribution among harmonics greatly differed between aerial and underwater components of single vocalizations (Figures 1.4 and 1.5).

Discussion

Harbour seals in the present study emitted inverted ‘U’ or ‘V’-shaped MACs characterised by a fundamental frequency averaging 434 ± 2 Hz , which was comparable to the average (350 Hz; Ralls et al. 1985) and range (200-600 Hz; Khan et al. 2006) reported in their Atlantic and Pacific conspecifics. Likewise, average MAC duration (411 ± 4 ms) fell within the range (31 ± 14 s - 1100 ± 700 ms) reported in earlier harbour seal studies (Ralls et al. 1985, Perry and Renouf 1988, Van Parijs and Kovacs 2002, Khan et al. 2006). Harbour seal pups from the St. Lawrence Estuary therefore produced MACs with similar general characteristics as have been reported in other populations.

Vocal stereotypy of pups

To our knowledge, this study is the first to investigate vocal stereotypy in both airborne and underwater harbour seal MACs independently. This approach allows for an enhanced understanding of the possible roles of these two MAC types in pup vocal recognition by the female. Fundamental frequency, energy quartiles, FM slopes and call duration were the most individualised parameters in both airborne and underwater MACs. Fundamental frequency, FM and call duration (Renouf 1984, Khan et al. 2006) have also been identified as individualised parameters in airborne MACs from various pinniped species (*e.g.*, Renouf 1984, Phillips and Stirling 2000, Charrier et al. 2002, 2010, Charrier and Harcourt 2006; Collins et al. 2006, Khan et al. 2006). The fundamental frequency therefore represents a highly individualised feature of pinniped MACs, which can be explained by its strong dependence upon the structural anatomy of the vocal tract (Kelemen 1963). The resistance of FMs to degradation due to attenuation with distance and masking by noise (Wiley and Richard 1982) makes it another reliable parameter in which to encode information in long-distance communication systems and noisy environments. Both airborne and underwater harbour seal pup MACs thus contain diverse features encoding for individual identity.

The individual distinctiveness of airborne and underwater MACs was further confirmed by DFAs, as a combination of individualised acoustic parameters (f_0, Q_{25}, Q_{75}, *dt*, *AFM* and *DFM*) could reattribute calls to the correct individual more often than expected by chance. Overall percent-correct scores for airborne (42.6 ± 0.5%) and underwater (44.2%) MACs were comparable, suggesting that both call types share a similar level of individual stereotypy. These percent-correct scores were higher than those obtained in a previous harbour seal study (29% for airborne calls from captive Pacific harbour seal pups; Khan et al. 2006). However, as percent-correct scores obtained from DFAs can be influenced by the acoustic parameters used as predictors (Khan 2004), sample size (Bee et al. 2001, Insley et al. 2003a) and cross-validation technique used (Collins et al. 2006), it is impossible to determine whether this discrepancy reflects contrasting stereotypy levels between harbour seal populations. Straightforward comparisons of vocal stereotypy among studies should therefore be interpreted with caution. Nevertheless, percent-correct scores tend to be higher in otariids than in phocids, which is consistent with the contrasting selective pressures on mother-pup recognition associated with maternal strategies and densities at breeding sites (Table 1.7; Riedman 1990, Insley 1992, Boness and Bowen 1996, Boness et al. 2002). The 42.6 and 44.2% correct classification rates obtained in this study are greater than those obtained in other phocids using similar methods (*i.e* cross-validated DFAs), but lower than those reported in otariids (Table 1.7). The intermediate maternal strategy adopted by harbour seals (Boness et al. 1994), compounded by pup's early mobility (Bowen et al. 1999) might thus have resulted in stronger selection for pup vocal stereotypy than other phocid species showing no frequent/extended mother-pup separation during the nursing period.

The DFAs also revealed important inter-individual variations in percent-correct scores (Tables 1.2 and 1.3). This could reflect different vocal stereotypy levels between individuals, which would likely affect females' efficiency to recognize their pup's calls among others. However, DFA results do not necessarily reflect female's abilities to recognize their pups, and playback experiments are therefore required to validate this suggestion. Individuals for which calls recorded at different ages were pooled in DFAs did not show lower percent-correct scores, indicating that age-related variations of acoustic parameters did not affect vocal stereotypy sufficiently to alter reassignment efficiency. Moreover, a high percent-correct scores (78.3 %) was obtained for a pups as young as one day-old, indicating that harbour seal MACs are individually distinct within the first days of life.

Individual traits and acoustic parameter

Effects of sex on source-related acoustic parameters can be mediated directly by the larynx since this organ is affected by sex-related testosterone levels. In this study, both airborne and underwater MACs produced by males were more frequency modulated in the descending part of the call and showed higher f_0. Similarly, a previous study reported higher FM coefficients in male than female harbour seal pup MACs (Khan et al. 2006). Male airborne MACs from this study were also initially longer. This could result from greater lung volume, as male harbour seal pups were reported to be 5% heavier and 2% longer at birth than females (Ellis 1998, Van de Walle 2013). Moreover, males' airborne MACs showed lower Q_{25}, Q_{50}, f_{max1} and f_{max2} but higher f_{max4} and f_{max5} than females. This indicates a tendency for wider frequency bandwidths and greater concentration of energy in lower frequencies in male calls. Sex-related effects on spectral parameters differed for underwater MACs, in which f_{max1} was higher but f_{max2} to f_{max5} (non-significant effect for f_{max3} and f_{max4}) were lower for males than females. These sexual differences in filter-related acoustic parameters may also result from the size dimorphism at birth in this species, which is susceptible to influence the width of the vocal tract independently of body length. As reported by Khan et al. (2006), calls from harbour seal pups of both sexes were contrastingly modified with age for many parameters. Such age*sex effects may be attributable to differential vocal anatomy development, which can result from contrasting sex hormone level variations (e.g., Fischer et al. 1995) during the nursing period.

Age can modify source-related features of pup vocalizations that are independent of body size. For example the growth of the vocal folds, modulating the fundamental frequency of vocal signals (Taylor and Reby 2010), is not strictly related to body size due to its soft tissue anatomy (Fitch 1997, 2000b). Aged-related variations in harbour seal pup MACs could further be attributable to the motivational state of the pups when calling their mother, which can change as pups mature and induce modifications in the acoustic parameters of their calls (Scherer 1986). The f_0 and related parameters have been found to vary with the context in which animals call in various mammals (*e.g.*, baboon, *Papio* sp.: Fisher et al. 2002; domestic dog: Yin 2002; American elk, *Cervus canadensis*: Feighny et al. 2006; Weddell seal, *Leptonychotes weddellii*: Collins et al. 2011). As expected, the f_0 of both airborne and underwater MACs decreased (except for underwater MACs in females) as pups aged. The positive effect of age on f_0 in females ($1\ \mathrm{Hz{\cdot}d^{-1}}$) might be attributable to the skewed distribution of the age variable and the limited sample size (n = 13; Figure 1.3b) used in models for underwater MACs. Age-effect coefficients of underwater MACs must therefore be interpreted with caution. Airborne MACs also became less frequency modulated, slightly longer in duration, and their 50% energy quartile tended to concentrate towards lower frequencies. The extent of most of these variations differed between sexes. These ontogenic changes are consistent with Khan et al.'s (2006) finding that maximum and minimum frequency, as well as frequency range and modulation decreased with age in airborne harbour seal pups MACs. Likewise, the fundamental frequency values decreased and the energy spectrum became more concentrated on lower frequencies with age in Subantarctic fur seal (*Arctocephalus tropicalis*) MACs (Charrier et al. 2003a). With regard to underwater MACs, the first 50% of the energy spectrum shifted to higher frequencies, with f_{max3} and f_{max4} increasing, whereas f_{max5} became in frequency as pups aged. All amplitude ratios increased with pup age, indicating that pups emphasized less the first frequency peak as they matured.

As body size directly determines the length of the vocal tract (Fitch 2000a, 2000b), body length-related changes in acoustic features are generally associated with filter-induced variations in vocalizations (Taylor and Reby 2010). Such variations include the distribution of the energy among harmonics (Taylor and Reby 2010). In harbour seal airborne and underwater MACs, all amplitude ratios decreased with body length, indicating that larger pups produce calls in which the energy is more concentrated in a single harmonic. Body length effects were also detected for many f_{max}s and energy quartiles in both call types, further indicating spectral-related effects of pup size on their vocalizations. Body size also had a negative effect on f_0 in both airborne and underwater MACs. This suggests that harbour seal pup laryngeal structures mature concurrently with growth in length (Taylor and Reby 2010) during the nursing period. Body size-related effects on the fundamental frequency and spectral content (but not on energy quartiles) were also reported in a similar analysis of goat (*Capra hircus*) kid calls (Briefer and McElligott 2011).

Some of the effects of pup sex, age and body size revealed in this study differed according to call type (airborne vs underwater). The latter is not surprising since in air, pups generally opened their mouth while calling, whereas pups vocalized with their mouth closed under water (*pers. obs.*). Moreover, their head position while resting on land and swimming under water differed. These contrasting calling postures are likely to influence the shape of pups' vocal tract and supra-laryngeal resonant cavities, and therefore the features of their calls and their relationship with individual traits.

Of the seven most individualized acoustic parameters (*i.e* with highest PIC values), five (*dt*, f_0, Q_{50}, *AFM* and *DFM*) were significantly influenced by pup age while four (Q_{25}, Q_{75}, f_0 and *AFM*) were related to body length for both airborne and underwater MACs. Yet, the process of mother-pup vocal recognition requires that 1) the pup produces MACs providing information about its identity, and 2) the mother perceives the signal and compares it to a template of her pup's MACs stored in memory to decide whether the MACs heard were emitted by her pup (Bradbury et al. 1998). If MACs are effectively used by females to recognize their pups, effects of age and body size on acoustic parameters therefore imply a continuous update of female references templates in the course of the rearing period.

Characterization of amphibious calls

Because amphibious MACs are single calls emitted simultaneously in-air and under water while pups are in the water with their head over the surface, source-related acoustic parameters are not expected to vary between both components of a same call. Accordingly, the f_0 of underwater and aerial components of amphibious MACs recorded in this study did not differ (see Figure 1.5 and Table 1.6). Likewise, the duration of the calls was unchanged and FM slopes closely covaried between both components, indicating that the structure of calls remained unchanged in both media. In a similar analysis, Perry and Renouf (1988) also found that average FM did not differ between aerial and underwater recordings of harbour seal pup MACs. However, the latter study showed a difference in mean duration of calls emitted in both media. However, this discrepancy could represent an artefact of the analysis method, as Perry and Renouf (1988) did not perform pairwise comparisons and their data included some recordings that did not have their equivalent component in both media. Nonetheless, both components are emitted from different anatomical structures: the aerial component radiates through the pup's mouth, while the underwater component is emitted at the animal's neck. These components therefore undergo different filtering processes within the vocal tract and may consequently vary in their filter-related features. In this study, f_{max}s were interchanged and amplitude ratios were uncorrelated between underwater and aerial components of single calls (Figure 1.5). Similarly, Perry and Renouf (1988) reported that lower harmonic bands present in aerial components of harbour seal pup MACS were missing from their underwater equivalent. The amphibious calls of the hippopotamus (*Hippopotamus amphibious*) show a similar trend, with underwater components exhibiting a wider frequency range than their aerial equivalents (Barklow 2004). These findings suggest that differential filtering processes occur prior to emission of aerial and underwater components of pup calls. Moreover, depending upon the pup's head position relative to the water surface, mouth opening (*i.e.*, variation of resonance cavities) and thickness of blubber layer around the neck (which could act as a low frequency filter, as suggested by Perry and Renouf 1988), the differences observed between aerial and underwater components of single amphibious calls are subject to vary. Interestingly, all of the acoustic parameters for which aerial and underwater components covaried (dt, Q_{50}, AFM, DFM, f_0) were among the seven most individualised (*i.e.*, higher PIC values) variables measured in this study. If these acoustic features are actually used for mother-pup vocal recognition, females could therefore learn a single version of their offspring's call and be able to recognise it when hearing it either under water or in air. Such individual-stereotypy of constant parameters both in-air and under water could thus favour efficient vocal recognition of pups by their mother and so would ease reunions between the pair.

In summary, this study found that free-ranging harbour seal pups emit individually-stereotyped calls from one day of age that might be used by females for vocal recognition of their pup. Such long-distance recognition would favor mother-pup reunion upon female's return to the colony from foraging trips at sea. Harbour seal MACs undergo various changes as pups grow and age, requiring the constant updating of the female's memorized template to recognise her pup throughout the nursing period. Finally, although some acoustic features vary between aerial and underwater components of single amphibious calls, the most individualised parameters remain relatively unchanged. This should enhance detection and recognition of pups by their mother in both media. However, the production of individually-distinct calls does not necessarily imply that these are used for individual recognition. Hence, playback experiments would be required to verify these assumptions.

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Table 1. 1. Descriptive statistics of harbour seal pup MACs. Numbers in brackets indicate parameter ranges. Statistics of amphibious MACs were performed on underwater components of the calls.

Acoustic parameter	Airborne MACs (*n*=678)	Underwater MACs (*n*=114)	Amphibious MACs (*n*= 280)
dt (ms)	417 ± 4 [193 - 1113]	450 ± 16 [170 – 1054]	426 ± 8 [207 - 952]
Q_{25} (Hz)	1019 ± 9 [357 - 1671]	466 ± 16 [45 – 1020]	618 ± 15 [162 – 1458]
Q_{50} (Hz)	1403 ± 12 [590 – 3783]	872 ± 31 [360 – 1757]	1200 ± 22 [364 – 2422]
Q_{75} (Hz)	2264 ± 38 [944 – 7944]	1682 ± 74 [707 – 5212]	1921 ± 43 [707 – 7558]
f_0 (Hz)	432 ± 2 [270 – 620]	423 ± 4 [340 – 580]	442 ± 4 [300 – 620]
f_{max1} (Hz)	1115 ± 13 [359 – 2172]	896± 23 [301– 1771]	722 ± 29 [294 – 2737]
f_{max2} (Hz)	1165 ± 18 [153 – 2282]	946 ± 32 [372 – 2643]	1095 ± 30 [361 – 2553]
f_{max3} (Hz)	1186 ± 22 [129 – 3636]	1268 ± 35 [423 – 2223]	1285 ± 31 [357 – 2737]
f_{max4} (Hz)	1492 ± 34 [286 – 6250]	1581 ± 40 [564 – 2676]	1561 ± 33 [299 – 2791]
f_{max5} (Hz)	2100 ± 45 [303 – 9182]	1972 ± 42 [589 – 2958]	1985 ± 37 [370 – 3202]
AFM (Hz·s^{-1})	766 ± 23 [82 – 8485]	878 ± 77 [93 – 4516]	777 ± 26 [73 – 3023]
DFM (Hz·s^{-1})	-924 ± 23 [-4262 – -31]	-822 ± 85 [-5692 – -94]	-938 ± 30 [-2524 – -72]
A2/A1	0.599 ± 0.009 [0.065 – 1.000]	0.46 ± 0.02 [0.05 – 1.0]	0.56 ± 0.02 [0.04 – 1.00]
A3/A1	0.362 ± 0.008 [0.034 – 0.984]	0.22 ± 0.02 [0.01 – 0.87]	0.36 ± 0.02 [0.03 – 0.95]
A4/A1	0.224 ± 0.006 [0.011 – 0.888]	0.121 ± 0.009 [0.008 – 0.555]	0.220 ± 0.008 [0.013 – 0.816]
A5/A1	0.128 ± 0.004 [0.004 – 0.666]	0.074 ± 0.006 [0.005 – 0.321]	0.128 ± 0.006 [0.001 – 0.505]

Table 1. 2. Results of stepwise cross-validation discriminant function analysis from 596 airborne harbour seal MACs emitted by 61 pups. The two last numbers of the individual ID indicate the pup cohort (2011, 2012 or 2013).

