# Ségrégation écologique au sein d'une communauté de delphinidés tropicaux : utilisation de l'espace et des ressources et fonctionnement social

Jérémy Kiszka

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# Ségrégation écologique au sein d’une communauté de delphinidés tropicaux : utilisation de l’espace et des ressources et fonctionnement social

Thèse présentée par Jeremy Kiszka
Pour l’obtention du grade de Docteur de l’Université de La Rochelle

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<u>Composition du jury</u> :
Pr. Etienne Danchin (CNRS, UMR 5174, Toulouse), Président du jury
Dr. Andrew J. Read (Duke University, USA), rapporteur
Dr. Christophe Guinet (CNRS-CEBC, Chizé), rapporteur
Dr. Florence Caurant (LIENSs, Université de La Rochelle), examinateur
Pr. Vincent Ridoux (LIENSs, Université de La Rochelle), directeur de thèse

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# Avant-propos

Cette thèse a été financée par le Conseil Général de Mayotte, dans le cadre d'une convention tripartite entre le Conseil Général de Mayotte, l'Université de La Rochelle et l'Office National de la Chasse et de la Faune Sauvage (convention CDM/ONCFS/ULR, avril 2007 - avril 2010). Ces deux dernières institutions ont également participé à la réalisation d'un programme de recherche sur les delphinidés de Mayotte en partenariat avec la Direction de l'Agriculture et de la Forêt (convention DAF/ONCFS/ULR, mai 2005).

L'organisation de ce manuscrit est celui d'une thèse sur publications. Quatre articles constituent les quatre principaux chapitres. Trois autres articles ont également été réalisés dans le cadre de la thèse mais ont été placés en annexe, car jugés comparativement plus marginaux. Le manuscrit est donc constitué d'une introduction présentant le cadre sociétal et théorique de la thèse, d'une section présentant les matériels et méthodes utilisés, des quatre articles principaux, d'une discussion (synthèse des résultats, discussion et perspectives), des références bibliographiques et des annexes.

Les articles présentés dans le corps de la thèse présentent les thèmes suivants :

- Structure d'une communauté de cétacés odontocètes autour d'une île tropicale (Mayotte, Canal de Mozambique). Cet article présente de manière descriptive la communauté de cétacés odontocètes de Mayotte, dont les delphinidés. Il aborde essentiellement des aspects de diversité spécifique, de distribution spatiale et d'abondance relative. Cet article est sous presse dans *African Journal of Marine Science.*
- Ségrégation écologique des delphinidés de Mayotte. Cet article aborde un aspect majeur de la thèse, à savoir le partage des habitats et des ressources par les delphinidés qui vivent en sympatrie autour de Mayotte, selon les trois dimensions principales d'une niche écologique : espace (habitats), temps (budgets d'activités) et ressource (signatures isotopiques). Cet article est soumis à *Marine Ecology Progress Series.*
- Associations interspécifiques de deux espèces jumelles (*Stenella longirostris* et *Stenella attenuata*) autour de Mayotte. Cet article examine les mécanismes impliqués dans la formation d'associations entre ces deux espèces qui vivent en sympatrie

directe (optimisation de la détection et de l'usage des ressources ? lutte contre les prédateurs ? avantages sociaux ?). Cet article est en préparation.

- Structure de population à fine échelle et ségrégation intra-spécifique du grand dauphin de l'Indo-Pacifique (*Tursiops aduncus*) autour de Mayotte. Cet article aborde, à des échelles temporelles emboitées, la structure de population de cette espèce et des phénomènes de ségrégation écologique intra-spécifique. Cet article est soumis à *Behavioural Ecology and Sociobiology.*

Enfin, plusieurs autres articles ont été réalisés durant la thèse. Ces derniers ont été placés en annexe. Ils touchent également au thème principal de la thèse, mais ont été placés en annexe parce qu'ils traitent de résultats préliminaires acquis en début du projet, ou acquis dans un autre secteur géographique, ou encore parce qu'ils abordent des aspects comportementaux et éthiques de certaines pratiques de prélèvement biologique, les biopsies, utilisées dans le corps du travail.

Les articles placés en annexe sont :

- Etude préliminaire de la ségrégation écologique des delphinidés autour de Mayotte. Cet article, réalisé dans le cadre d'un stage de Master 2 (Alexandra Gross) a permis d'étudier de manière préliminaire le partage des habitats et des ressources selon les axes « habitat » et « écologie alimentaire » de la niche écologique grâce à des données d'observation (issues de campagnes dédiées et opportunistes) et d'un faible échantillon de biopsies de peau et de lard. Cet article a été publié dans *Estuarine Coastal and Shelf Science* (2009).
- Réactions comportementales à l'échelle des individus et des groupes de delphinidés à la pratique des biopsies par arbalète. Cet article aborde l'impact de cette pratique permettant la collecte d'échantillons de peau et de lard de delphinidés et propose des recommandations. Le manuscrit est accepté dans *Animal Welfare.*
- Ségrégation écologique des delphinidés de l'île de Moorea (Polynésie Française). Ce travail a été réalisé en collaboration avec le CRIOBE de Polynésie (Centre de Recherche Insulaire et Observatoire de l'Environnement), l'Université d'Auckland (Nouvelle Zélande) et l'Université de La Rochelle (LIENSs). Il vise à déterminer les relations trophiques des delphinidés vivant en sympatrie autour de Moorea. Cet article est sous presse dans *Journal of Experimental Marine Biology and Ecology.*

# Partie 1 :

# Introduction générale

## 1.1 Contexte sociétal

### *1.1.1 Les delphinidés : modèles diversifiés et indicateurs écologiques*

A travers le monde, 36 espèces de delphinidés sont actuellement reconnues. Leur taille et leur morphologie sont très variables : du céphalorhynque d'Hector (*Cephalorhynchus hectori*) de 146 cm pour environ 57 kg à l'orque (*Orcinus orca)* pouvant atteindre la taille maximale 980 cm et un poids d'environ 10 tonnes (Jefferson *et al.*, 2008). Les delphinidés occupent tous les océans du globe, des zones côtières aux habitats océaniques, des pôles aux tropiques. Ils exploitent une très grande diversité d'habitats (fluviatiles, côtiers et océaniques) et de ressources (benthiques à épi- ou méso-pélagiques dans les 1000 premiers mètres de l'océan). Par ailleurs, ces organismes ont des modes de vie très diversifiés. Leur domaine vital s'étend de quelques km² pour certaines espèces côtières résidentes (certaines populations de grands dauphins *Tursiops truncatus*) à plusieurs milliers de km² pour plusieurs delphinidés océaniques (espèces de genre *Lagenorhynchus,* par exemple). Ainsi, ils exploitent à la fois des milieux ouverts en formant de très grands groupes pouvant atteindre plusieurs milliers d'individus ou des zones côtières fermées comme des baies ou même des rivières en petits groupes de quelques individus (Gowans *et al.*, 2007). Enfin, ces organismes sont très sociables, mais les degrés de socialité sont relativement variables au sein de la famille des delphinidés. Ceci permet aux individus un meilleur accès à un partenaire sexuel, le soin aux petits, ou encore la recherche de nourriture (Danchin *et al.*, 2005). Cette socialité a fortement contribué à favoriser la colonisation de milieux variés dans l'environnement hétérogène et parfois hostile de l'océan. Les delphinidés se caractérisent par plusieurs types de structure : des sociétés fluides non apparentées avec des associations qui durent quelques heures à quelques années (type « fission-fusion ») que l'on observe chez le grand dauphin (Connor *et al.*, 2000) et de nombreux autres petits dauphins, aux sociétés apparentées dont les associations peuvent durer toute la vie et qui sont centrées autour de matriarches (type « matriarcal), comme c'est le cas chez les orques et plusieurs espèces de la sous-famille des *Globicephalinae* (Gowans *et al.*, 2007).

Les delphinidés représentent des maillons clés des écosystèmes marins et des indicateurs pertinents de leur santé, et ce pour plusieurs raisons. Il s'agit de prédateurs supérieurs qui exploitent une grande variété de ressources alimentaires (poissons, céphalopodes, crustacés) et qui accumulent les contaminants à des concentrations parfois très élevées, comme c'est le cas pour certains métaux toxiques comme le mercure (Caurant *et al.*, 1996). Les delphinidés sont des prédateurs supérieurs situés au sommet des réseaux trophiques. Ils sont longévifs (stratégie de croissance K), ont un faible taux de reproduction et une maturation tardive. L'état de santé des populations de delphinidés reflète donc également l'état de santé des maillons inférieurs des écosystèmes marins (Wells *et al.*, 2004 ). En tant qu'indicateurs, ils s'avèrent également intéressants du fait de leur bonne accessibilité (notamment pour les espèces côtières et résidentes). Les delphinidés (et les cétacés de manière plus générale) représentent d'excellents indicateurs de la biodiversité des écosystèmes marins. En effet, la mesure de la diversité et de la densité de ces prédateurs est rendue aisée par leur bonne détectabilité et ce sur de grandes échelles spatiales. Ainsi, des diversités et des densités importantes de prédateurs supérieurs (comme les delphinidés) révèlent la présence de structures océanographiques induisant une plus forte productivité du milieu. Enfin, il a pu être mis en évidence qu'il existait un lien entre l'utilisation stratégique des prédateurs supérieurs et la conservation à l'échelle écosystémique. Ainsi, les plans de conservation centrés sur les prédateurs supérieurs peuvent être mis en place pour la conservation de la biodiversité au sens large (Sergio *et al.*, 2006). Ceci met donc en évidence l'importance des prédateurs supérieurs, dont les delphinidés, en tant qu'indicateurs de la biodiversité.

### *1.1.2 Les delphinidés : des espèces emblématiques et protégées*

Depuis le milieu du 20$^{\text{ème}}$ siècle, les delphinidés jouissent d'un statut d'espèces emblématiques par leur médiatisation à travers les documentaires et la fiction. Leur image est très populaire, tout particulièrement dans les pays occidentaux. Leur statut d'espèces emblématiques en fait des espèces protégées par de nombreuses conventions internationales (Conventions de Berne, de Nairobi, de Washington, par exemple). Dans de nombreux pays, ces espèces sont protégées contre la destruction volontaire et la perturbation intentionnelle, à l'image de la France. Toutefois, depuis près de 20 ans, la notion de protection des habitats tend à prendre le relais sur celle de protection des espèces. Depuis 1992, la Directive Européenne « Habitats » permet de renforcer le statut de protection de certaines espèces de mammifères marins côtiers en créant des zones spéciales de conservations permettant de protéger les espèces par la protection des habitats dont elles dépendent.

Paradoxalement, même si les delphinidés et de nombreuses espèces de mammifères marins jouissent d'un statut de protection important à l'échelle globale (malgré de fortes disparités géographiques), de nombreuses espèces sont menacées dans le monde du fait des captures accidentelles dans les engins de pêche, de l'exploitation directe mais aussi de la destruction de leurs habitats et des dérangements (Culik, 2004). La menace la plus importante à l'échelle globale demeure les captures accidentelles dans les pêcheries (notamment au filet maillant et à la senne, DeMaster *et al.*, 2001). Par exemple, les populations de dauphins à long bec (*Stenella longirostris orientalis*) et de dauphins tachetés pantropicaux (*Stenella attenuata attenuata*) du Pacifique Est tropical ont été décimées par les captures accidentelles dans la pêcherie thonière. A l'heure actuelle, la taille de ces populations ne montre aucun signe d'augmentation (Gerrodette & Forcada, 2005). Ailleurs, dans le golfe de Californie, les filets maillants ont décimé le marsouin de Californie ou *vaquita* (*Phocoena sinus*), espèce endémique de cette région, qui est actuellement en danger critique d'extinction (D'Agrosa *et al.*, 2000). En 2007, une espèce de dauphin de fleuve de la famille des lipotidés, le baiji (*Lipotes vexilifer*), endémique du fleuve Yang Tsé, s'est éteinte du fait des captures accidentelles et de la forte dégradation de son habitat (Turvey *et al.*, 2007). Le problème des captures accidentelles est tout particulièrement aigu dans les pays en voie de développement, où les alternatives à la pêche sont peu envisageables (Read *et al.*, 2006) et où, sous la pression de la raréfaction des ressources halieutiques, nombre de pêcheries présentant des captures accidentelles de mammifères marins deviennent graduellement des pêcheries de subsistance ciblant ces espèces (IWC, 2010).

En tant que prédateurs supérieurs, les delphinidés représentent des indicateurs importants des processus écosystémiques et de la répartition de leurs proies. Les aires marines protégées apparaissent comme un outil de gouvernance utile pour leur conservation au regard des activités humaines qui peuvent interagir avec eux (Hooker & Gerber, 2004). En France, en 2006, l'Agence des Aires Marines Protégées (établissement public sous tutelle du Ministère de l'Ecologie, de l'Energie, du Développement Durable et de la Mer) a été créée pour répondre aux engagements de la France en matière de conservation de la biodiversité marine. Elle constitue notamment un appui aux politiques de création et de gestion d'aires marines protégées.