Pup ID	Pup sex	Number calls analyzed	Percent correct classification	Percent correct classification expected by chance	Pup age at recording (days)
O8212	M	6	78.3	1.0	1
O4213	M	15	73.6	2.5	2, 10
O2811	M	6	73.3	1.0	2
J9812	F	8	65.9	1.3	2
O7512	F	14	64.8	2.4	4
O3013	F	7	65.7	1.2	2
O6013	M	13	62.7	2.2	14, 33
O7012	F	14	66.2	2.4	14, 21
O5313	M	19	58.8	3.2	16, 29, 35
O2813	M	16	57.8	2.7	1, 34
O1111	M	6	58.7	1.0	2
O0211	F	7	61.4	1.2	2
O2113	M	14	56.8	2.4	8
O8112	M	6	59.3	1.0	3
O1711	M	7	53.9	1.2	2
O3113	M	20	60.0	3.4	4, 31, 33
J6012	M	12	56.4	2.0	17, 21
O7213	F	14	55.1	2.4	13, 19
O4513	M	7	54.2	1.2	9
J9212	F	29	52.4	4.9	16, 19, 41
J8812	F	9	53.3	1.5	3
J8012	M	10	50.4	1.7	23
O5113	F	14	43.9	2.4	3, 23
J9512	M	16	49.3	2.7	18, 21
O2613	F	11	44.7	1.9	4
O8912	F	7	40.9	1.2	7
O2913	F	6	38.9	1.0	32
O6213	M	7	42.4	1.2	28
O3413	M	8	42.4	1.3	4
O1211	M	6	46.0	1.0	4
O1013	M	12	40.6	2.0	3
O5013	F	13	42.2	2.2	12, 14
O9212	M	21	40.3	3.5	9, 20
O4813	F	6	42.1	1.0	26
O1113	M	11	33.8	1.9	9
O7212	M	12	39.0	2.0	19, 26
O8512	F	8	29.6	1.3	1
O6313	F	10	26.9	1.7	18, 27
O4413	M	6	30.5	1.0	2
O5413	F	6	25.8	1.0	12
O3813	F	11	30.3	1.9	6, 16
O4913	F	7	32.0	1.2	4
O4713	M	13	28.4	2.2	16
O7612	F	10	28.3	1.7	14
J9712	F	10	20.9	1.7	18
J8612	M	6	23.6	1.0	21
J7112	M	8	20.2	1.3	12
O8312	F	7	15.6	1.2	2
O4313	M	7	14.7	1.2	17
O2013	M	6	18.3	1.0	4
O3513	F	7	11.7	1.2	11
O3313	M	7	14.3	1.2	13
O0813	M	6	12.5	1.0	25
O0213	F	6	10.5	1.0	22
J8312	M	6	9.5	1.0	18
O7112	F	6	5.8	1.0	4
O1213	F	7	5.7	1.2	2
O2513	F	6	4.6	1.0	2
J8112	F	9	3.7	1.5	29
O2413	M	6	1.3	1.0	3
O4613	M	6	0.0	1.0	19

Table 1. 3. Results of stepwise cross-validation discriminant function analysis from 95 underwater harbour seal MACs emitted by 12 pups. The two last numbers of the individual ID indicate the pup cohort (2012 or 2013).

Pup ID	Pup sex	Number calls recorded	Percent correct classification	Percent correct classification expected by chance	Pup age at recording (days)
O0113	F	11	81.82	11.58	2
O7013	M	7	85.71	7.37	30
J9712	F	12	66.67	12.63	3, 18
O2013	M	6	66.67	6.32	10
O6613	F	6	66.67	6.32	38
O4513	M	14	28.57	14.74	9
J0213	M	6	16.67	6.32	2
O4213	M	6	50.00	6.32	2
O1813	M	7	14.29	7.37	10
O2613	F	7	14.29	7.37	4
O3913	F	7	14.29	7.37	11
J9512	M	6	0.00	6.32	18

Table 1. 4. Results of linear mixed models assessing the effects of age, body length, sex and the age*sex interaction on 16 vocal parameters measured on airborne harbour seal MACs (678 calls from 70 individuals). *P-values* were calculated by comparing coefficients provided by the models to those generated from randomisation of the response variable (nb of iterations = 1000; Mazerolle, 2013). Coefficients in these tables represent slopes of linear regressions for the effects of age and body length, and intercept differences between males and females for the effect of sex. The coefficient of the interaction term (age*sex) is the difference in the age coefficient between males and females. Bold type highlights significant effects ($p < 0.05$). Acoustic parameter abbreviations are defined in text. Asterisks indicate parameters that were log-transformed to fulfill the homoscedacity assumption. Females are the referent for the sex effect.

Acoustic Parameter	Age (d)			Body length (cm)			Sex			Age*Sex		
	coefficient	*p-value*	*VIF*	coefficient	*p-value*	*VIF*	coefficient	*p-value*	*VIF*	coefficient	*p-value*	*VIF*
dt	1.5	**0.00**	3.7	0.4	0.13	2.2	-55.1	**0.00**	1.6	0.4	0.10	3.2
Q_{25}	-1.3	0.07	3.9	5.7	**0.00**	2.3	-88.7	**0.00**	1.5	3.3	**0.01**	3.1
Q_{50}*	-0.003	**0.00**	3.9	0.001	0.15	2.4	-0.079	**0.00**	1.5	0.002	**0.06**	3.1
Q_{75}*	0.001	0.16	4.3	-0.012	**0.00**	2.7	0.009	0.17	1.3	-0.002	0.11	3.1
f_0	-0.4	**0.05**	4.2	-2.1	**0.00**	2.5	25.9	**0.00**	1.3	-1.0	**0.00**	3.1
f_{max1}	-0.6	0.15	3.5	6.3	**0.01**	2.1	-70.8	**0.02**	1.7	0.1	0.19	3.3
f_{max2}	2.7	0.06	3.0	0.1	0.19	1.8	-102.6	**0.02**	2.2	3.4	0.07	3.6
f_{max3}	1.0	0.15	3.0	-4.0	**0.01**	1.8	-84.5	0.05	2.2	7.6	**0.02**	3.7
f_{max4}	-4.1	0.09	3.0	-7.8	0.05	1.8	278.8	**0.00**	2.2	-7.3	**0.04**	3.7
f_{max5}	-4.0	0.12	3.2	-11.3	0.05	1.9	530.8	**0.00**	2.0	-23.2	**0.00**	3.5
AFM	-11.2	**0.00**	3.5	-9.3	**0.01**	2.2	-14.3	0.16	1.6	9.6	**0.00**	3.1
DFM	5.5	**0.02**	3.6	4.4	0.08	2.1	-222.8	**0.00**	1.7	-2.2	0.12	3.2
A2/A1	0.0	0.17	3.0	-0.0	0.10	1.7	0.0	0.09	2.3	0.0	0.12	3.7
A3/A1	0.0	0.20	3.2	-0.0	**0.00**	1.9	0.0	0.084	2.0	0.0	0.13	3.5
*A4/A1**	0.001	0.16	3.4	-0.025	**0.00**	2.0	-0.248	**0.00**	1.8	0.003	0.12	3.3
*A5/A1**	-0.006	**0.04**	3.5	-0.014	**0.01**	2.0	-0.303	**0.00**	1.8	0.009	**0.03**	3.3

Table 1. 5. Results of linear mixed models assessing the effects of age, body length, sex and the interaction between age and sex on 16 vocal parameters measured on underwater harbour seal MACs (114 calls from 13 individuals). *P-values* were calculated by comparing coefficients provided by the models to those generated from randomisation of the response variable (nb. of iterations = 1000; Mazerolle, 2013). Bold type highlights significant effects ($p < 0.05$). Acoustic parameter abbreviations are defined in text. Asterisks indicate parameters that were log-transformed to fulfill the homoscedacity assumption. Females are the referent for the sex effect.

Acoustic parameter	Age (d)			Body length (cm)			Sex			Age*Sex		
	coefficient	*p-value*	*VIF*	coefficient	*p-value*	*VIF*	coefficient	*p-value*	*VIF*	coefficient	*p-value*	*VIF*
dt	-5.9	**0.04**	1.4	14.5	**0.01**	1.5	51.9	0.13	2.3	9.3	**0.05**	3.1
Q_{25}	9.0	**0.00**	1.2	-12.2	**0.00**	1.4	62.1	0.06	2.3	-6.5	**0.02**	3.0
Q_{50}	7.3	**0.02**	1.3	-6.9	0.06	1.5	-54.8	0.12	2.3	-0.2	0.20	3.0
Q_{75}*	-0.006	**0.04**	1.3	0.009	**0.04**	1.5	-0.121	0.05	2.3	0.004	0.12	3.0
f_0	1.0	**0.02**	1.6	-3.0	**0.00**	1.7	27.1	**0.01**	2.3	-2.5	**0.00**	3.1
f_{max1}	-0.2	0.19	1.7	-2.4	0.12	1.7	148.1	**0.01**	2.4	-6.5	**0.04**	3.2
f_{max2}*	-0.003	0.12	1.7	-0.002	0.17	1.7	-0.174	**0.03**	2.4	0.012	**0.03**	3.3
f_{max3}	7.7	**0.02**	1.7	-10.9	**0.02**	1.6	-8.0	0.19	2.4	-4.5	0.12	3.2
f_{max4}	13.5	**0.00**	1.7	-12.3	**0.02**	1.7	-88.3	0.11	2.4	2.23	0.16	3.2
f_{max5}	-10.2	**0.01**	1.8	-2.9	0.15	1.7	-227.2	**0.01**	2.4	2.3	0.15	3.2
AFM*	0.015	**0.03**	1.6	-0.058	**0.00**	1.6	0.166	0.08	2.3	0.002	0.18	3.1
DFM	-21.6	**0.00**	1.5	26.1	**0.01**	1.6	-608.5	**0.00**	2.3	33.4	**0.00**	3.1
$A2/A1$	0.0	**0.00**	1.4	0.0	**0.00**	1.5	0.0	0.18	2.3	0.0	0.17	3.1
$A3/A1$*	0.011	0.05	1.4	-0.012	0.09	1.5	0.160	0.11	2.3	0.000	0.20	3.1
$A4/A1$*	0.037	**0.00**	1.3	-0.024	**0.03**	1.5	0.358	**0.04**	2.3	-0.023	**0.05**	3.0
$A5/A1$*	0.032	**0.00**	1.4	-0.009	0.12	1.5	0.281	0.06	2.4	-0.014	0.09	3.1

Table 1. 6. Results of test hypothesis on slopes (null hypothesis: slope =1) for robust linear regressions modeling the relationship between aerial and underwater values of 16 acoustic parameters measured on 255 amphibious MACs produced by 55 harbour seal pups. The significance level is set to 1% to account for measurement accuracy. Bold type indicate significant acceptance of the null hypothesis.

Acoustic parameter	Coefficient estimation	*F*	*p-value*	Confidence interval of coefficients	
				0.5%	99.5%
dt	1.0	0.45	**0.50**	0.9	1.2
Q_{25}	0.2	137.15	0.00	0.0	0.4
Q_{50}	0.4	65.56	0.00	0.2	0.6
Q_{75}	0.2	129.93	0.00	0.1	0.4
f_{max1}	0.2	75.96	0.00	-0.1	0.4
f_{max2}	0.0	141.94	0.00	-0.2	0.2
f_{max3}	0.2	121.16	0.00	0.01	0.4
f_{max4}	0.1	151.30	0.00	-0.1	0.3
f_{max5}	0.2	227.58	0.00	0.1	0.3
AFM	0.6	82.38	0.00	0.51	0.7
DFM	0.7	55.57	0.00	0.7	0.8
f_0	1.0	4.15	**0.04**	0.9	1.0
A2/A1	0.0	287.34	0.00	-0.1	0.2
A3/A1	0.1	303.80	0.00	-0.1	0.2
A4/A1	0.1	163.54	0.00	0.0	0.3
A5/A1	0.1	112.38	0.00	-0.1	0.3

Table 1. 7. Ecological factors and percent-correct scores obtained from discriminant function analyses on various pinniped species. Asterisks indicate DFA results that were not cross-validated.

Species	Density on breeding sites	Maternal absence during nursing period	Percent-correct scores of DFA on pup calls	Reference for DFA results
Odobenids				
Odobenus rosmarus rosmarus	High	No	67	Charrier et al. 2010
Otariids				
Otaria byronia	High	Yes	89*	Fernandez-Juricic et al. 1999
Arctocephalus forsteri	High	Yes	79	Page et al. 2002
A. tropicalis	High	Yes	83	Page et al. 2002
Callorhinus ursinus	High	Yes	79*	Insley 1992
A. gazella	High	Yes	52	Page et al. 2002
A. australis	High	Yes	60	Phillips et Stirling 2000
Neophoca cinerea	Moderate-Low	Yes	77*	Charrier et Harcourt 2006
Phocids				
Leptonychotes weddellii	Moderate-Low	Short	53*, 29	Collins et al. 2005, 2006
Mirounga angustirostris	High	No	64*	Insley 1992
Halichoerus grypus	Moderate	No	32	McCulloch et al. 1999
Monachus schauinslandi	Low	No	14	Job et al. 1995
Phoca vitulina	Moderate	Short	29, 43	Khan et al. 2006, présente étude

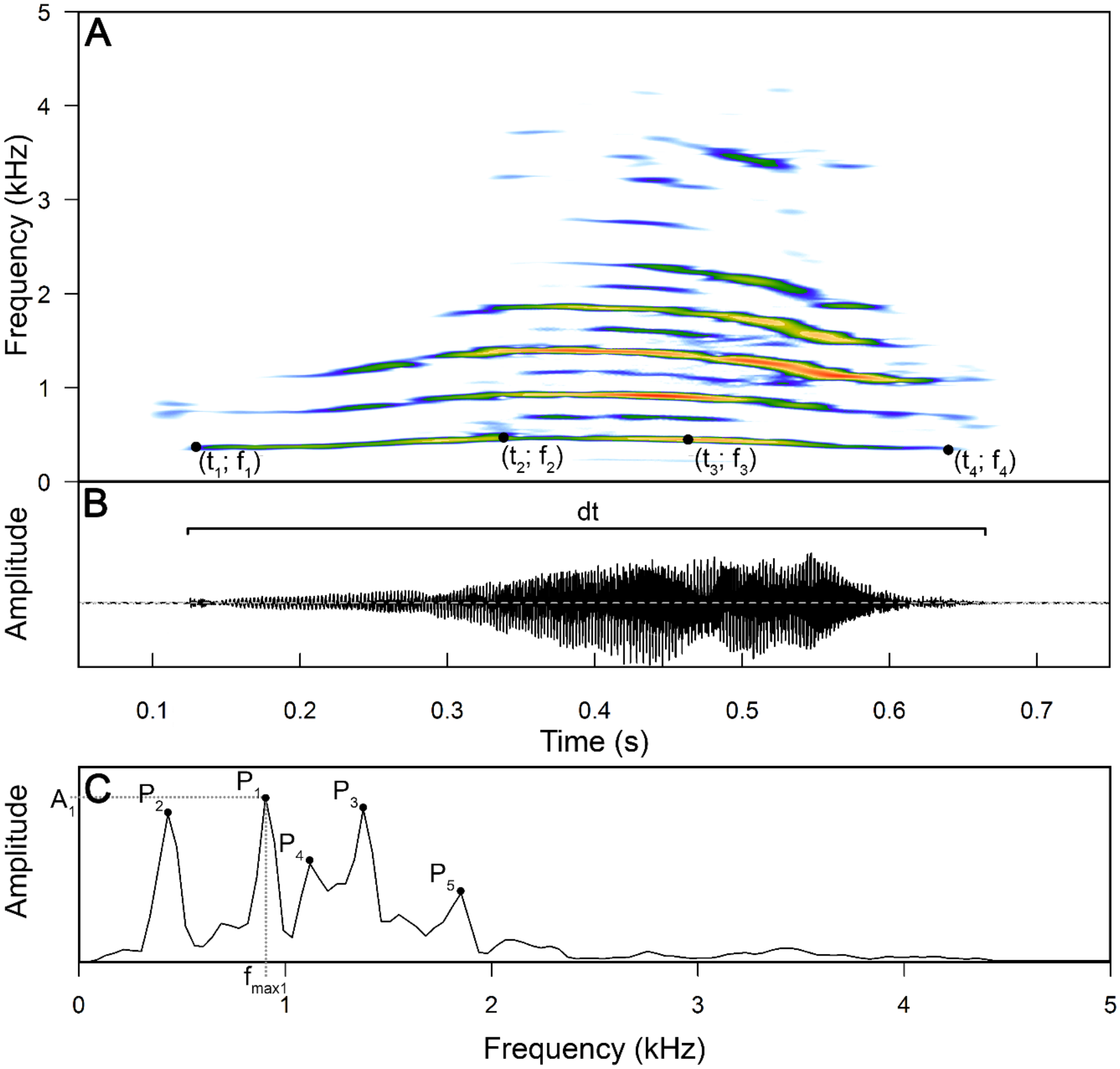

Figure 1.1. Structure of a typical airborne harbour seal pup MAC displaying the acoustic parameters measured for the acoustical analysis. A) Spectrogram (FFT window size, 1024 Hz) presenting beginning of the call (t_1; f_1), inflection points (t_2; f_2) and (t_3; f_3) and end of the call (t_4; f_4); B) Oscillogram used to measure the duration of the call (*dt*) and C) Frequency spectrum displaying first to fifth peaks of amplitude (P_1 to P_5) that provided the f_{max}s and amplitude values used to calculate amplitude ratios (relative to A_1). Figure generated using SEEWAVE v.1.7.3 (Sueur et al. 2008).

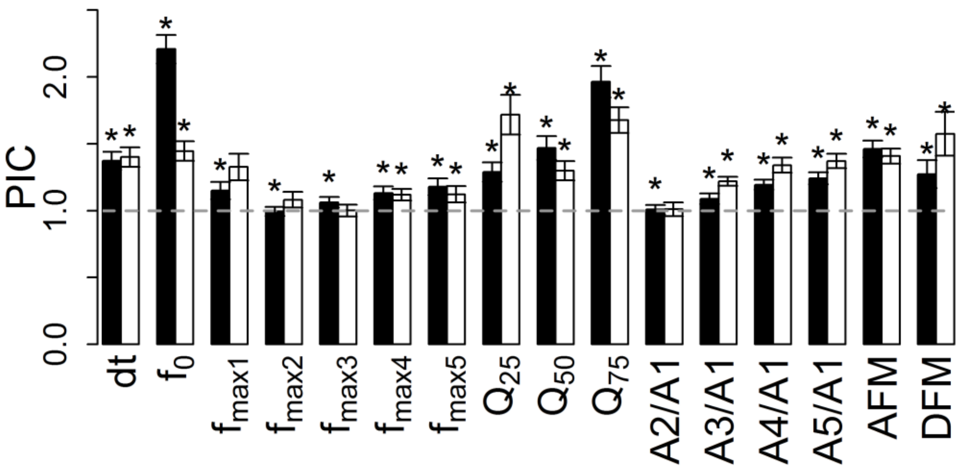

Figure 1.2. PIC values of acoustic parameters measured on harbour seal pup MACs. Black and white bars represent airborne (n= 678) and underwater (n=114) MACs, respectively. Asterisks indicate parameters for which significant ($\alpha < 0.05$) inter-individual differences in means where identified. Parameters selected as potential predictors in the DFA were: *dt*, f_0, Q_{25}, Q_{50}, Q_{75}, *AFM* and *DFM*.

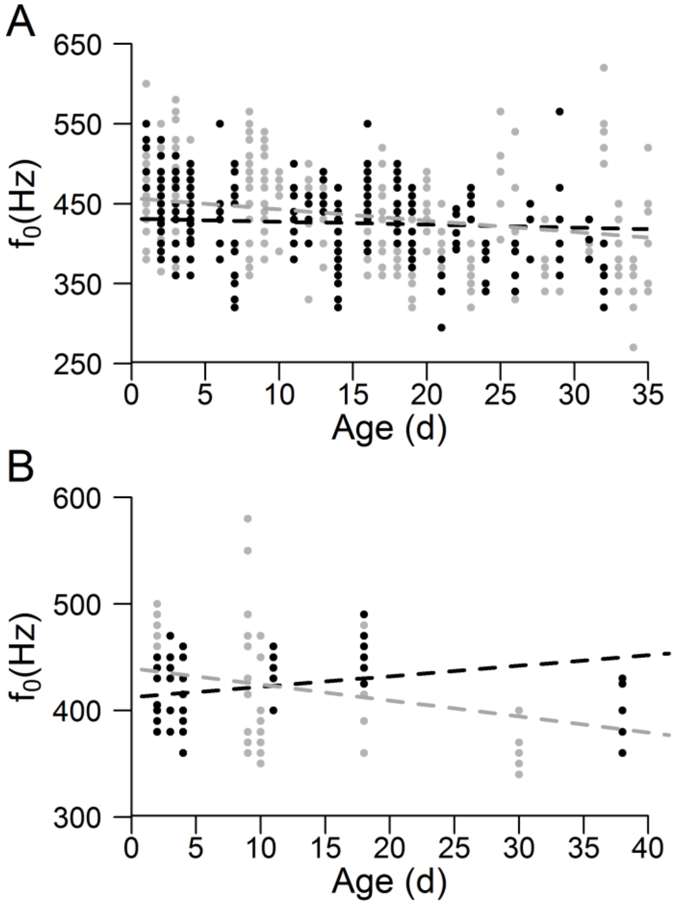

Figure 1.3. Effect of pup age on fundamental frequency (f_0) of harbour seal pup A) airborne (n_{call} = 675, n_{pup} = 70) and B) underwater (n_{call} = 114, n_{pup} = 13) MACs. Black and grey dots represent females and males, respectively. Dashed lines show the predictions estimated by the linear mixed models for both sexes.

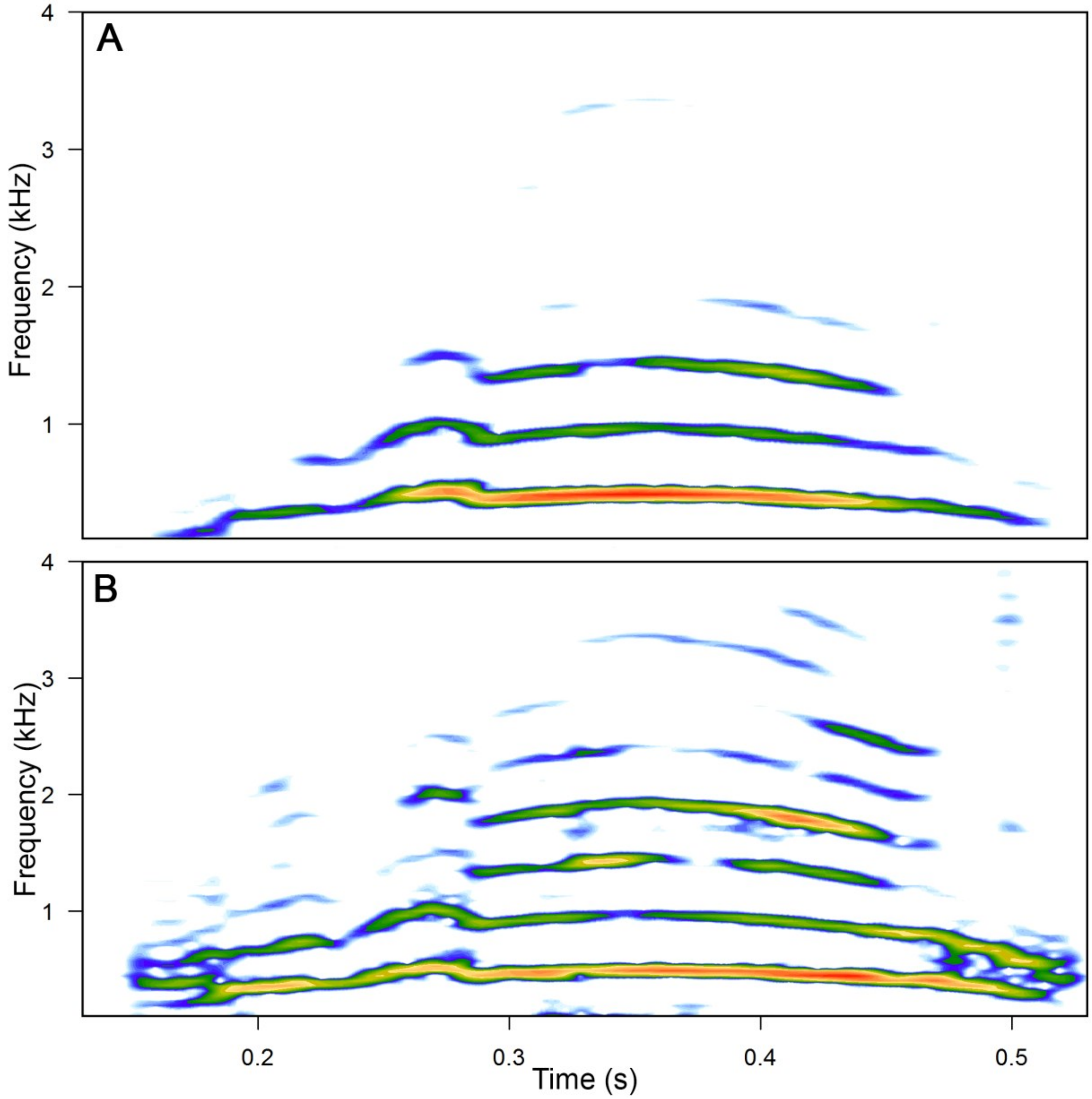

Figure 1.4. Spectrograms (FFT window size, 1024 Hz) illustrating the (A) aerial and (B) underwater components of a harbour seal pup amphibious MAC. Figure generated using SEEWAVE v.1.7.3 (Sueur et al. 2008).

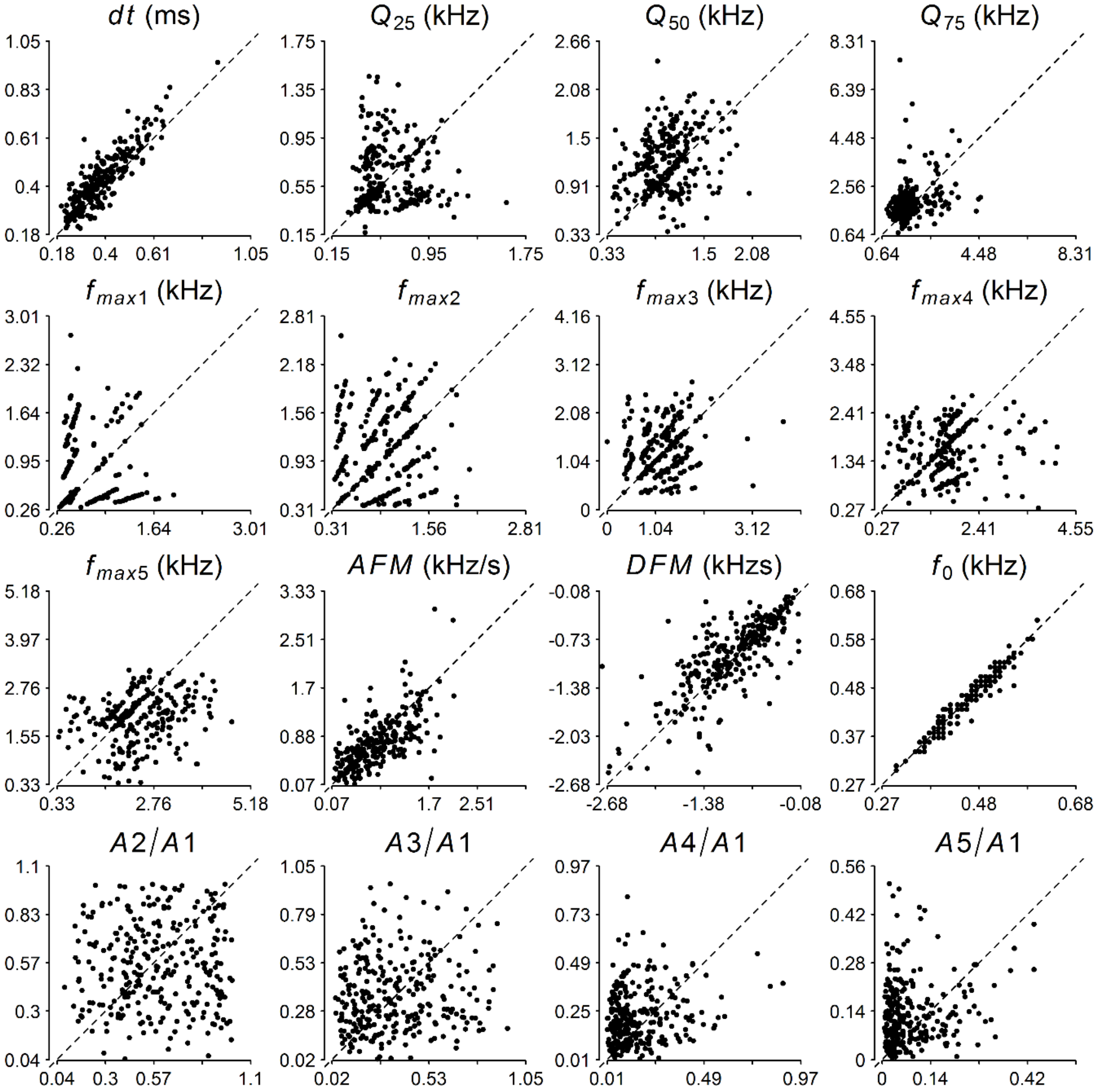

Figure 1.5 Relationship between aerial (x axis) and underwater (y axis) components of the 16 acoustic parameters measured on 280 amphibious harbour seal pup MACs (n_{pup} = 55). Dashed lines present the hypothesis of equality between both components (x = y).

Chapitre 2 – Mother-pup vocal recognition in harbour seals: Call stereotypy and habitat acoustic properties may drive female discrimination abilities

Résumé

Au sein des pinnipèdes, les systèmes de reconnaissance vocale mère-chiot reflètent les stratégies d'allaitement adoptées par les deux grandes familles du groupe. Chez les otariidés, les absences maternelles sont régulières et prolongées au cours de la lactation et les chiots sont relativement mobiles. Par conséquent, la reconnaissance vocale mère-jeune est typiquement bidirectionnelle chez ces espèces. Les phocidés adoptent quant à eux une stratégie impliquant peu ou pas de séparations mère-petit associée à des systèmes de reconnaissance vocale moins développés. Le phoque commun représente un cas particulier parmi les phocidés puisque les femelles s'alimentent durant la période de lactation (durée ≈ 34 d). De plus, le chiot phoque commun est exceptionnellement mobile avant le sevrage. Des expériences de playback testant la capacité des mères à reconnaître la voix de leur chiot ont été réalisées sur 18 femelles phoques communs (*Phoca vitulina*) de l'estuaire du St-Laurent. De plus, des tests de propagation acoustique ont été menés afin de caractériser la résistance à la dégradation des cris du chiot. Les femelles ont montré une plus forte réponse comportementale suite à la diffusion de cris de leur propre chiot comparativement à la diffusion de cris d'un chiot non apparenté. Cette capacité était corrélée au niveau d'individualité porté par les vocalisations des chiots. Les femelles plus protectrices ont répondu plus fortement aux tests de playback quel que soit le type de cris diffusés. Des tests de propagation suggèrent également que certains sites utilisés par les couples mère-petits sont plus favorables que d'autres au processus de reconnaissance vocale.