### *1.1.3 Les delphinidés à Mayotte : statut et conservation*

Parmi la diversité connue de delphinidés, 22 espèces occupent les zones tropicales au moins temporairement et 16 sont exclusivement inféodées aux eaux tropicales et tempérées chaudes (Rice, 1998). Plus de 90 % des espèces tropicales de delphinidés ont été observées dans le sud-ouest de l'océan Indien (Kiszka *et al.*, 2009a). Le reste constitue des espèces endémiques à distributions restreintes. Autour de Mayotte, en 2007, 19 espèces de cétacés ont été recensées (Kiszka *et al.*, 2007a). Parmi ces espèces, 11 delphinidés appartenant à 9 genres ont été enregistrées : le grand dauphin de l'Indo-Pacifique (*Tursiops aduncus*), le dauphin à bosse de l'Indo-Pacifique (*Sousa chinensis*), le dauphin à long bec (*Stenella longirostris*), le dauphin tacheté pantropical (*Stenella attenuata*), le péponocéphale (*Peponocephala electra*), le globicéphale tropical (*Globicephala macrorhynchus*), le pseudorque (*Pseudorca crassidens*), l'orque pygmée (*Feresa attenuata*), le dauphin de Risso (*Grampus griseus*), le dauphin de Fraser (*Lagenodelphis hosei*) et le grand dauphin commun (*Tursiops truncatus*). Récemment, la présence de deux nouvelles espèces a été confirmée : l'orque (*Orcinus orca*) et le dauphin à bec étroit (ou sténo, *Steno bredanensis*) (Sea Blue Safari, communication personnelle). Ces données nouvelles portent à 13 espèces (de 11 genres) le nombre d'espèces de delphinidés recensées autour de Mayotte.

La communauté des delphinidés autour de Mayotte est donc très diversifiée. Ceci serait dû à la présence d'une grande diversité d'habitats marins autour de l'île, des zones côtières aux zones océaniques (Kiszka *et al.*, 2007a). L'abondance des populations de delphinidés de Mayotte a été estimée de manière préliminaire pour plusieurs espèces : *T. aduncus* (41, CI 95%, 30 – 67), *S. longirostris* (703, CI 95%, 643 – 1046), *S. attenuata* (375, CI 95%, 342 – 557) (Pusineri *et al.*, 2009). L'abondance du dauphin à bosse a également été estimée par photo-identification. Seuls trois individus ont été recensés et sont ré-observés régulièrement. Plusieurs menaces d'origine anthropique pèsent actuellement sur les populations de delphinidés autour de Mayotte. Elles incluent les dérangements issus du trafic maritime et de l'observation commerciale des mammifères marins, la diminution des ressources alimentaires (notamment pour les espèces côtières comme le grand dauphin et le dauphin à bosse) et la dégradation des habitats côtiers (Pusineri & Kiszka, 2007). Récemment, il a pu être montré que les grands dauphins de l'Indo-Pacifique de Mayotte étaient affectés par des maladies de peau similaires à la lobomycose. Ceci pourraient être dû à des modifications de l'environnement côtier (Kiszka *et al.*, 2009b).

Les delphinidés de Mayotte connaissent des niveaux de vulnérabilité différents. Par exemple, le dauphin à bosse est plus menacé que le grand dauphin du fait de la très faible taille de ses effectifs. Le grand dauphin est lui plus menacé que les espèces océaniques (du genre *Stenella* par exemple) du fait de son habitat côtier plus dégradé, du trafic maritime et de la surpêche. Globalement toutefois, les delphinidés de Mayotte jouissent d'un statut de conservation favorable, à l'inverse du dugong (*Dugong dugon*), menacé par les captures accidentelles et l'envasement des herbiers sous-marins (Kiszka *et al.*, 2007b ; Pusineri & Quillard, 2008).

## 1.2 Contexte théorique

### *1.2.1 Le concept d’habitat*

Le terme d’habitat est utilisé en écologie pour désigner le lieu ou vit un organisme. Par exemple, l’habitat du gorille des plaines (*Gorilla gorilla*) regroupe les forêts secondaires tropicales alors que celui du tigre (*Panthera tigris*) inclut la forêt tropicale humide, les forêts de conifères enneigées ou les marécages (Sunquist, 1985). Par ailleurs, certains organismes effectuent d’importantes migrations, ce qui rend l’identification de leur habitat d’autant plus difficile (Chapman & Reiss, 1999). Il existe deux types de modèles de distribution des organismes dans un habitat. Le premier, la distribution libre idéale, postule que la densité locale dépend de l’adéquation du site : les espèces se distribuent préférentiellement dans des habitats dont les conditions sont optimales. Son opposé prétend que les conditions ne sont jamais optimales car il existe de la compétition (pour l'espace, l’alimentation, la reproduction…) et des contraintes environnementales (Campan & Scapini, 2002). Certains écologistes ont rapidement réalisé que les plus petits organismes, notamment ceux vivant dans des zones très restreintes spatialement (sur une plante, un animal ou une strate du benthos en milieu marin), la notion d’habitat devrait être précisée. Le terme de micro-habitat fut donc employé (Chapman & Reiss, 1999).

### *1.2.2 Le concept de niche et de ségrégation écologique*

Le concept de niche écologique est ancien (Grinell, 1924). Celui-ci avait tout d’abord un sens d’habitat. Les définitions existantes pour la niche écologique sont nombreuses et très variables d’un auteur à l’autre. La définition la plus simple et la plus classique désigne la niche écologique comme étant l’ensemble des conditions abiotiques et biotiques dans lesquelles vit l’espèce (Hutchinson, 1957). La niche écologique d’une espèce est un complexe multifactoriel caractérisé par trois composantes majeures (ou dimensions) : l’habitat (distribution spatiale, influence des paramètres physiques et biologiques du milieu), les ressources alimentaires (régime alimentaire, niveau trophique) et l’espace temps (variations saisonnière et diurne de l’utilisation des habitats et des ressources). Pour certains organismes comme les mammifères, on ajoute parfois une composante comportementale (Campan & Scapini, 2002). La niche écologique est propre à chaque espèce et représente l’ensemble des conditions et des ressources dans laquelle celle-ci vit et se perpétue. L’une des principales lois en écologie est que chaque espèce a sa propre niche écologique (Grinnell, 1924). En d’autres termes, deux espèces ne peuvent occuper la même niche et coexister. Si c’est le cas, ces deux espèces entrent en compétition et l’une d’entre elles est vouée à disparaître. Toutefois, deux espèces peuvent partiellement occuper la même niche. Ce niveau de chevauchement peut même aboutir à la formation d’une association poly-spécifique (ou interspécifique), dont l’origine peut être l’optimisation de la recherche alimentaire et de la prédation, la lutte contre les prédateurs ou encore le renforcement des activités sociales (Whitesides, 1989; Terborgh, 1990 ; Heymann & Buchanan-Smith, 2000 ; Stensland *et al.*, 2003). Déterminer la niche d’une espèce est complexe et nécessite de collecter des données dans la nature, ce qui est rendu difficile dans les milieux peu accessibles (comme le milieu marin). En effet, il est difficile de représenter graphiquement la niche écologique d’un organisme quand celle-ci comporte plus de deux paramètres (Figure 1.1). Les outils statistiques proposent alors des représentations de niches comme des hyper volumes à n-dimensions (Barbault, 1992).