Abstract

In pinnipeds, mother-pup vocal recognition abilities reflect the maternal reproductive strategies adopted by the two main families. In otariids, the mother-pup pair is frequently and extendedly separated during lactation, and young are relatively mobile. Accordingly, vocal recognition is typically mutual between mothers and pups. In contrast, the phocid strategy implies few pre-weaning mother-pup separations, hence mother-young vocal recognition abilities are less developed in this family. Harbour seals are particular among phocids as females forage afore weaning their pups, which are exceptionally mobile throughout the 21 to 42-day nursing period. Playback experiments were performed on 18 harbour seal (*Phoca vitulina*) breeding females to assess their abilities to recognize the voice of their pup. Moreover, propagation tests were performed to investigate the resistance to degradation of pup calls. Females were more responsive to calls of their own pup than to those of non-filial pups, even when recorded up to 27 days prior to playback. This ability was correlated to the level of individuality conveyed in pup calls. Mothers displaying highest protective behaviours towards their pup prior to playback were more responsive although less selective to broadcast stimuli. Considerable differences in the propagation efficiency of pup calls were detected between areas used for mother-pup reunions. This study provides evidence that wild harbour seal females recognize the voice of their pup among others, and that they memorize anterior versions of their pup calls albeit age- and size-related effects on voice. Propagation tests further suggest that some sites used by mother-pup pairs are more suited for vocal recognition than others.

Introduction

Communication systems are likely to evolve in a species or population when it benefits both senders and receivers of the signal (Bradbury, Alcock et al. 1998). Individual recognition confers valuable benefits in a variety of social contexts such as territoriality, aggressive competition, nepotism directed to kin, and parental care (Trivers 1974, Barnard and Burk 1979, Hepper 1991, Temeles 1994). Consistently, the ability to recognize individuals is widespread across a range of animal taxa and sensory modalities (Falls 1982, Halliday 1983, Tibbetts and Dale 2007). The different sensory channels are associated with contrasted effectiveness of transmission, localizability, energetic cost, temporal modulation, etc. (Bradbury et al. 1998, Davies and Krebs 2009). The modalities used in a given context of individual recognition result from species/population ecological constraints acting as selection pressures on these signal properties.

Parent-offspring recognition limits misdirected parental care, increasing offspring survival and therefore reproductive success of caregivers (Clutton-Brock 1991, Royle et al. 2012). It also reduces the risks of injuries associated to the young during interactions with unrelated, potentially aggressive adults (*e.g.*, Troisi et al. 1988, Harcourt 1992). As it can provide mutual benefits to both parties, parent-offspring recognition is common in species providing parental care. While visual and olfactory cues are used for egg recognition in the nest or at close range for the confirmation of offspring identity (*e.g.*, Pike 2011, Pitcher et al. 2011, Helantera et al. 2014), vocal communication generally evolves in situations requiring identity signals effective over long distances (Bradbury et al. 1998). The occurrence of parent-offspring vocal recognition has been uncovered in several taxa (*e.g.*, birds: Falls 1982; ungulates: Espmark 1971, Torriani et al. 2006, Sebe et al. 2007; bats: Knornschild and Von Helversen 2008, Knornschild et al. 2013; primates: Hammerschmidt and Fisher 1998, Fisher 2004; carnivores: Sieber 1986, Charrier et al. 2001b, 2009). The complexity of the parent-offspring vocal recognition system is generally associated with the difficulties encountered by the pair to remain in contact and find each other during the rearing period. Therefore, mutual parent-young recognition is demonstrated in species characterised by high population densities at breeding sites (Trillmich 1981, Aubin and Jouventin 2002), frequent parent-offspring separations (Aubin and Jouventin 2002, Briefer and McElligott 2011) and mobile offspring (Jones et al. 1987, Sayigh et al. 1999). Comparative studies of parent-offspring vocal recognition abilities thus provide valuable information as to the selective pressures shaping communication systems. Moreover, it allows for a greater understanding of the role of vocal recognition in young growth and survival as well as in adult reproductive success.

Pinnipeds have a great potential for comparative studies of recognition due to the established phylogeny between families (Berta and Churchill 2012) and the contrasting maternal strategies adopted by otariids and phocids (Boness and Bowen 1996). Otariids are income breeders that alternate between nursing episodes on land and foraging trips at sea leading to frequent and extended maternal absences from the breeding colony (Schulz and Bowen 2004). During female absences, otariid pups generally gather at the periphery of the colony to rest and play together (Bowen 1991), and are thus relatively mobile and active in the course of the long lactation period (4-18 months; Schulz and Bowen 2004). As for phocids, females usually fast alongside their pup throughout the relatively short nursing period (4-60 d; Schulz and Bowen 2004). They are capital breeders, relying on fat reserves stored before parturition to produce the highly energetic milk necessary for successful rearing of their pup (Boness and Bowen 1996). Phocid pups are mostly sedentary, involved in limited social interactions with non-filial adults or young and rarely undertaking movements within the breeding colony (Bowen 1991). These differences in maternal strategies and pup mobility reflect contrasting ecological constraints for the evolution of mother-pup vocal recognition systems between the two main families of pinnipeds. Accordingly, evidence suggests that mutual mother-pup vocal recognition is the norm in otariids whereas recognition abilities in phocids are more variable (total absence or uni-directional; see Insley et al. 2003a for review).

In spite of the phylogenetic dichotomy regarding the features of the reproductive strategies among pinnipeds, breeding females of a few phocid species do not follow the typical phocid maternal strategy as they forage in the course of the lactation period (Hammill et al. 1991, Lydersen and Kovacs 1993, Boness et al. 1994, Wheatley et al. 2008). Harbour seal (*Phoca vitulina*) females perform short foraging trips beyond one week post-partum, and spend most of their time at sea during the lactation period (Boness et al. 1994, Bowen et al. 1999). Harbour seal pups are also exceptional among phocids as they are highly active and mobile in the water throughout the lactation period (Bigg 1981, Bowen et al. 1999, Jorgensen et al. 2001), which lasts between 21 and 42 d (Riedman 1990). These traits imply greater selection pressures for an effective mother-pup vocal recognition system in harbour seals compared to most phocids. Harbour seals therefore represent a species of interest for comparative mother-pup vocal recognition studies.

Harbour seal pups frequently emit calls that disappear from their vocal repertoire soon after weaning (Renouf 1984), suggesting their essential role in maintaining contact with the mother. Previous work has revealed that harbour and Northern elephant seal vocalisations convey individual-stereotypy levels intermediate between those found in otariids and other phocids (*c.f.* Chapter 1 and Insley 1992). However, although individual stereotypy in vocalisations is a prerequisite for individual recognition, it does not necessarily imply that females can perceive such information and use it to identify the emitter (Beecher 1982). A captive harbour seal female was successfully trained to discriminate between single calls from non-filial pup pairs (Renouf 1985), confirming that females have the sensory and neurological capacities to perceive differences between pup vocalisations. However, as the broadcasted stimuli in this experiment consisted of a single, repeated call from each pup, it cannot be established whether the female relied on inter-individual or inter-vocalisation differences when discriminating the broadcasted calls (pseudoreplication; Kroodsma 1989). This hinders the determination as to whether harbour seal pup inter-individual call variability is sufficient for females to recognise the voice of her pup. Moreover, the fact that a female can learn to discriminate between calls from non-filial pups does not imply that such ability is effectively used for recognition of offspring in a natural context (notion of generalisation; (McGregor et al. 1992). Finally, this experiment leaves open to what extent females can perceive variations in pup vocalisations in their often noisy habitat.

Given the contrasted topography, proximity to anthropogenic activities and exposure to waves, wind and currents characteristic of harbour seal habitat (Thompson et al. 1997, Robillard et al. 2005, Burns 2009), the efficiency of pup call acoustic propagation might vary between and within colonies. Additionally, acoustic parameters of vocalisations are usually degraded differentially with distance (e.g., Wiley and Richard 1982). Depending on the cues used in vocal recognition of offspring (if any), such asymmetrical propagation of call features may potentially influence female vocal recognition abilities.

The first objective of this study was to experimentally test the abilities of free-ranging harbour seal females to discriminate the voice of their pup among others. These discrimination abilities are discussed in regards to female motivational state and personality, along with individual stereotypy of pups' voice. In a second step, resistance to degradation of harbour seal pup calls was investigated through propagation tests. Intra- and inter-colony transmission efficiency differences, as well as contrasting degradation levels among acoustic parameters were examined. These results are interpreted in the perspective of mother-pup recognition and reunion site selection.

Material and methods

Study site and animal handling

This study was conducted on two harbour seal colonies on the South shore of the St. Lawrence River estuary (Figure 2.1). The Bic colony (48°24' N, 68°51' W; N ≈ 100 pups/year, *pers. obs.*) is extended around an island and nearby rocky reefs within a 40 km^2 area. Located about 60 km downstream, the Métis colony (48°41' N, 68°01' W; N ≈30 pups/year, *pers. obs.*) covers a 10 km^2 area along the shoreline. These sites were visited (weather permitting) alternately throughout the 2013 breeding season (from Mid-May to July).

Capture and tagging protocols are detailed in Sauvé et al. (2014). Upon each capture, the pup was weighed (± 0.5 kg; Salter spring scale, West Bromwich, England) and a maternal protection level (MPL) was determined according to female's protective behaviour towards her pup during the chase preceding capture (0: absent, 1: swims away from pup as boat approaches; 2: keeps pup in sight at a distance > 50 m; 3: remains within [10-50 m] of pup ; 4: stays < 10 m of pup and 5: jumps into the boat to join pup). Handling time rarely exceeded 10 min from capture to release. When the female was present, we noted whether mother-pup reunion occurred within 5 min following pup release. As most pups were not captured immediately after parturition, pup age (d) was determined by indirect methods detailed in Van de Walle (2013).

Recording procedure

Upon each capture, airborne MACs (mother attraction calls) emitted by the pup were recorded for ≈ 60 s following capture and prior to any handling, and after it was released into the water. Recordings were performed using a shotgun microphone (Sennheiser ME 67, Sennheiser electronic GmbH & Co. KG, Wedemark, Germany) connected to a Marantz PMD 661 digital recorder (Marantz Europe, Eindhoven, Netherlands) at a 44.1 kHz sampling frequency.

Playback experiments

To assess whether breeding harbour seal females are able to discriminate their offspring's calls among calls from other pups, females were tested with two experimental stimuli: MACs from 1) their own pup (control) and 2) from a non-filial pup. Each experimental stimulus consisted of two series of five airborne MACs separated by a 3 s break of silence. Within each series, calls were interspaced by natural silence intervals (0.3 to 0.7 s) and series contained at least two different MACs since collecting ten good signal-to-noise ratio calls for each pup was not always possible. Signals were built using Avisoft SAS lab Pro (Avisoft Bioacoustics, Berlin, Germany; v5.2.07) and Goldwave (Goldwave Inc., St. John, NL, Canada; v5.67). As MAC characteristics change with pup age and body size (see Chapter 1) stimuli were created using MACs from the most recent recording available for each pup. Additionally, tracks containing MACs from pups of similar ages were used for both treatments (own and non-filial pup) within a given playback session to avoid any bias associated with pup age in the female's response to playback.

A playback session started immediately after a pup was captured while its mother was still in the area. During each playback session, a stimulus was broadcast from the boat and the female's behavioural response was noted during the following 90 s. An additional 90 s interval allowed the female to return to her initial motivational state before the second stimulus was broadcast and the behavioural response noted for another 90 s. Treatment order (calls from own or non-filial pup played first) was randomised. At the end of the playback session, the pup was released into the water and observed to ensure that mother and pup reunited. Stimuli were played at a natural amplitude (98-100 dB SPL, A-weighting fast response), as measured at 0.5 m from calling pups with a sound-level meter (Brüel & Kjaer 2235, Brüel & Kjaer, Nærum, Denmark), using a MP3 player (Edirol R-09 WAVE/MP3 Recorder, Roland Corporation U.S., Los Angeles, CA, USA) connected to both a portable loudspeaker (Permio 8, TAG, Saint Jean de Védas, France) held above the surface of the water (< 50 cm) and an underwater speaker (LL916, Lubell Labs, Columbus, Ohio, USA) placed at a minimum depth of 1 m. Stimuli were therefore broadcasted simultaneously in-air and under water.

Female behavioural responses to playback were monitored by an observer located in the boat and a digital video camera (GoPro Hero 3 Silver Edition, Woodman Labs, San Mateo, CA, USA) attached to the underwater speaker. This allowed the calculation of three variables depicting female's response to playback: 1) the number of times the female looked in the direction of a speaker (*NL*), either by surfacing while looking towards the aerial loudspeaker or by passing in front of the video camera; 2) the closest distance of approach to the aerial speaker estimated by the observer (*DA*; m); and 3) the latency to first apparition (LA; s) at the surface or in front of the underwater camera. Playback tests were performed in dense population areas where different females happened to swim nearby as the observer was monitoring the response of the tested female. To insure unequivocal characterisation of the pup's mother's response to both stimuli, surfacing female faces were photographed both throughout the playback experiment and during the final mother-pup reunion to compare the fur colour patterns with pictures taken previously while the mother-pup pair was reunited.

The three behavioural response variables (*NL*, *DA* and *LA*) were introduced into a principal component analysis (PCA) to generate independent variables describing female's strength of response to the playback stimuli (McGregor et al. 1992). Principal component (PC) scores were computed for PCs with eigenvalues > 1. Paired *t*-tests were thus performed on these PC scores to assess for differences in response to playback according to treatment (own vs non-filial pup). To investigate the effect of females' and pups' characteristics as well as experimental settings on the behavioural responses to playback stimuli, PC scores were introduced as response variables in linear mixed models (LMM, package nmle; Pinheiro et al. 2012) fitted with REML with treatment, pup age at playback (d), Δage (pup age at the day of the playback test - pup age when calls used as stimuli were recorded; d), MPL and treatment order (*t.order*) as fixed effects and female's ID as a random effect. To obtain the best model explaining female's response to the playback series according to the considered explanatory variables, stepwise model selection based on the likelihood-ratio test (package lmtest; Zeilis and Hothorn 2002) was performed until eliminating fixed effects no longer generated better models than the previous one.

Two factors were investigated to determine whether pup voice individual-stereotypy level (ISL) affected female recognition abilities. First, the effects of pup voice ISL on females' response to the playback was calculated as the coefficient of a linear model on ΔPB and ISL, where ΔPB was the difference in PC scores obtained from both playback treatments (PC_{own} - $PC_{non\text{-}filial}$) for a given female, and ISL was estimated by her pup's percent-correct classification scores generated by a discriminant function analysis on 7 acoustic parameters (detailed in Chapter 1). Second, a one-tailed *t*-test was performed to assess whether ISL were greater for pups that reunited with their mother within 5 minutes following pup release. To provide an insight as to the magnitude of both of these relationships, a Cohen's *d* was computed using the formula $d = 2t\big/\sqrt{df} = 2r\big/\sqrt{1-r^2}$, where *t*: Student's statistic, *df*: degrees of freedom from the *t*-test and *r*: Pearson correlation coefficient (Borenstein et al. 2009).

Propagation tests

The two studied colonies differ in their exposure to waves, wind and streams. Indeed, mother-pup reunion sites (i.e., aquatic areas, often close to haul-out sites, where mothers and pups reunite after a separation) at the Bic colony are mostly protected since the island acts a wave- and wind-shield, whereas the costal Métis colony is more exposed. Sites within each colony also vary in their level of exposure to the elements. As waves, winds and streams mask and induce pattern loss in sounds, they are likely to influence the distance to which pup MACs can be detected by females at each reunion site.