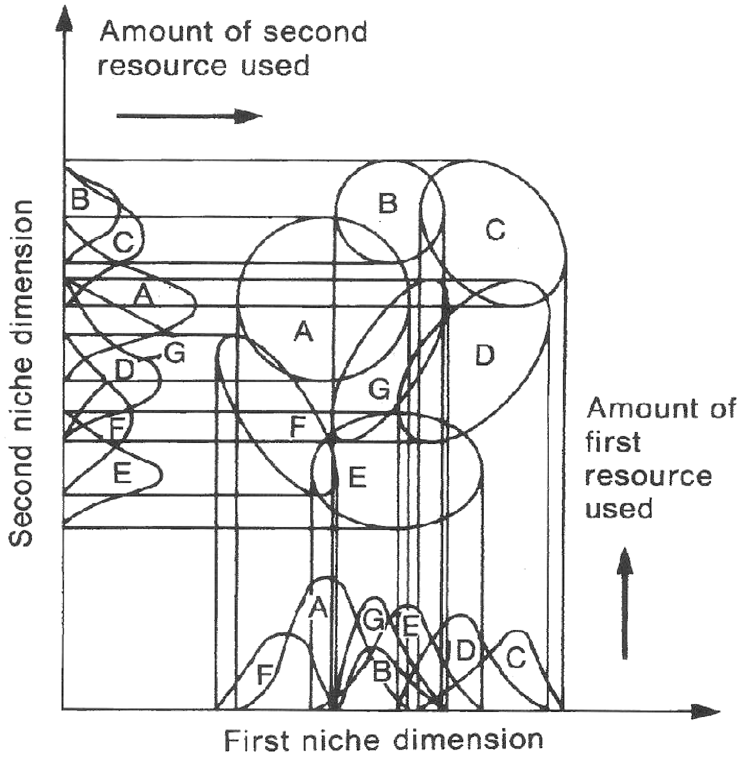


**Figure 1.1 :** Représentation schématique à deux dimensions des niches de différentes espèces. Les niches se recouvrent peu malgré le chevauchement des ressources observé sur chaque axe (Chapman & Reiss, 1999).

### *1.2.3 Compétition inter- et intra-spécifique*

Il est important de distinguer la niche fondamentale (la niche théorique pouvant être occupée par un organisme, sans compétiteur et sans prédateur) et la niche réalisée (niche réellement occupée par l’organisme) (Hutchinson, 1958). Il ne parait pas concevable que deux espèces présentant la même niche écologique puissent coexister. Une exploitation des mêmes ressources dans un même habitat induit une compétition. Cette compétition peut opposer les individus d’une même espèce (compétition intra-spécifique) ou de plusieurs espèces (compétition interspécifique). La compétition peut revêtir deux aspects : d’une part, l’interférence, c'est-à-dire une interaction directe et souvent violente entre les individus ; d’autre part, l’exploitation de la même ressource limitante, ce qui peut aboutir à l’exclusion d’un des compétiteurs. C’est ce qui est développé dans le principe d’exclusion compétitive de Gausse, qui prévoit que deux espèces ayant des « exigences écologiques » identiques ne peuvent coexister indéfiniment, la plus compétitive finissant par éliminer l’autre (May & MacArthur, 1972). Plusieurs facteurs peuvent contribuer à déterminer quelle espèce est la plus susceptible d’être exclue. Les espèces les plus flexibles dans leur alimentation et dans le choix de leurs ressources sont théoriquement celles qui parviennent à se maintenir. Les espèces les plus spécialisées sur une ressource sont les plus fragiles en cas de changement quelconque ou de compétition. Les espèces à gamme d’alimentation plus large peuvent aisément trouver une autre ressource à exploiter (Danchin *et al.*, 2005).

Les individus d’une même espèce ont des besoins pour survivre, pour se développer et pour se reproduire qui sont identiques. Toutefois, la demande immédiate de ressources peut dépasser la disponibilité immédiate de celles-ci. Les individus d’une même espèce peuvent alors entrer en compétition. La compétition intra-spécifique peut se manifester de diverses manières et varie surtout en fonction des taxons. Le comportement territorial est la première forme de compétition intra-spécifique. Il augmente les chances de survie en fragmentant les ressources disponibles (*Optimal feeding territory size* ; Shoener, 1983). Les individus qui ne sont pas cantonnés dans un territoire ne se reproduisent pas et la compétition joue ainsi un rôle de régulateur des populations. Le maintien d’une hiérarchie sociale est également un facteur de compétition intra-spécifique. Il est notamment fréquent chez les mammifères mais aussi chez les insectes. Ainsi, les cohortes plus âgées peuvent détruire de plus jeunes cohortes, limitant leur développement. Enfin, la compétition intra-spécifique pour l’alimentation est une des formes les plus courantes. Elle augmente avec la densité de la population et sa conséquence est la baisse du taux de croissance des populations. Chez les grands mammifères par exemple, cela peut se traduire par une augmentation de l’âge à maturité sexuelle ou la baisse du taux de femelles gravides (Dajoz, 2000).

### *1.2.5 Le concept de communauté d'organismes*

Les premières définitions de la communauté sont nées des études botaniques. En effet, Oosting (1956) définit une communauté comme « une agrégation de plantes vivantes ayant des relations entre elles et avec leur environnement ». Plus récemment, on a introduit dans cette définition les aspects de compétition, de complémentarité et de dépendance (Grubb, 1987). La synthèse de ces deux définitions présente la communauté comme un ensemble d'espèces vivant ensemble dans un environnement ou un habitat commun, et qui interagissent en tant que société. Durant les 60 dernières années, les études en écologie à l'échelle des communautés se sont fortement développées. Elles ont d'abord commencé sur les communautés de végétaux (Lack, 1947) et se sont ensuite étendues à des organismes de plus en plus complexes et inaccessibles comme les grands herbivores (Chapmann & Reiss, 1999) ou encore les prédateurs supérieurs marins (e.g. Ridoux, 1994 ; Cherel *et al.*, 2008 ; Pusineri *et al.*, 2008 ; Gross *et al.*, 2009). Les études des communautés cherchent généralement à comprendre les mécanismes de partage des habitats et des ressources.

### *1.2.6 La communauté à l'échelle intra-spécifique*

L'usage commun dans la littérature du terme de « communauté » réfère généralement à un assemblage d'espèces interagissant entre elles (Roughgarden, 1989). Pourtant, ce terme peut également être employé à l'échelle de l'espèce et se définit alors comme un ensemble d'individus interagissant au sein d'un domaine vital commun (Goodall, 1986 ; Wrangham, 1986). Le domaine vital est une zone habituellement fréquentée par un animal ou un groupe d'animaux (Burt, 1943). Cette nouvelle définition est née des études éthologiques entreprises sur les chimpanzés (*Pan troglodytes*). Chez les delphinidés, le terme de communauté a été employé pour décrire l'existence de groupes de grands dauphins utilisant des domaines vitaux distincts et/ou formant des groupes préférentiellement associés (Wells, 1986 ; Lusseau *et al.*, 2005 ; Urian *et al.*, 2009). Il semblerait que ces communautés ne constituent généralement pas des unités démographiques génétiquement distinctes et les individus peuvent circuler d'une communauté à l'autre au cours du temps (Wells, 1986 ; Connor *et al.*, 2000). Toutefois, les communautés d'individus sont définies par des associations d'individus se caractérisant par des degrés importants de fidélité au site. Ces derniers peuvent être accentués par la philopatrie natale chez les deux sexes (Connor *et al.*, 2000).

### *1.2.7 Ségrégation écologique et compétition chez les prédateurs supérieurs marins*

L’étude de la ségrégation écologique au sein de communautés de prédateurs supérieurs marins est relativement récente. Elle s’est surtout développée dans les années 1990. De manière générale, les situations montrent très souvent que les niches écologiques des espèces vivant en sympatrie diffèrent, notamment sur l’axe de l’alimentation. Toutefois, des études montrent que certains prédateurs peuvent avoir des niches alimentaires très proches. Autour de l’archipel de Crozet (îles françaises subantarctiques), les oiseaux de mer se ségrégent de manière variable en fonction de la niche occupée par une guilde donnée. En effet, les oiseaux plongeurs (manchots, pétrels plongeurs et cormoran) se caractérisent par des indices de chevauchement de niche alimentaire plus importants que les oiseaux se nourrissant en surface (albatros, certains pétrels) (Ridoux, 1994). Les niches alimentaires peuvent être très proches entre certaines espèces (notamment chez les espèces congénères), mais les axes spatiaux et temporels de la niche écologique de ces mêmes espèces peuvent faire intervenir d’autres mécanismes de ségrégation. Ainsi, les individus d’une même guilde ont des niches écologiques distinctes dès qu’elles se nourrissent à des moments différents ou dans des secteurs différents. Les travaux sur le partage des niches écologiques des prédateurs supérieurs marins sont nombreux, notamment depuis le début des années 2000. Ils sont très souvent axés sur les niches alimentaires ou sur l’habitat, mais la dimension temporelle n’est pas systématiquement intégrée. Ceci peut donc induire des interprétations de compétition interspécifique lorsque ce n’est pas nécessairement le cas.

De nombreuses communautés de prédateurs supérieurs marins ont été étudiées sur le plan de la ségrégation écologique, dont les oiseaux (Ridoux, 1994 ; Cherel *et al.*, 2008 ; Jaeger, 2009), les poissons osseux (Potier *et al.*, 2004 ; Ménard *et al.*, 2007), les requins (Estrada *et al.*, 2003 ; Domi *et al.*, 2005) ou encore les mammifères marins (e.g. Das *et al.*, 2003 ; Whitehead *et al.*, 2003 ; MacLeod *et al.*, 2004 ; Zhao *et al.*, 2004 ; Praca, 2008 ; Pusineri *et al.*, 2008 ; Gross *et al.*, 2009).

## 1.2 Questions posées et plan de l’étude

Au sein des communautés, incluant les communautés d’organismes évoluant en sympatrie et les communautés d’individus pour une espèce donnée, il existe des processus de ségrégation écologique permettant une utilisation durable des habitats et des ressources. Chaque espèce doit occuper sa proche niche écologique, définie par trois dimensions : l’habitat, les ressources et les variations temporelles. Le partage d’une même ressource (et d’un même habitat) entrainerait une compétition, que ce soit au sein d’une même espèce (compétition intra-spécifique) ou entre les individus de différentes espèces (compétition interspécifique). La coexistence de plusieurs espèces est assurée si celles-ci ont des niches réalisées qui sont distinctes. Autour de l’île de Mayotte, une grande diversité d’espèces de delphinidés vit en sympatrie au sein d’un espace géographique très restreint. Cet espace est constitué d’une mosaïque d’habitats très marqués, côtiers à océaniques. La présence d’une douzaine d’espèces de delphinidés (dont au moins six tout au long de l’année), ayant des traits morphologiques proches, implique l’existence de processus de ségrégation écologique définis par les trois dimensions de la niche. L’hypothèse principale est que chaque espèce occupe sa proche niche écologique, définie par la combinaison des dimensions d’habitat, de ressources alimentaires et de variations temporelles.

La seconde problématique abordée se focalise ensuite à l’échelle spécifique chez la principale espèce de delphinidé fréquentant les eaux intérieures du lagon de Mayotte : le grand dauphin de l’Indo-Pacifique (*T. aduncus*). Considérant l’existence de processus de ségrégation écologique au sein d’une même espèce, l’hypothèse de l’étude est que le grand dauphin du lagon se ségrége spatialement et forme des communautés distinctes d’individus se partageant les habitats favorables à l’espèce en domaines vitaux propres à chaque communauté, rassemblant des individus qui s’associent préférentiellement. Ceci permettrait une utilisation partagée des habitats et des ressources. Une approche complémentaire visera à déterminer si les grands dauphins ont des stratégies distinctes d’utilisation des ressources, qui pourraient avoir une origine culturelle. Enfin, la dernière hypothèse de ce volet de l’étude est que les communautés sont formées par des individus apparentés, ce qui pourrait confirmer l’origine culturelle de la formation de ces communautés.

Nous nous attacherons d’abord à décrire la communauté de delphinidés et des autres cétacés odontocètes vivant autour de Mayotte. Nous aborderons les aspects de diversité (richesse spécifique, indices de diversité), d’abondance relative et de distribution spatiale (partie 3).

Cette approche descriptive permettra de mieux appréhender les caractéristiques de la communauté de delphinidés présente autour de Mayotte.

Par la suite, nous aborderons l'un des deux axes majeurs de l'étude, à savoir la ségrégation écologique des principales espèces de delphinidés, notamment le dauphin à long bec, le dauphin tacheté pantropical, le grand dauphin de l'Indo-Pacifique mais également (dans une moindre mesure) le péponocéphale et le dauphin de Fraser (partie 4). Nous analyserons la ségrégation écologique des delphinidés selon les trois dimensions de la niche écologique : l'habitat (en relation avec les variables abiotiques de l'environnement), les ressources alimentaires (au travers des traceurs isotopiques du carbone et de l'azote) et le temps (variations saisonnières et diurnes de l'utilisation des habitats et des ressources).