To investigate MACs' efficiency of propagation in different reunion sites from both colonies, underwater and aerial propagation tests were carried out. They consisted of ten repetitions of a single natural pup call (MAC), played with a MP3 player (Edirol R-09 WAVE/MP3 Recorder) either in-air (Permio 8 loudspeaker) or under water (LL916 underwater speaker) at a natural amplitude (98-100 dB SPL at 0.5 m in air) and re-recorded either in air (Edirol R-09 WAVE/MP3 Recorder) or under water (Cetacean Research C54XRS hydrophone connected to a Marantz PMD 661) at increasing distances from the loudspeaker. In-air broadcast signals were re-recorded at 1 m (control), 4 m, 8 m, 16 m, etc. until calls could not be heard by the experimenters (maximal distance range: [256-2048] m). Similarly, underwater signals were re-recorded at 1 m (control), 25 m, 50 m, 100 m, etc. Distances between the speaker and the microphone were measured using a range finder (Bushnell ScoutArc® 1000, Bushnell Corp., Overland Park, NS, USA) for distances less than 100 m and a handheld GPS (Garmin GPSMAP 60Cx, Garmin, Olathe, KS, USA) otherwise. This procedure was performed on seven different reunion sites (three at Métis, four at Bic; see Figure 2.2) under similar weather conditions (light wind, low waves). Propagation tests were conducted in directions from which females were more likely to swim back to the colony and search for their pup after a feeding trip at sea.

To quantify the degradations of the acoustic signals during propagation, three acoustic parameters were measured on propagated calls: frequency modulation (FM) patterns, amplitude modulation (AM) patterns and the average energy spectrum. The modification of the FM pattern was assessed using the spectrogram cross-correlation function, which simultaneously analyses temporal, amplitude and frequency components (Clark et al. 1987, Khanna et al. 1997). Single spectrograms were created for each propagated call (Hamming window, FFT length= 1024, frame size = 100 %, overlap = 96.87 %) and pairwise comparisons were calculated using Avisoft Correlator (Avisoft Bioaccoustics, Berlin, Germany; high pass cutoff = 0 Hz, tolerate frequency deviation=

1 Hz). To determine the AM degradation, the smoothed envelope was calculated using a Hilbert transformation (Mbu Nyamsi et al. 1994). Maximal cross-correlation coefficients accounting for a time lag of ± 10 ms were computed using R (version 3.1.0; R Development Core Team, 2011) between AM patterns from calls recorded at various distances and those recorded at 1 m (controls). Finally, the degradation of the frequency spectrum was measured by calculating the averaged frequency spectrum on the whole length of the call (Hamming window, frequency resolution = 0.336 Hz), and Pearson correlation coefficients between propagated and control calls were obtained. Propagated calls were analysed until the signal-to-noise ratios became too weak to allow reliable visual identification on the spectrograms. Additionally, propagated calls masked by significant noise (*e.g.* particularly loud rumble of waves, bird vocalizations, gust of wind) were excluded from the analyses to avoid introducing bias in correlation coefficients. For FM, AM and the frequency spectrum, average correlation coefficients from calls recorded at a given distance and at a given site were computed, and distances last distances after which their value dropped below 0.5 ($d_{0.5}$; m) were extracted. This $d_{0.5}$ variable was hereafter used as an index of sound propagation efficiency.

When appropriate, normality and homoscedacity criteria were tested with Shapiro-Wilk and Levene (package car; Fox and Weisberg 2011) tests, respectively. When the normality criterion was not respected, randomization tests (rand-test; modified from Mazerolle 2013b) with 500 permutations were used rather than *t*-tests to compare statistics between groups. Results were considered significant at $p < 0.05$ and are presented as means ± s.e., unless stated otherwise.

Results

Playback experiments

A total of 21 playback sessions were performed, of which three were discarded from further analysis since pictures taken during the experiment revealed uncertainties about the identity of the tested female as being the pup’s mother. This resulted in 18 high-confidence sessions, all performed on different females. Maternal protection levels (MPL) of the 18 tested females ranged from 2 to 4.

The results of the PCA performed on the three behavioural variables are summarized in Table 2.1. The absolute values of the standardized loadings were > 0.50 on at least one PC for the three variables, indicating that all of them were relevant in the PCA (Hair 1995). According to Kaiser’s criterion, only the first PC (*PC1*) had an eigenvalue > 1 and was subsequently retained. All original behavioural measures contributed about equally to *PC1* and loaded significantly (loadings > |0.50|) on this factor. Moreover, the signs of the loadings were consistent with *PC1* representing a strength of response to playback variable (*e.g.*, shorter latency, closer approach towards the speakers, and greater number of looks toward the speakers: all indicate a strong response; therefore *LA* and *DA* showed negative loadings on *PC1* whereas the loading for *NL* was positive; McGregor et al. 1992).

A Tukey test for pairwise multiple comparisons on means indicated that, regardless of the treatment (own vs non-filial pup), females with low protection levels (MPL =2 or 3) displayed weaker responses to the playback stimuli (*i.e.*, *PC1* scores) than highly protective females (MPL=4; $p= 0.04$ for both MPL pairs (2-4 and 3-4); Figure 2.3a). However, females displaying MPLs of 2 and 3 did not show differential intensity of response to playback stimuli (independently of treatment; $p = 0.98$). These categories of females were thereafter combined, thus the MPL variable introduced in the model selection procedure included only two categories: low (MPL <4) and high (MPL= 4) protection levels. Model selection further led to the elimination of the treatment order from the fixed effects (see Table 2.2 for details). The results of the best modelling of *PC1* scores are presented in Table 2.3. The only significant effects on female's response to the playback were 1) MPL, with highly protective females responding more intensely than females with a low protection level, regardless of the treatment ($\beta_{high} = 1.0$, $p= 0.03$); and 2) the treatment, with signals from females' own pup resulting in greater responses ($\beta_{own} = 1.1$, $p < 0.01$). The latter result is further confirmed by a paired *t*-test on *PC1* scores, which revealed that females showed a significantly greater overall response to calls of their own pup than to those of non-filial pups ($p < 0.01$, $t_{17}= 3.36$, Figure 2.3b). A paired *t*-test revealed that females with low protection levels displayed greater response to calls from their own pups than to non-filial young ($p < 0.01$, $t_{15}= 3.8$) whereas highly protective females did not show differential response to playback according to the treatment ($p = 0.53$, $t_1= -0.08$).

Female preferential response to her pup during playback (*i.e.*, $PC1_{own} – PC1_{non\text{-}filial}$) and pup call stereotypy (ISL) tended to exhibited a positive correlation (slope= 2.5 ± 1.3, $p = 0.08$, $d= 1.06$; $n = 15$; Figure 2.4a). Similarly, pups that reunited with their mother within 5 minutes after their release in the water had on average a greater ISL (ISL = 38 ± 3 %, n=42) than those that did not (ISL = 27 ± 5 %, n=14), although this difference was not significant ($t_{16.75} = 1.54$, $P = 0.07$, $d= 0.56$; Figure 2.4b).

Propagation tests

The patterns of both AM and FM, as well as the frequency spectrum of propagated MACs were exponentially degraded with increasing distance from the source (Figures 2.5 and 2.6). Average correlation coefficients for each distance and each site are presented in Tables 2.4 and 2.5, while Figure 2.7 indicates FM, AM and frequency spectra $d_{0.5}$ values obtained for both in-air and underwater propagation experiments. There was no difference in mean $d_{0,5}$ between colonies either for FM (rand-test; $p = 0.48$ and 0.37), AM (rand-test; $p = 0.28$ and 0.56) or frequency spectra (rand-test, $p = 0.55$ and 0.37) for both media of propagation (in-air and under water, respectively). However, sound propagation efficiency ($d_{0.5}$) varied considerably within colonies (Figure 2.7).

In underwater trials, the frequency spectrum was the least degraded acoustic feature with distance at every site tested, followed by FM and AM patterns in second and last ranks, respectively (Tables 2.4 and 2.5). Similarly, frequency spectra showed a weaker degradation with distance in 57% (4/7) of in-air propagation tests, while FM was most efficiently transmitted in 29% (2/7) of the trials.

Sites from Métis sorted in decreasing in-air propagation efficiency (*i.e.*, $d_{0.5}$ and coefficients of correlation in decreasing order) are 1 > 2 > 3 for FM patterns and 2 > 1 > 3 for both AM patterns and frequency spectra (Figure 2.7 and Table 2.4). For underwater propagation efficiency, the Métis site ranks are 3 > 1 > 2 for both FM patterns and frequency spectra, while ranks for AM patterns are 3> 2 > 1. When sorted similarly, Bic site ranks for in-air propagation are 6 > 4 > 7 > 5 for FM patterns; 6=7 > 5 > 4 for AM patterns and 5 > 7 > 6 > 4 for the frequency spectra. Rankings for underwater propagation are 4 > 5 > 7 > 6 for both FM and AM patterns while they are 4 > 7 > 5 > 6 for the frequency spectrum (Figure 2.7 and Table 2.5).

Discussion

Playback experiments

Our playback experiments revealed that harbour seal females respond differently to pup calls depending upon 1) their protective maternal behaviour (*i.e.*, MPL), and 2) whether the aforementioned calls were emitted by their own or an unrelated pup (*i.e.*, playback treatment). These findings are supported by both modelling (LMM) of the response to playback variable (*PC1* scores) and hypothesis tests on means.

The MPL variable describes the intensity displayed by a female to maintain contact with her pup throughout the perturbation caused by the capture procedure. It combines female motivation, personality (boldness personality trait; Wilson et al. 1994) and hormonal state (lactogenic and sex steroid hormones; Numan 1994). Bolder (*i.e.*, highly protective) females displayed stronger responses to the playback, surfacing more often and closer to the loudspeaker, showing-up faster following the broadcast of MACs and appearing more frequently in front of the underwater video camera, regardless of the treatment (own *vs* non-filial pup calls). It has been reported that animal boldness can be associated with greater amount of time spent near offspring, greater parental care and higher weaning success (Budaev et al. 1999, Reale et al. 2000). Similarly, our results allow us to postulate that bolder harbour seal females, by responding more intensely to any pup calls, would maintain better contact with their offspring during the nursing period. This could have important outcomes on both female reproductive success and pup growth and survival.

This study also demonstrated that females displaying low protection levels responded more strongly to calls of their own pups than to those of non-filial young. This provides evidence that harbour seal females have the ability to recognize their pup's voice from others. Females therefore perceive and use individual vocal markers previously identified in harbour seal pup MACs (Renouf 1984, Perry and Renouf 1988, Khan et al. 2006, Chapter 1 from this study) for individual vocal recognition purposes. It is unlikely that some harbour seal females in this study literally lack recognition abilities. The absence of differential response to playback between treatments (own vs non-filial) for highly protective females might be attributable to their hormonal status, bold personality and related strong motivation to reunite with their pup, which may incite them to pay less attention to the vocalization characteristics and to react strongly to any MAC heard when searching for their pup.

Parent-offspring vocal recognition systems differ among taxa, species and populations according to selection pressures for this ability (*e.g.*, Beecher 1982, Jouventin 1982, Insley 1992, Jouventin and Aubin 2002, Insley et al. 2003a). High population density, land breeding and maternal absences from the breeding site represent ecological factors that seem to favor maternal vocal recognition abilities in phocids (Table 2.6). Although harbour seals breed in relatively low population density areas, most breeding sites from the St. Lawrence estuary (rocky reefs) are generally flooded at high tide (Boulva and McLaren 1979, Lesage et al. 1995), forcing pups to take to the water within hours after birth (Bigg 1981). Female foraging trips at sea during the lactation period (Boness et al. 1994) imply an effective need to relocate their pup when they return to the breeding colony. In instances where pups accompany their mother at sea, a recognition system effective over long distances is also required for the pair to reunite after female diving bouts, as pups perform shorter dives than females (Bowen et al. 1999). Considering all these ecological factors favoring the evolution of mother-pup recognition in harbour seals, our findings demonstrating that females have the ability to recognize their pup's voice is not surprising.

Some harbour seal populations breed on sand beaches, therefore facing lesser landscape variation with tide levels. These more stable meeting sites could ease the use of spatial cues by females searching for their pup after a foraging trip (*e.g.*, Trimble and Insley 2010) and thus influence the reliance on vocal communication. Furthermore, McCulloch and collaborators found that grey seals from two distinct colonies exhibited contrasting vocal recognition abilities (McCulloch et al. 1999, McCulloch and Boness 2000), and suggested that population genetic history could explain apparent paradoxical results. As harbour seals are widespread along North Atlantic and Pacific coasts (Thompson et al. 1997, Burns 2009), it would be interesting to perform playback experiments on harbour seal females from other populations to assess for divergences in vocal recognition abilities.

The absence of *Δage* effect on the playback responses involves that females were not more responsive to the latest version of their pup calls, suggesting that they retain older versions of their offspring vocalizations despite several modifications throughout rearing (see Chapter 1). Long-term vocal recognition was also demonstrated at higher levels in otariids, as Subantarctic and Northern fur seal females recognized the calls of their pup several months/years after birth and weaning (Insley 2000, Charrier et al. 2003b). Since harbour seal pup MACs disappear from animal's repertoire following weaning (Renouf 1984), it is unlikely that long-term vocal recognition abilities procure any adaptive benefit in this species (*e.g.*, post-weaning cooperation allowed by kin recognition). As Charrier et al. (2003) suggested, memorization of older pup call versions is likely to represent a by-product of strong learning experienced by females during the course of the rearing period.

Greater ISL in pup calls was associated with greater female differential response to playback between treatments (own *vs* non-filial pup calls). Moreover, pups that reunited with their mothers within 5 min following handling had greater ISL in their calls than those that didn't. These results suggest that females are more efficient in recognising their pup voice when it is highly individualised. Pup call ISL rather than female discrimination capacity is therefore likely to be the limiting factor in the harbour seal mother-pup vocal recognition system. Females rearing pups emitting weakly individualised calls are thus likely to depend more on spatial cues to locate their offspring and on non-acoustic recognition modes, primarily olfaction (Miller 1991, Dehnhardt 2002) to confirm pup identity upon reunion.

Propagation tests

The three acoustic features used to describe MAC propagation efficiency exhibited considerable differences as to their distance-related degradation. The frequency spectrum was the least degraded parameter measured in this study. This indicates that spectral features of pup MACs propagate with a high reliability, and might thus be used by females for individual recognition over long distances. Accordingly, an acoustical analysis previously revealed that the fundamental frequency (f_0) and energy quartiles (Q_{25}, Q_{50} and Q_{75}) are highly individually-stereotyped in harbour seal pup MACs (see Chapter 1). There was no trend for AM or FM patterns to propagate more efficiently than the other during in-air propagation tests. Therefore, both of these parameters appear as additional acoustic cues that could be reliably used by females for in-air individual recognition of their pup over long distances. However, in underwater propagation tests, AM was degraded more rapidly than FM. Under calm weather conditions, noise and medium absorption are likely to be more important in shallow coastal waters where currents and physical barriers (*e.g.*, seaweed, rocks) are present than over the surface. This could explain the relatively poor propagation of AM patterns obtained in underwater trials compared to aerial propagation tests. In a previous study, both ascending and descending FM slopes were found to convey high individuality levels in harbour seal MACs (Chapter 1). Frequency modulation has also been shown to be 1) highly resistant to degradation with distance and 2) involved in recognition processes in other colonial species (Aubin and Jouventin 2002, Charrie et al. 2009, 2010, Pitcher et al. 2012). By providing evidence that the most individually-stereotyped acoustical parameters in harbour seal pup MACs are also the ones that propagate most efficiently in the habitat, propagation tests further suggest that spectral characteristics and FM pattern are likely to be the ones used by females for vocal recognition of their offspring. However, playback tests with modified MACs are required to validate this hypothesis.

Overall, both colonies were comparable regarding their sound propagation performances on all 3 acoustic features measured. Nevertheless, propagation tests revealed an important within-colony heterogeneity of sound transmission efficiency, indicating that reunion sites are associated with differential constraints on signal propagation efficiency. Overall, locations best suited for aerial sound propagation (greater $d_{0.5}$ and correlation with the control) at the Métis colony were sites 1 and 2, site 3 being always the worst site. Sites 1 and 2 represent a single mother-pup meeting area tested in both directions (see Figure 2.2). Propagation trajectories were parallel to the rocky coast, which might channel sound waves, as opposed to the open and sandy bay at site 3. By contrast, the most efficient underwater sound propagation site at Métis was site 3. This can be explained by the protection from dominant currents and waves provided by the bay, and by the absence of underwater reefs impeding sound propagation as found in sites 1 and 2. The important aerial degradation of acoustic signals at site 3 could thus be compensated by its high underwater transmission efficiency. Chances of mother-pup reunion at this site can be optimized only when pups call in the water.