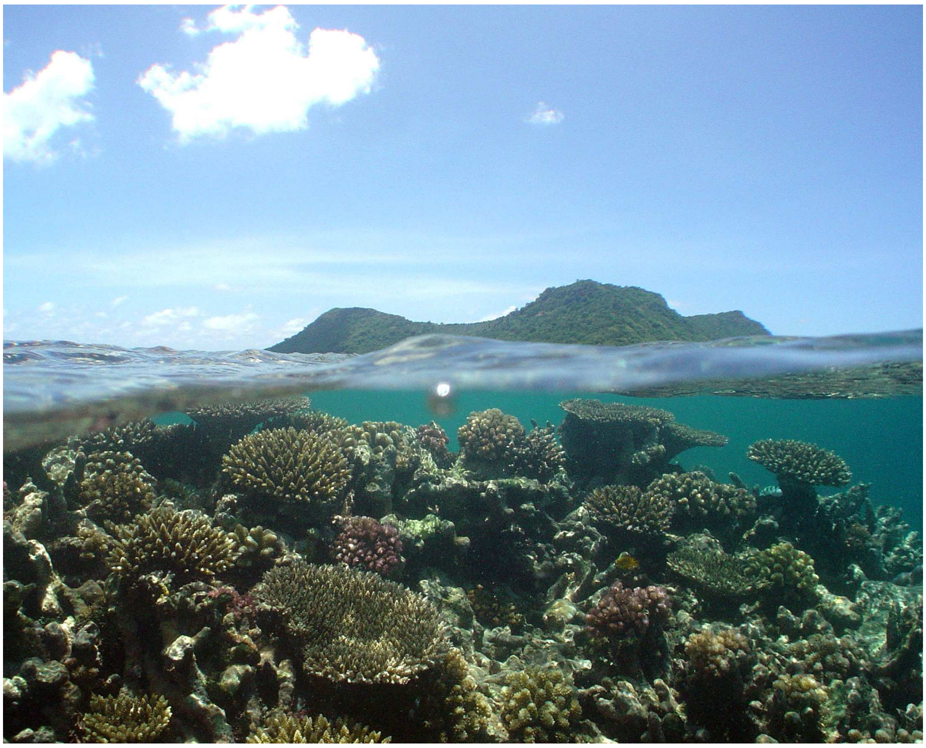
Par ailleurs, nous nous intéresserons à l'un des aspects de l'écologie des delphinidés vivant en sympatrie, à savoir les associations poly-spécifiques (ou interspécifiques). Ces associations semblent de prime abord en opposition avec la théorie des niches puisqu'elles font référence à la présence d'au moins deux espèces sur un même territoire qui parfois utilisent partiellement les mêmes ressources. Trois facteurs majeurs peuvent être à l'origine de la formation d'associations poly-spécifiques : l'utilisation commune d'une ressource, la lutte contre les prédateurs et la pratique des interactions sociales. A Mayotte, les associations entre deux espèces jumelles, le dauphin à long bec et le dauphin tacheté pantropical, sont très fréquentes. Nous tenterons donc de déterminer la signification écologique de la formation de ces associations, puisqu'elles induisent au moins partiellement un usage commun de l'espace et/ou des ressources, et semblent en conséquence opposées au principe de ségrégation compétitive (partie 5).

Pour répondre à la question de ségrégation à l'échelle infra-spécifique, nous étudierons la structure de la population du grand dauphin de l'Indo-Pacifique à travers plusieurs échelles temporelles : de l'échelle évolutive (génétique) à l'échelle de la vie de l'individu (écologie et fonctionnement social ; partie 6). Nous combinerons les approches génétiques et écologiques (utilisation de l'espace et des ressources par les traceurs isotopiques) pour déterminer si la population de Mayotte est structurée (plan génétique) et ségrégée (formation de communautés constituées par des individus partageant un domaine vital commun). Nous tenterons également de répondre à la question de la nature de la structuration des communautés (les communautés formées sont-elles génétiquement distinctes ? Sont-elles constituées par des animaux apparentés ?).

Les quatre principaux chapitres de l'étude seront précédés par une description du site d'étude, des modèles biologiques étudiés et de leur environnement mais également des outils analytiques classiquement utilisés pour appréhender les processus de ségrégation écologique au sein d'une communauté d'organismes, notamment chez les prédateurs supérieurs (partie 2). Enfin, une synthèse des résultats sera effectuée, suivi d'une discussion de ceux-ci et des perspectives de recherche dans ce domaine d'étude (partie 7).

# Partie 2 :

# Site d’étude, matériels et méthodes



## 2.1 Le lagon de Mayotte et ses abords océaniques

### *2.1.1 Caractéristiques générales*

Mayotte (45°10'E, 12°50'S) est une île océanique située dans le nord-est du Canal de Mozambique (sud-ouest de l'océan Indien). Cette île, sous administration française (en cours de départementalisation), fait partie de l'ensemble géographique de l'archipel des Comores. Le territoire a une superficie de 376 km² et se compose de deux îles principales (Petite et Grande Terres). Une trentaine d'îlots d'origine volcanique ou corallienne est distribuée tout autour de l'île. Mayotte est entourée par un complexe récifo-lagonaire d'environ 1500 km², soit l'un des plus vastes au monde et le plus important dans la région occidentale de l'océan Indien. Ce complexe a une largeur variant entre 3 et 15 km et comprend diverses formations récifales : les récifs frangeants, les récifs internes et les récifs barrières. La pente insulaire est très abrupte, parcourue par de nombreux canyons et parsemée de volcans sous-marins (Figure 2.1, 2.2).

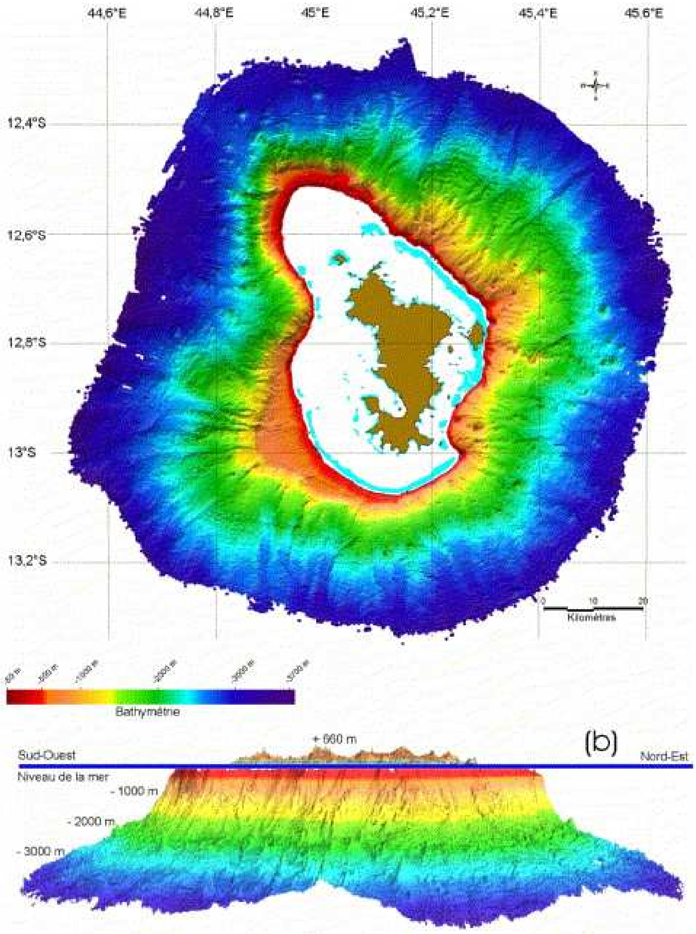


**Figure 2.1 :** Modélisation des fonds sous-marins de Mayotte d'après la bathymétrie du SHOM (Service Hydrographique et Océanographique de la Marine).

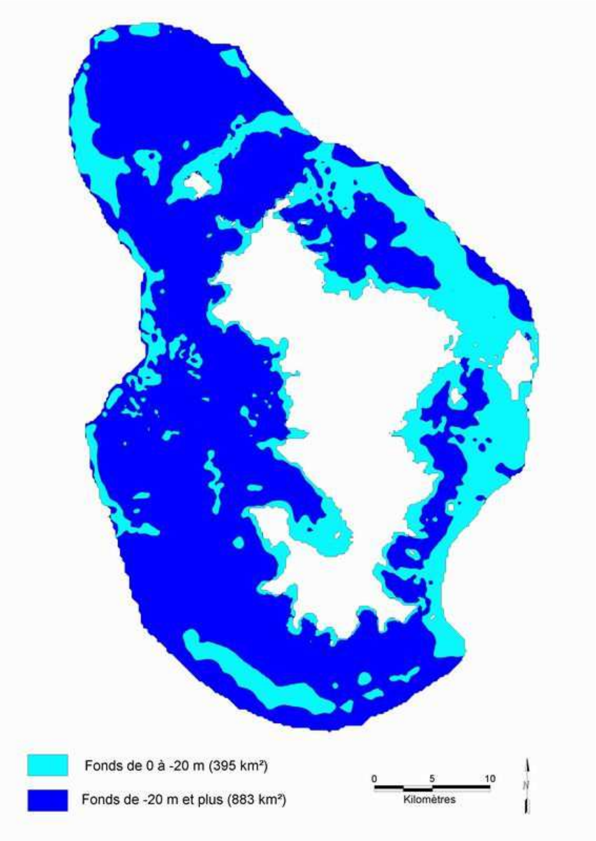


**Figure 2.2 :** Profondeur du lagon de Mayotte (source : BRGM).

### *2.1.2 Climat et écosystèmes marins autour de Mayotte*

Le climat de Mayotte est régi par la Zone de Convergence Intertropicale ; il est de type tropical maritime avec deux saisons contrastées : l’hiver austral (saison sèche, régime d’alizés) et l’été austral (saison humide, régime de mousson). Les saisons intermédiaires sont plus brèves. La température moyenne annuelle de l’air est d’environ 26-27°C et celle des eaux de surface du lagon de 27-28°C. L’humidité dans l’air varie entre 70 et 95 % et les précipitations annuelles oscillent entre 1080 et 2300 mm. A Mayotte, le régime des marées est semi-diurne avec une amplitude d’environ 4 m. Les conditions climatiques sont favorables au développement des récifs coralliens ainsi qu’aux écosystèmes associés comme les mangroves ou les herbiers de phanérogames marines. La géomorphologie générale du lagon résulte du travail simultané de la subsidence (enfoncement de l’île sous son propre poids) d’une part et de la croissance des colonies coralliennes d’autre part. A cela s’ajoutent l’action des aléas érosifs (pluies et rivières à l’origine de la création des passes récifales) et climatologiques (assèchement du lagon lors de la dernière glaciation, il y a environ 20 000 ans). Lorsque l’on évoque l’ensemble des constructions récifales de l’île, on parle alors de complexe récifo-lagonaire (Figure 2.3). Cet immense éco-complexe qui ceinture l’île de Mayotte, comprend plusieurs entités.

- Des récifs frangeants, de 50 à 800 m de large sur 195 km de long, entourent l'ensemble de l'île et des îlots. Ils s'interrompent parfois à l'embouchure des rivières, en fond de baies, et sont alors remplacés par un fond vaseux.
- Un lagon d'une profondeur moyenne de 35 à 40 m peut dépasser par endroits les 80 m. Les fonds du lagon sont plats ou peu accidentés, essentiellement constitués de matériel sédimentaires sablo-vaseux.
- Des récifs internes incluent une double barrière interne au sud-ouest de l'île d'une longueur de 18 km, formée par une subsidence en deux phases. Ce type de formation récifale est très rare puisqu'il n'existe que trois doubles barrières dans le monde.
- Un récif barrière, long de 140 km et large de 800 à 1500 m, présente des zones continues (sud et nord-est) et des zones submergées à des profondeurs variables (nord et ouest). Il est entrecoupé de douze passes récifales majeures.

A ces écosystèmes coralliens se trouvent associés des mangroves et des herbiers de phanérogames marines, constituant également des habitats importants pour le cycle biologique de nombreuses espèces marines et de poissons en particulier.

- Les mangroves, qui s'organisent en bandes de végétation successives parallèles au trait de côte, couvrent environ 735 hectares actuellement et se répartissent tout au long du littoral mahorais. Deux grands types de mangroves se rencontrent autour de l'île : (i) les mangroves « d'estuaires », installées dans les baies où débouchent un ou plusieurs cours d'eau, et (ii) les mangroves de « front de mer » qui forment une ceinture parallèle au rivage. Sept espèces de palétuviers sont recensées à Mayotte.
- Les herbiers de phanérogames marines se développent aussi bien sur les platiers et les pentes du récif frangeant que sur les platiers et pentes internes du récif barrière. Avec 13 espèces recensées, Mayotte constitue un site de haute diversité pour les phanérogames marines. La superficie globale des herbiers de Mayotte est estimée à 760 hectares.

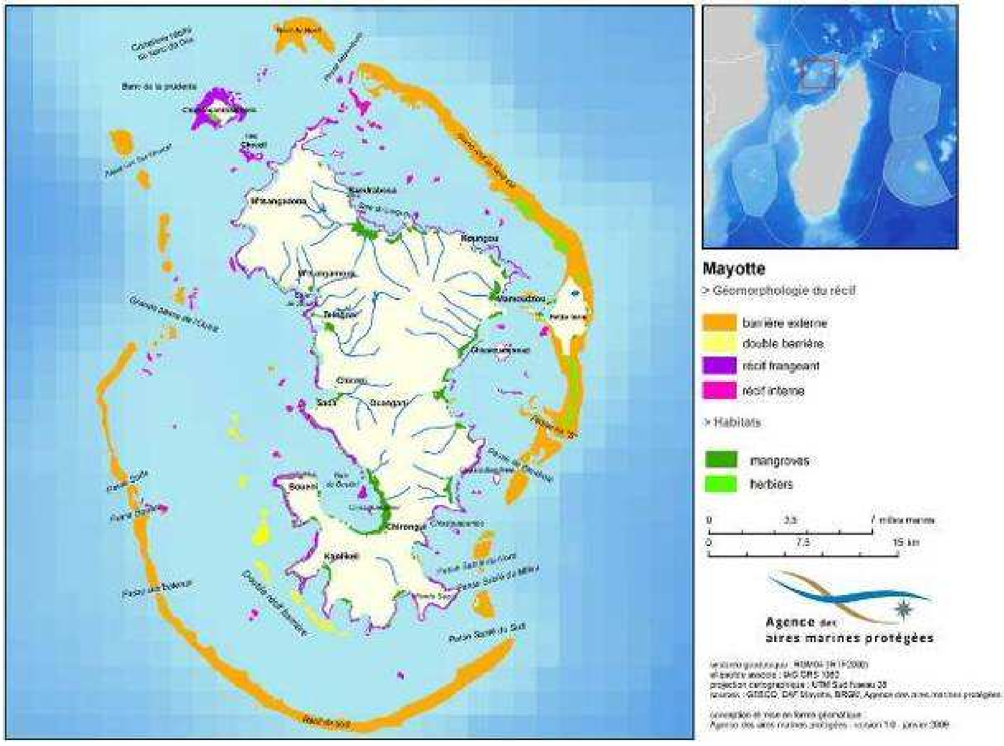


**Figure 2.3 :** Présentation des habitats du complexe récifo-lagonaire de Mayotte (source : Agence des Aires Marines Protégées).