At the Bic colony, the three acoustic features measured led to different rankings for in-air propagation. Nevertheless, the best correlation coefficients were obtained at site 6 for both AM and FM patterns. Although no fine-scale site-use data was collected in the study area, the elongated rocky reef and surrounding aquatic area at site 6 was observed to be extensively used as haul-out and mother-pup reunion sites, respectively. Channeling of the sound by the barrier might explain the high propagation efficiency found at this location. Site 7, a protected bay frequently used for mother-pup reunion, also had good in-air propagation properties for both the AM pattern and the frequency spectrum. Underwater sound propagation at Bic was the most efficient at site 4, which seemed infrequently used by mother-pup pairs to haul-out or reunite, while the highest sound degradation was found for site 6. Site 4 is a particularly deep water area compared to the other sites tested. There was therefore less turbulence and no obstacles to sound propagation at the location of the hydrophone (depth $\approx$2 m) at this site, which might explain the better underwater propagation efficiency. Considering these results, it appears difficult to determine which tested sites are best suited for mother-pup vocal recognition and successful reunion at the Bic colony. For instance, sites 6 and 7 might represent interesting trade-offs between acoustic properties, protection from the elements and haul-out opportunities.

In both colonies, the distribution of mother-pup pairs was not proportional to the space available at each site (G. Beauplet and C.C. Sauvé, *unpublished observations*), suggesting that site characteristics might influence spatial use by breeding harbour seals (Ban and Trites 2007). Accordingly, exposure to waves, substrate as well as anthropogenic disturbance and noise levels are known to influence pinniped haul-out site choice (e.g., Suryan and Harvey 1999; Ban and Trites 2007; Acevedo-Gutierrez and Cendejas-Zarelli 2011; Cordes et al. 2011). As they are likely to affect mother-pup recognition efficiency, acoustic properties could represent additional characteristics influencing harbour seal haul-out and reunion site selection during the rearing season. Performing similar propagation tests in different weather conditions could provide insights as to the influence of wind, waves and currents on acoustic properties of meeting sites and help unravel the relative importance of sound transmission efficiency for habitat selection by harbour seal mother-pup pairs. Furthermore, the impact of site acoustic properties on the efficiency of mother-pup vocal communication could be assessed by additional playback experiments at the different sites coupled with mother-pup haul-out and meeting sites distribution surveys.

Acknowledgments

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Table 2. 1 Factor matrix from the principal component analysis on response to playback (*n*=36 tests) performed on harbour seal females. Variables are detailed in text.

Behavioural response variable	Standardized factor loadings		
	PC1	PC2	PC3
Number of looks (*NL*)	**0.58**	-0.47	-0.67
Distance of approach (D*A*)	**-0.58**	0.34	-0.74
Latency to first apparition (*LA*)	**-0.57**	-0.82	0.07
Eigenvalue	**2.10**	0.47	0.44
Proportion of variance explained	0.70	0.15	0.147
Cumulative proportion of variance explained	0.70	0.85	1.000

Table 2. 2 Summary of the model selection procedure on the behavioural responses to the playback stimuli (i.e., *PC1* scores, see Table 2.1). Coefficient estimations for a first complete linear mixed model (LMM) were obtained and the less significant effect was eliminated from the next model. Likelihood ratio tests indicated whether the simplified model was more fit than the complete one. These steps were repeated until the simplified model was no longer better than the previous. See text for definition of variables. Referents for treatment, MPL and t.order are 'non-filial', 'low' and 'own = first track', respectively. Bold type indicates the best modelling of *PC1* scores identified by the procedure.

Model	Coefficient *p*-values					Log-likelihood	p likelihood ratio test
	treatment	age	Δage	MPL	t.order		
PC1 score ~ treatment + age + Δage + MPL + t.order + $|ID_{pup}$	< 0.01	0.38	0.40	0.03	0.48	-60.80	} 0.74
PC1 score ~ treatment + age + Δage + MPL + $\mathbf{|ID_{pup}}$	< 0.01	0.43	0.51	0.03		-60.85	} 0.03
PC1 score ~ treatment + age + MPL + $|ID_{pup}$	< 0.01	0.57		0.03		-58.53	

Table 2. 3 Results of the best linear mixed model (see Table 2.2) assessing the effects of treatment (own vs alien young), pup age, pup age difference between call recording and playback session, and mother protection level on PC1 scores representing females' strength of response to the playback stimuli ($n_{♀} = 18$). Female ID was included as a random effect. Variables loading on *PC1* are presented in Table 2.1. 'Non-filial' and 'low' are the referents for the treatment and protection level effects, respectively.

Effect	Coefficient	DF	t	P
Treatment (own)	1.1	15	3.35	**< 0.01**
Pup age (d)	0.0	15	0.81	0.43
Age difference (d)	0.0	15	-0.67	0.51
Protection level (high)	1.0	16	2.64	**0.03**

Table 2. 4 Mean coefficients of correlation between acoustic features measured at various distances compared to control (measured at 1m) for the different tested sites at the Métis colony. Site numbers refer to those illustrated on Figure 2.2a). Grey highlighting indicates correlation coefficients > 0.50.

		In-air							Underwater					
		FM		AM		Frequency spectra			FM		AM		Frequency spectra	
Site no.	Distance (m)	mean	s.e.	mean	s.e.	mean	s.e.	Distance (m)	mean	s.e.	mean	s.e.	mean	s.e.
1	1	0.86	0.01	0.91	0.01	0.92	0.01	1	0.98	0.01	0.75	0.04	0.99	0.01
	4	0.84	0.01	0.93	0.01	0.90	0.01	25	0.63	0.04	0.43	0.02	0.89	0.01
	8	0.79	0.01	0.91	0.01	0.86	0.01	50	0.67	0.02	0.28	0.03	0.79	0.02
	16	0.68	0.01	0.76	0.04	0.88	0.01	100	0.43	0.03	0.09	0.02	0.63	0.03
	32	0.64	0.01	0.90	0.01	0.89	0.01	200	0.13	0.01	0.10	0.04	0.21	0.01
	64	0.62	0.01	0.79	0.02	0.81	0.01							
	128	0.61	0.01	0.67	0.03	0.67	0.01							
	256	0.61	0.01	-0.08	0.04	0.30	0.02							
2	1	0.88	0.02	0.94	0.01	0.95	0.01	1	0.900	0.008	0.67	0.03	0.92	0.01
	4	0.52	0.01	0.83	0.01	0.52	0.01	25	0.814	0.007	0.59	0.02	0.85	0.01
	8	0.57	0.01	0.89	0.01	0.84	0.01	50	0.33	0.03	0.32	0.03	0.48	0.02
	16	0.55	0.01	0.87	0.01	0.90	0.01	100	0.30	0.01	0.13	0.04	0.43	0.02
	32	0.57	0.01	0.85	0.01	0.87	0.01							
	64	0.52	0.01	0.89	0.01	0.68	0.03							
	128	0.59	0.02	0.86	0.01	0.90	0.01							
	256	0.49	0.01	0.78	0.02	0.72	0.01							
	512	0.49	0.01	0.32	0.03	0.60	0.02							
	1024	0.24	0.02	0.05	0.03	0.38	0.01							
3	1	0.77	0.04	0.93	0.01	0.95	0.01	1	1.0	0.01	0.86	0.03	1.0	0.01
	4	0.58	0.03	0.92	0.01	0.57	0.02	25	0.87	0.01	0.76	0.02	0.94	0.01
	8	0.58	0.06	0.89	0.01	0.81	0.03	50	0.95	0.01	0.76	0.03	0.96	0.01
	16	0.59	0.03	0.89	0.01	0.83	0.02	100	0.82	0.03	0.74	0.01	0.93	0.01
	32	0.54	0.05	0.87	0.01	0.76	0.02	200	0.87	0.01	0.65	0.02	0.89	0.01
	64	0.52	0.04	0.89	0.01	0.64	0.02	400	0.61	0.02	0.37	0.02	0.71	0.03
	128	0.49	0.08	0.5	0.1	0.44	0.03	800	0.37	0.02	0.04	0.03	0.44	0.02
	256	0.43	0.06	0.27	0.05	0.38	0.01	1600	0.26	0.02	0.04	0.03	0.47	0.01

Table 2. 5 Mean coefficients of correlation between acoustic features measured at various distances compared to control for the different tested sites at the Bic colony. Site numbers refer to those illustrated on Figure 2.2b). Grey highlighting indicates correlation coefficients > 0.50.

		In-air							Underwater					
		FM		AM		Frequency spectra			FM		AM		Frequency spectra	
Site no.	Distance (m)	mean	s.e.	mean	s.e.	mean	s.e.	Distance (m)	mean	s.e.	mean	s.e.	mean	s.e.
4	1	0.94	0.01	0.99	0.01	0.99	0.01	1	0.99	0.01	0.85	0.05	1.0	0.01
	4	0.85	0.03	0.92	0.02	0.97	0.01	25	0.85	0.03	0.73	0.02	0.96	0.01
	8	0.93	0.01	0.99	0.01	0.97	0.01	50	0.90	0.03	0.79	0.02	0.98	0.01
	16	0.75	0.03	0.82	0.04	0.88	0.01	100	0.74	0.04	0.57	0.03	0.81	0.02
	32	0.72	0.04	0.87	0.02	0.90	0.02	200	0.53	0.06	0.45	0.07	0.71	0.04
	64	0.91	0.01	0.97	0.01	0.97	0.01	400	0.76	0.02	0.53	0.03	0.78	0.02
	128	0.75	0.02	0.79	0.03	0.82	0.01	800	0.53	0.03	0.25	0.04	0.60	0.02
	256	0.49	0.02	0.63	0.04	0.66	0.02	1600	0.20	0.04	0.18	0.06	0.54	0.06
	512	0.36	0.03	0.41	0.03	0.50	0.01							
5	1	0.80	0.02	0.92	0.01	0.89	0.01	1	0.93	0.01	0.62	0.04	0.94	0.01
	4	0.77	0.03	0.96	0.01	0.94	0.01	25	0.87	0.01	0.52	0.03	0.90	0.01
	8	0.65	0.03	0.94	0.01	0.87	0.01	50	0.90	0.01	0.65	0.02	0.92	0.01
	16	0.71	0.03	0.94	0.01	0.87	0.02	100	0.70	0.03	0.53	0.02	0.83	0.01
	32	0.51	0.03	0.74	0.02	0.75	0.02	200	0.68	0.03	0.37	0.04	0.71	0.03
	64	0.45	0.05	0.90	0.01	0.87	0.02							
	128	0.53	0.04	0.95	0.01	0.93	0.01							
	256	0.43	0.04	0.75	0.02	0.81	0.02							
6	1	0.88	0.03	0.94	0.01	0.95	0.01	1	0.57	0.05	0.38	0.06	0.81	0.04
	4	0.78	0.02	0.94	0.01	0.94	0.01	25	0.57	0.02	0.31	0.03	0.74	0.02
	8	0.70	0.03	0.91	0.01	0.88	0.01	50	0.42	0.05	0.10	0.05	0.64	0.03
	16	0.72	0.03	0.86	0.02	0.89	0.01	100	0.38	0.04	0.03	0.04	0.62	0.03
	32	0.73	0.03	0.92	0.01	0.90	0.01	200	0.19	0.01	0.02	0.05	0.30	0.01
	64	0.69	0.03	0.92	0.01	0.93	0.01							
	128	0.62	0.03	0.79	0.01	0.83	0.01							
	256	0.64	0.03	0.76	0.01	0.69	0.02							
	512	0.61	0.04	0.32	0.02	0.43	0.01							
7	1	0.87	0.02	0.99	0.01	0.99	0.01	1	1.0	0.01	0.87	0.03	1.0	0.01
	4	0.79	0.02	0.98	0.01	0.97	0.01	25	0.83	0.03	0.76	0.01	0.97	0.01
	8	0.67	0.03	0.98	0.01	0.97	0.01	50	0.81	0.01	0.45	0.02	0.91	0.01
	16	0.66	0.03	0.98	0.01	0.97	0.01	100	0.79	0.01	0.40	0.01	0.91	0.01
	32	0.73	0.02	0.96	0.01	0.89	0.01	200	0.55	0.05	0.31	0.02	0.88	0.01
	64	0.34	0.04	0.89	0.02	0.93	0.01	400	0.09	0.01	-0.04	0.02	0.12	0.01
	128	0.48	0.04	0.74	0.02	0.88	0.01							
	256	0.38	0.03	0.76	0.03	0.76	0.01							

Table 2. 6 Comparison of ecological factors likely to act as selection pressures on mother-pup recognition systems, and results of studies assessing maternal vocal recognition abilities in five phocid species

Species	Population density[a]	Maternal foraging (% time at sea)[b]	Breeding substrate[b]	Pup mobility	Lactation length[b,c] (d)	Maternal vocal recognition
Northern elephant seal (*Mirounga angustirostris*)	H	0	Land	Low[d]	22-29	Yes[j]
Grey seal (*Halichoerus gyprus*)	H-M	0	Fast-ice or land	Null to High[e,f]	15-21	Pop. dependent[k,l]
Weddell seal (*Leptonychotes weddellii*)	M-L	40	Fast-ice	Moderate-High[g]	45-50	No[m]
Harbour seal (*Phoca vitulina*)	L	55	Land	High[h]	21-42	Yes[n]
Hawaiian monk seal (*Monachus schauinslandi*)	L	0	Land	Low[i]	35-42	No[o*]

Population density: low (L), medium (M), high (H)

References: A) Riedman 1990; B) Schulz and Bowen 2004, C) Riedman 1990; D) Reiter et al. 1978; E) Haller et al. 1996; F) Jenssen et al. 2010; G) Burns 1999; H) Bowen et al. 1999; I) Boness et al. 1998; J) Petrinovich 1974; K) McCulloch and Boness 2000; L) McCulloch et al. 1999; M) Van Opzeeland et al. 2012; N) present study; O) Job et al. 1995

*from observations, no experimental study

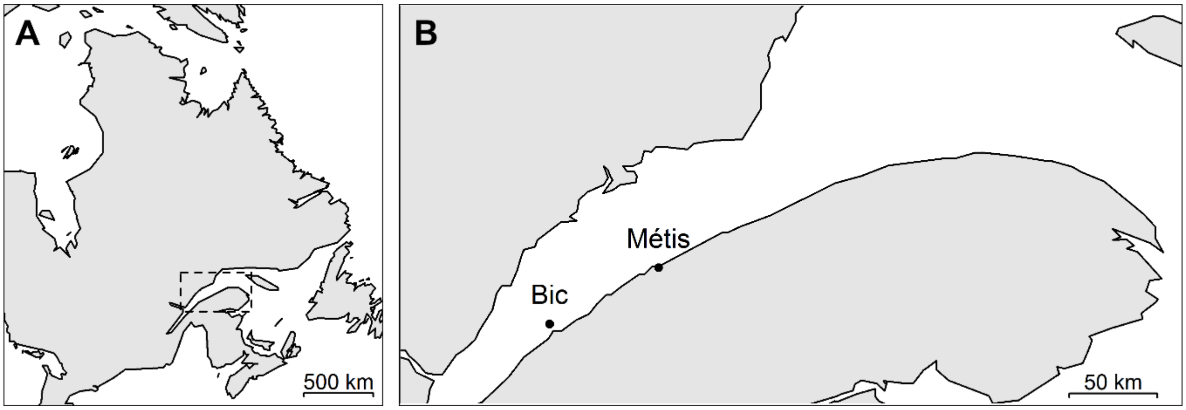

Figure 2. 1 Location of the colonies under study within a) Eastern Canada and b) the St-Lawrence River estuary. Map generated using *R* (packages maps and mapdata; Becker et al. 2013, Becker et al. 2013).

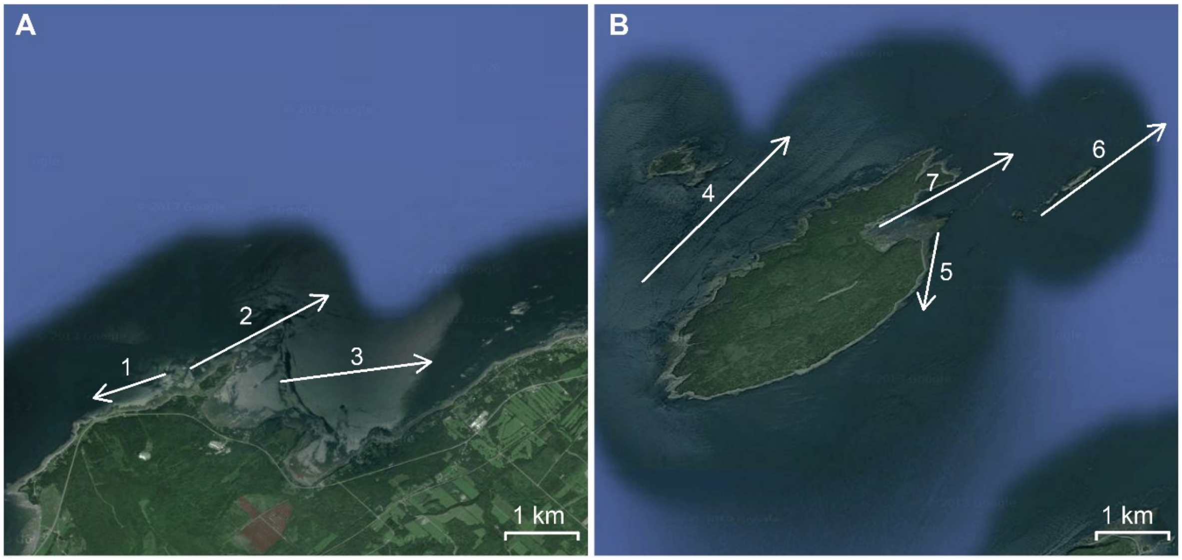

Figure 2. 2 Location of the propagation tests performed in-air at the a) Métis and b) Bic colonies. Arrows, topped with site numbers, are drawn from the recording location of propagated calls at 1 m to the longest distance tested for each trial (*i.e.*, 1024 m for sites 1 and 5, and 2048 m for other sites). Underwater propagation tests were performed from the same source with greater recording distances. Maps generated with *R* (package RgoogleMaps; Loecher 2013).

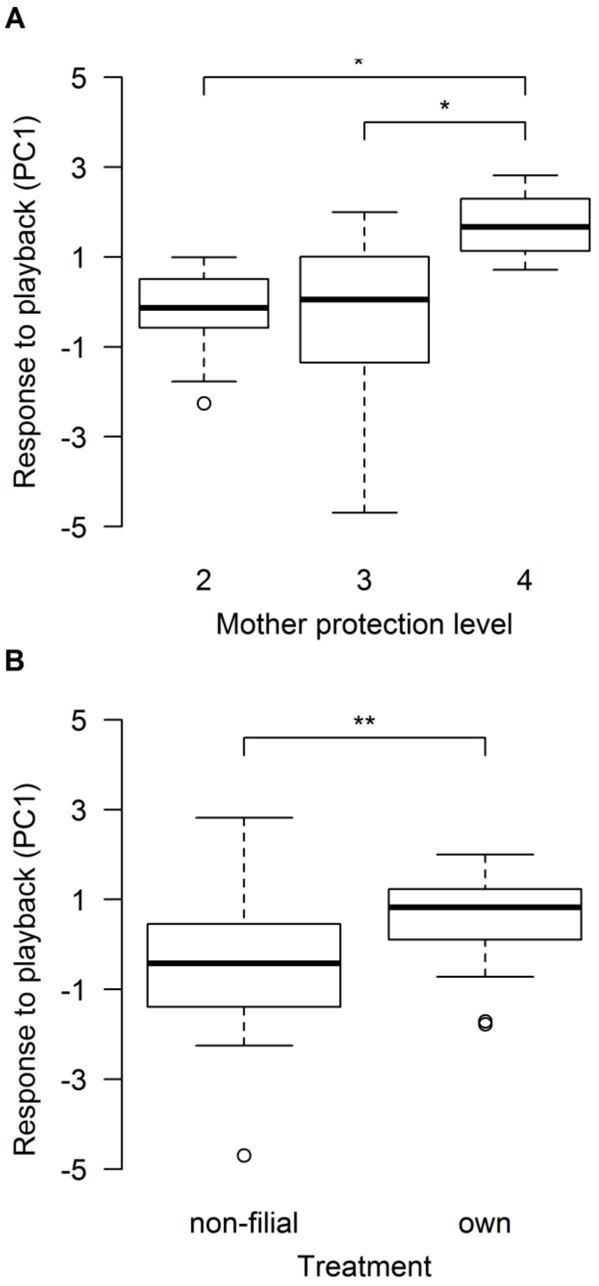

Figure 2. 3 Boxplots displaying female's response to playback, measured as PC1 scores from the PCA detailed in Table 2.1, relative to A) Mother protection level, regardless of treatment (see text for details) and B) Treatment. Asterisks indicate the following significance levels for differences in means tests (paired t-test and Tukey test for panels A and B, respectively): * $P < 0.05$, ** $P < 0.01$.

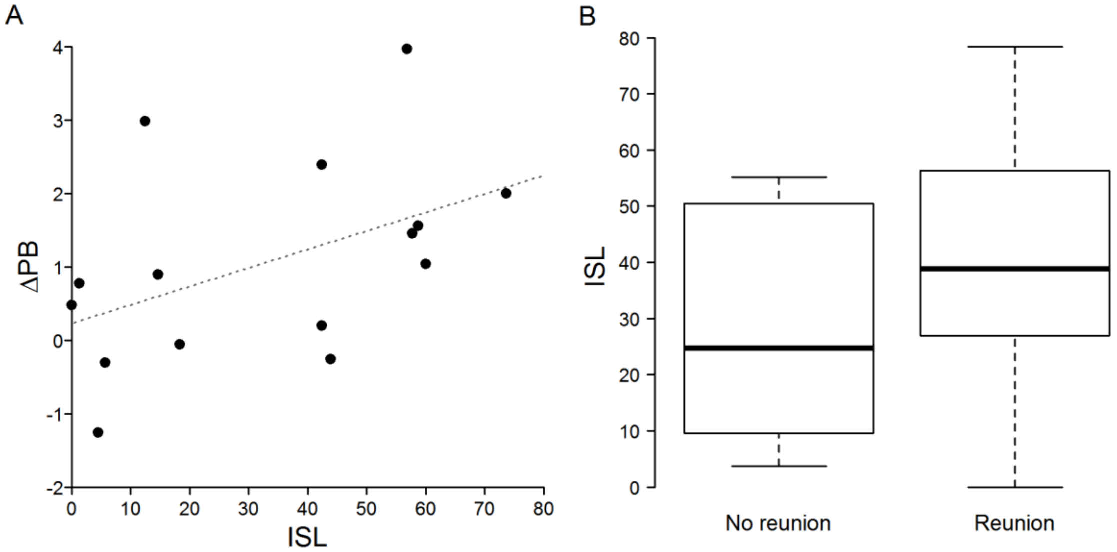

Figure 2. 4 Effect of pup voice ISL (individual percent correct classification rate from DFA on six acoustic parameters, detailed in Chapter 1) on female recognition abilities and mother-pup reunion. A) Differential response to playback ($\Delta PB = PC1_{own} – PC1_{non\text{-}filial}$) as a function of ISL, the grey line illustrates the linear prediction estimation ($p = 0.08$, $n = 15$). B) ISL in regards to whether pups did or did not reunite with their mother within 5 min after their release in the water. Differences in means were close to significance ($t_{16.75} = 1.54$, $p = 0.07$, $n = 42$).

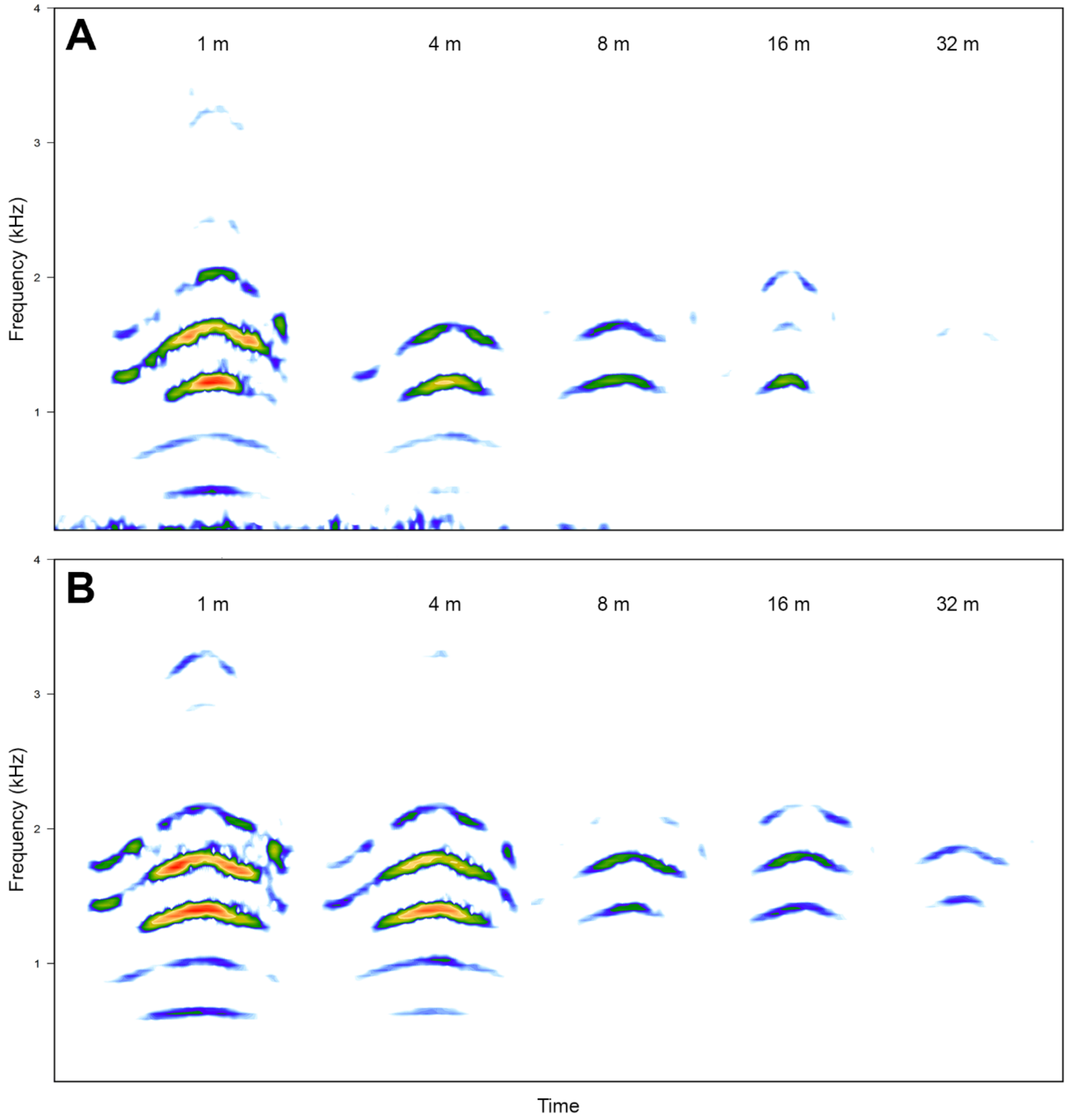

Figure 2. 5 Spectrograms of propagated aerial pup MACs recorded at increasing distances at A) site 5 and B) site 6. Figure generated using SEEWAVE R v.1.7.3 (Sueur et al. 2008).

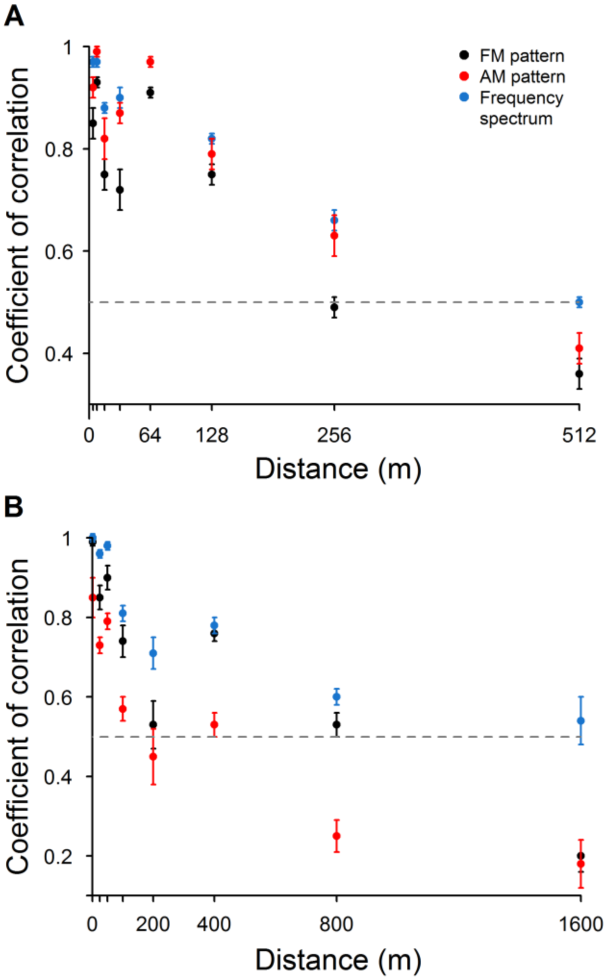

Figure 2. 6 Mean correlation coefficients of acoustic features measured on MACs recorded at increasing distances from the source compared to the control recording at 1 m for A) in-air and B) underwater propagation tests at site 4 (see Figure 2.2 for identification of site numbers). The dotted line indicates the 0.5 correlation threshold used to compare sites. Error bars present s.e. on means.

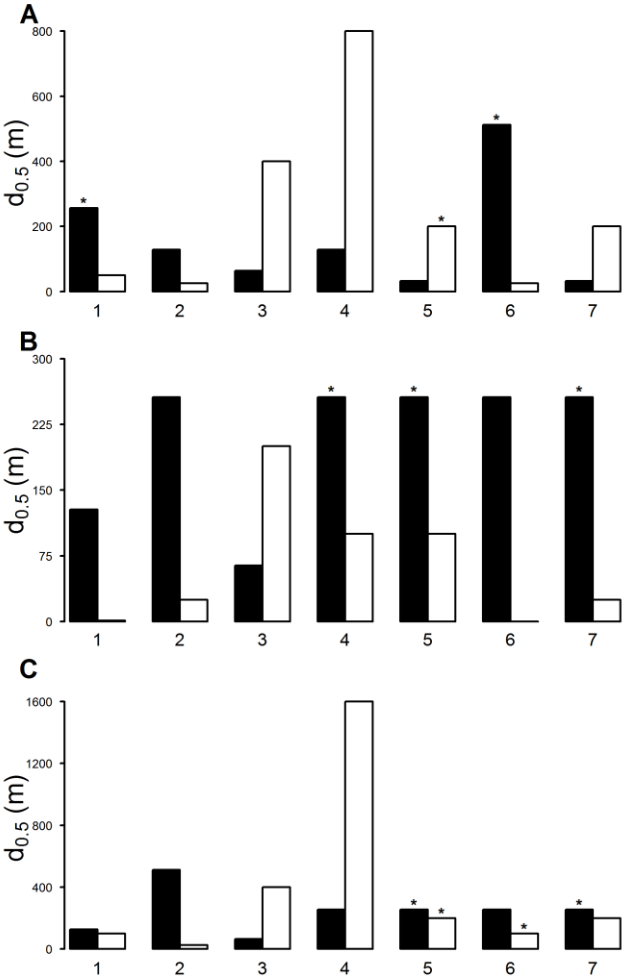

Figure 2. 7 Last distances before which mean A) FM, B) AM and C) frequency spectra correlation coefficients between propagated and control MACs (i.e., MACs recorded at 1m from the source) fell below 0.5 for the seven sites tested (see Figure 2.2 for identification of site numbers). Black and white bars represent in-air and underwater propagation tests, respectively. Asterisks indicate propagation trials where correlation coefficients remained > 0.5 at the maximal distance at which propagated calls were analyzed.

Conclusion

Étant donné l'état des connaissances relatives à leur phylogénie et à leurs stratégies d'allaitement, les pinnipèdes représentent un groupe d'intérêt pour les études comparatives de reconnaissance parent-jeune. Le phoque commun se distingue par une stratégie d'allaitement intermédiaire entre celles des phocidés et des otariidés, ainsi que par la forte mobilité pré-sevrage des chiots. Ces particularités sont susceptibles d'avoir influencé les forces de sélection ayant modelé le système de reconnaissance mère-jeune chez cette espèce. Ainsi, l'objectif général de cette étude était de caractériser le système de reconnaissance vocale mère-chiot chez le phoque commun. Pour ce faire, trois aspects de ce système ont été étudiés. D'abord, une analyse acoustique des vocalisations du chiot a été réalisée. Ensuite, les capacités de reconnaissance vocale du chiot par les femelles ont été testées lors d'expériences de playback. Finalement, l'efficacité de transmission des cris du chiot à différents sites de rencontre mère-petit a été évaluée et comparée grâce à des tests de propagation acoustique.

Caractérisation des vocalisations du chiot

L'analyse acoustique des vocalisations est une étape essentielle de la caractérisation d'un système de reconnaissance vocale. En effet, la présence d'une signature individuelle dans les vocalisations est un prérequis pour que les individus puissent se reconnaître par leur voix. Si son existence n'est pas démontrée, cela complique l'interprétation des résultats d'expériences de playback. En effet, il est alors impossible de déterminer si une absence de différence entre les traitements lors du playback est due à l'incapacité du receveur de discriminer entre les individus ou au signal qui encoderait une variation interindividuelle insuffisante pour permettre la discrimination (Beecher 1982, 1991). À notre connaissance, cette étude est la première à présenter une analyse acoustique pour chacun des trois types de cris (aériens, sous-marins et amphibies) émis par le chiot phoque commun. Elle est également la première à décrire l'ontogénie des cris de chiots phoque commun en milieu naturel et à considérer séparément les effets de l'âge et de la taille corporelle sur les différents paramètres acoustiques.

Les cris d'appel émis par les chiots (MAC, *mother attraction calls*) dans les milieux aériens et sous-marins portent des niveaux d'individualité fortement similaires (pourcentage de réassignation correcte globaux de 42.6% et 44.2%, respectivement) et intermédiaires entre ceux obtenus chez d'autres phocidés et otariidés par une méthode équivalente (*i.e.*, DFA à validation croisée; Table 1.7). Cela suggère que la stratégie d'allaitement intermédiaire adoptée par le phoque commun est associée à des forces de sélection équivalentes sur le système de reconnaissance vocale mère-jeune. Ces niveaux d'individualité dans les vocalisations sont également suffisants pour appuyer le rôle potentiel des cris du jeune pour la reconnaissance individuelle. De plus, à notre connaissance, la production de cris d'appels individualisés tant dans le milieu aérien que sous-marin n'a pas été rapportée chez d'autres pinnipèdes. Cela pourrait donc constituer une adaptation à la forte activité aquatique du phoque commun tout au long de la période de lactation (e.g.: Bigg 1981, Oftedal et al. 1987, Jorgensen et al. 2001) permettant aux chiots d'être entendus de leur mère qu'ils soient en plongée ou à la surface.

Parmi les paramètres acoustiques mesurés, les plus individualisés (plus grandes valeurs de PIC) sont la fréquence fondamentale (f_0), la durée du cri (*dt*), les pentes de modulation de fréquence (*AFM* et *DFM*) et les trois quartiles d'énergie (Q_{25}, Q_{50} et Q_{75}). Alors que les quatre premiers sont des paramètres liés à la source, les trois derniers sont associés au filtre du tractus vocal. Ces deux composantes contribuent donc à la signature individuelle encodée dans les cris du chiot. Cette redondance de l'information pourrait assurer le maintien de la signature individuelle malgré la croissance et la maturation du tractus vocal du chiot. En effet, cette étude révèle que plusieurs paramètres acoustiques des vocalisations du chiot sont modifiés avec l'âge et la taille corporelle. Comme la période de lactation est caractérisée par une croissance rapide des chiots, nos résultats suggèrent que les femelles doivent constamment mémoriser ces modifications pour être en mesure de reconnaître la voix changeante de leur jeune. De plus, cette étude révèle que cinq des sept paramètres acoustiques les plus individualisés (f_0, *dt*, *AFM*, *DFM* et Q_{50}) sont conservés entre les composantes aérienne et sous-marine des cris amphibies. L'utilisation de ces paramètres acoustiques pour la reconnaissance vocale pourrait faciliter la mémorisation de la voix du chiot par les femelles, puisque la signature individuelle est la même dans les deux milieux.

Reconnaissance des chiots par les femelles

Lors de la caractérisation d'un système de reconnaissance vocale, les expériences de playback sont nécessaires pour déterminer si les signatures individuelles portées par les vocalisations des émetteurs sont effectivement utilisées par les receveurs à des fins de reconnaissance. De plus, le design expérimental influence le degré de généralisation qu'il est possible de tirer des résultats du playback (McGregor et al. 1992). Ainsi, une étude antérieure a démontré qu'il est possible pour une femelle phoque commun d'apprendre à discriminer les cris de deux chiots préalablement enregistrés (Renouf 1985). Toutefois, cette expérience ne permettait pas de déterminer si ces capacités de discrimination sont effectivement utilisées par les femelles phoques communs en milieu naturel pour la reconnaissance vocale de leur jeune. Lors de la présente étude, le chiot était capturé, impliquant une séparation mère-petit. Cela faisait en sorte que les femelles étaient fortement motivées à retrouver leur petit. Les tests de playback décrits dans le Chapitre 2 ont donc permis d'observer le comportement de femelles en situation réelle de recherche de leur jeune, d'où la pertinence d'interpréter les résultats dans le contexte du maintien du contact mère-petit pendant la lactation.

Lors des tests de playback, les femelles ont répondu plus fortement à la diffusion de cris de leur propre chiot comparativement à la diffusion de cris de chiots non apparentés. Cela démontre que les femelles phoques communs 1) sont en mesure de percevoir la signature individuelle encodée dans les cris des chiots et 2) utilisent cette signature pour identifier leur jeune lorsqu'elles ont perdu le contact avec ce dernier. Cela fait du phoque commun le troisième phocidé (après l'éléphant de mer septentrional (Petrinovich 1974) et une population de phoques gris (McCulloch and Boness 2000)) chez lequel des tests de playback ont démontré des capacités de reconnaissance vocale mère-petit. Malgré un certain degré d'individualité porté par les cris des chiots (Collins et al. 2006), aucune reconnaissance vocale mère-petit n'a été démontrée chez le phoque de Weddell (Van Opzeelan et al. 2012), une deuxième population de phoques gris testée (McCulloch et al. 1999) et le phoque moine d'Hawaii (Job et al. 1995; observations seulement). Les capacités de reconnaissance vocale de la mère sont donc susceptibles de n'être présentes que chez les espèces ou populations de phocidés chez lesquelles de fortes pressions de sélection agissent sur le système de reconnaissance mère-petit. Chez le phoque commun, la forte mobilité du chiot (Bowen et al. 1999, Jorgensen et al. 2001) et les fréquentes absences maternelles durant les épisodes de chasse en cours de lactation (Boness et al. 1994) sont susceptibles d'avoir favorisé le développement d'un système de reconnaissance vocale individuelle chez les femelles.

L'analyse acoustique des cris a révélé que le niveau d'individualité vocale varie considérablement entre individus (estimée par le pourcentage individuel de réassignation correcte par la DFA, voir Tables 1.2 et 1.3). Or, la réponse préférentielle des femelles aux cris de leur propre chiot lors des tests de playback était corrélée au niveau d'individualité vocale de leur jeune. Les chiots ayant une voix plus stable ont donc été mieux reconnus par leur mère, suggérant que le niveau d'individualité vocale est un facteur limitant dans le processus de reconnaissance vocale mère-petit chez cette espèce. En l'absence d'autres modes de reconnaissance mère-petit, cela serait susceptible d'avoir des répercussions sur la force du contact mère-petit pendant la période de lactation, et par conséquent l'efficacité de l'administration des soins maternels, notamment l'allaitement. Cependant, l'olfaction jouerait un rôle dans la confirmation de l'identité suite à la réunion mère-petit chez les pinnipèdes (Lowell 1980, Insley et al. 2003a). Afin de déterminer si un rôle plus important de l'olfaction permet de compenser les difficultés de reconnaissance vocale chez les couples mère-petit où le chiot a une voix peu individualisée, il serait fort informatif de réaliser une étude intégrative. Par exemple, une analyse du niveau d'individualité porté par les cris couplée avec une expérience de reconnaissance olfactive (e.g.: Pitcher et al. 2011) permettrait de déterminer l'importance des systèmes de reconnaissance vocale et olfactive. Parallèlement, la pose d'enregistreurs de proximité sur les couples mère-petits (proximity loggers; Cross et al. 2012) mesurant le temps durant lequel mère et jeune sont en contact, ainsi qu'un suivi de croissance et de survie pré-sevrage fourniraient les informations nécessaires afin de caractériser la force du contact mère-chiot, son impact sur la qualité des soins maternels apportés et ultimement la survie des jeunes.

Les expériences de playback ont également révélé que la réponse des femelles aux cris diffusés est corrélée à l'intensité du comportement protecteur (MPL) exhibé à l'égard de leur chiot préalablement à sa capture. Comme cette tendance était observée indépendamment du traitement (propre jeune *vs* jeune non-apparenté), il est peu probable qu'elle soit attribuable à des différences de capacités de discrimination entre les femelles. Elle serait plutôt le résultat de différences quant aux niveaux de motivation à retrouver leur jeune ou au degré de témérité (Wilson et al. 1994) entre les femelles testées. Si un tel gradient de réaction suite à l'appel de leur chiot existe entre les femelles, il serait intéressant de vérifier si cela affecte la force du contact mère-petit pendant la période de lactation et s'il y a des répercussions sur le comportement d'allaitement, la croissance et la survie des jeunes. L'étude intégrative proposée précédemment permettrait également de répondre à cette question soulevée par les résultats de nos expériences de playback.

Efficacité de propagation des vocalisations du chiot

Les tests de propagation acoustique permettent de déterminer l'impact de l'habitat sur l'efficacité de diffusion d'un signal vocal. Ils fournissent des renseignements quant à la dégradation différentielle des paramètres acoustiques des vocalisations, des distances auxquelles la communication vocale est effective dans des conditions météorologiques optimales, ainsi qu'aux composantes du paysage les plus susceptibles de favoriser ou d'altérer la propagation des signaux acoustiques.

Les différents sites testés dans le cadre de cette étude varient largement quant à leur efficacité de propagation acoustique. La comparaison des caractéristiques des sites indique que l'absence d'obstacles physiques à la propagation (e.g.: récifs à fleur d'eau ou submergés), une importante profondeur de l'eau et une grande distance des zones de végétation représentent les conditions de propagation aérienne et sous-marine optimales. Puisque les femelles phoques communs utilisent la communication vocale pour retrouver leur chiot suite à une séparation, les propriétés acoustiques de l'habitat sont susceptibles d'être importantes pour le maintien du contact mère-petit durant la période de lactation. Il pourrait donc être intéressant de considérer l'efficacité de propagation acoustique comme un facteur explicatif additionnel dans les études portant sur la sélection de l'habtitat par le phoque commun, notamment pendant la période de lactation.

Parmi les paramètres mesurés sur les cris propagés, le spectre fréquentiel était considérablement moins dégradé avec la distance que les modulations de fréquence et d'amplitude, ce qui renforce la suggestion que la fréquence fondamentale et les quartiles d'énergie constitueraient des paramètres fiables de la signature individuelle pour la reconnaissance vocale des chiots phoques communs par leur mère.

Perspectives

Bien que la présente étude propose les paramètres acoustiques des cris qui pourraient potentiellement être utilisés par les femelles pour la reconnaissance de leur jeune, cela demeure hypothétique. La réalisation de tests de playback au cours desquels seraient diffusés des cris de chiots modifiés (un paramètres acoustique à la fois) permettrait d'identifier avec certitude les éléments de la signature individuelle effectivement utilisés par les femelles pour reconnaître la voix de leur chiot (e.g.: Charrier et al. 2002, Pitcher et al. 2012). Cette expérience permettrait de faire le lien entre les deux chapitres de ce mémoire, en associant les capacités de reconnaissance des femelles à l'analyse acoustique des cris des chiots. Elle mettrait en lumière les facteurs influençant l'utilisation des paramètres acoustiques pour la reconnaissance vocale mère-petit: faible modification avec l'âge et la taille?, conservation entre les composantes aérienne et sous-marine?, faible dégradation avec la distance?, etc.

Cette étude présente les premiers tests de playback réalisés sur des femelles phoque commun. Or, cette espèce est la plus répandue des phocidés et exploite une multitude de substrats comme sites d'échouage (Bigg 1981, Burns 2009). Dans l'estuaire du St-Laurent, les récifs sur lesquels les phoques communs s'échouent sont, pour la plupart, submergés à marée haute (Boulva and McLaren 1979, Lesage et al. 1995). Les sites de mise-bas et d'allaitement sont donc très fluctuants, ce qui pourrait être un facteur ayant favorisé l'évolution du système de reconnaissance vocale mère-petit décrit dans la présente étude. Les systèmes de reconnaissance vocale mère-petit peuvent diverger entre les populations d'une même espèce (e.g., phoque gris; McCulloch et al. 1999, McCulloch and Boness 2000). Il serait donc pertinent de réaliser l'analyse acoustique et les expériences de playback décrites dans cette étude au sein d'autres populations de phoques communs afin de déterminer si les capacités de reconnaissance et les niveaux d'individualité vocale rapportées ici s'appliquent à l'ensemble de l'espèce ou s'il y a des différences inter-populationnelles. À l'instar des études comparatives interspécifiques, les comparaisons entre populations permettraient de mettre en lumière les forces évolutives modelant les systèmes de reconnaissance vocale mère-jeune.

Par ailleurs, l'analyse acoustique des vocalisations des jeunes phocidés et l'évaluation des capacités de discrimination des femelles n'ont été réalisées que sur cinq des 19 espèces actuelles, alors que la proportion des espèces étudiées est plus grande chez les otariidés (sept sur 13; voir Table 1.7). Il importe donc de poursuivre la caractérisation de la reconnaissance vocale mère-chiot chez les phocidés et autres pinnipèdes afin d'obtenir une meilleure représentation de l'influence des contraintes écologiques sur l'évolution de ces systèmes de communication au sein de ce groupe de référence.

Finalement, il serait fort approprié d'uniformiser les paramètres acoustiques mesurés sur les vocalisations des chiots et les méthodes de quantification du niveau d'individualité porté par les cris entre les différentes études sur les pinnipèdes. Cela permettrait un meilleur potentiel de comparaison des résultats des analyses acoustiques entre les espèces et les populations.

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