### *2.1.3 Aperçu général de la biodiversité marine*

Le lagon de Mayotte abrite une biodiversité marine importante, incluant plus de 800 espèces de poissons, 300 espèces de coraux durs et mous, 280 espèces d'algues et de plantes marines, 535 espèces de mollusques et 6 espèces de reptiles, par exemple (Direction de l'Agriculture et de la Forêt, LAGONIA et APNEE, données non publiées). Peu d'études approfondies de la biodiversité marine et littorale ont été entreprises à Mayotte et de nombreuses espèces sont susceptibles de fréquenter les abords côtiers et océaniques de l'île.

Parmi la biodiversité marine présente autour de l'île, on retrouve 22 espèces de mammifères marins appartenant à 2 ordres : les siréniens (avec le dugong *Dugong dugon*) et les cétacés (dont 13 delphinidés, deux ziphiidés, deux kogiidés, un physétéridé et trois balénoptéridés ; Kiszka *et al.*, 2007a).

### *2.1.4 Modèles étudiés*

Les delphinidés étudiés à Mayotte sont les espèces fréquentant toute l'année les abords de l'île, que ce soit les eaux intérieures du lagon ou les abords externes de la barrière récifale. Ces espèces sont accessibles du fait de cette présence permanente et de leur forte densité. Les espèces étudiées en détail sont le grand dauphin de l'Indo-Pacifique (*T. aduncus*), le dauphin à long bec (*S. longirostris*), le dauphin tacheté pantropical (*S. attenuata*) et dans une moindre mesure (du fait de leur occurrence plus faible) le péponocéphale (*P. electra*) et le dauphin de Fraser (*L. hosei*). Les traits principaux de la morphologie et de l'écologie de ces espèces sont présentés ci-après.

### 2.1.4.1 Le grand dauphin de l'Indo-Pacifique (*Tursiops aduncus*)

Le grand dauphin de l'Indo-Pacifique est un delphinidé d'environ 240 cm qui peut atteindre 180 kg (Figure 2.4). Il est gris et se caractérise par de nombreuses tâches ventrales qui se développent avec l'âge. Il s'agit d'une espèce typiquement côtière qui se distribue dans l'océan Indien et dans le sud-ouest du Pacifique tropical, subtropical et tempéré chaud.

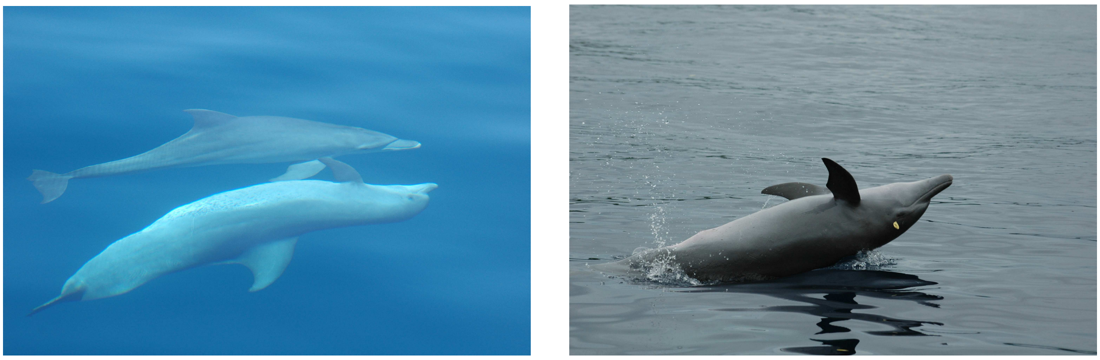


**Figure 2.4 :** Grand dauphin de l'Indo-Pacifique (*T. aduncus*).

Dans le sud-ouest de l'océan Indien, cette espèce est présente de l'Afrique du Sud (notamment le Kwazulu-Natal) à la Mer Rouge (Best, 2007). Dans les îles de cette région, le grand dauphin de l'Indo-Pacifique a été observé tout autour de Madagascar, à La Réunion, à Maurice, aux Seychelles et aux Comores, incluant Mayotte (Kiszka *et al.*, 2007, 2009a). Cette espèce se distribue essentiellement dans des eaux de moins de 30 mètres de profondeur, au moins durant le jour. Cette espèce tend à avoir un domaine vital de taille réduite et est fidèle à certains sites côtiers, comme c'est le cas en Afrique du Sud ou en Tanzanie (Stensland *et al.*, 2006 ; Best, 2007). Toutefois, l'espèce est capable de réaliser des mouvements migratoires de plusieurs centaines de kilomètres le long de côtes (420 km observés entre Algoa Bay et Plettenberg Bay, Afrique du Sud).

Le grand dauphin de l'Indo-Pacifique a un régime alimentaire très varié (poissons, crustacés, céphalopodes), incluant des proies benthiques, démersales et pélagiques associées aux milieux coralliens et aux substrats sableux et vaseux (Amir *et al.*, 2005 ; Best, 2007). Cette espèce chasse à la fois de manière individuelle et en groupe. Les groupes sont souvent de petite taille chez cette espèce (1 à plus de 200 individus). De très grands groupes comprenant plusieurs dizaines à plusieurs centaines d'individus ont été observés en Afrique du Sud. Toutefois, les groupes observés ailleurs comprennent le plus souvent entre 4 et 10 individus. Les rythmes d'activité de cette espèce varient, avec le comportement alimentaire qui prédomine le matin et le soir (Saayman *et al.*, 1973). La structure sociale du grand dauphin de l'Indo-Pacifique est de type « fission-fusion », avec des associations préférentielles entre individus du même sexe. Certaines alliances sont très stables et peuvent durer plus de 15 ans (Connor *et al.*, 2000).

### 2.1.4.2 Le dauphin à long bec (*Stenella longirostris*)

Le dauphin à long bec est une espèce mesurant environ 190 cm qui peut atteindre 60 kg. Il existe plusieurs sous-espèces à travers le monde, mais le type présent dans l'océan Indien est *S. longirostris longirostris*. La pigmentation est tricolore, gris foncé sur le dos, gris clair sur les flancs et blanc à rosâtre sur le ventre (Figure 2.5). L'espèce utilise des habitats diversifiés, puisqu'elle occupe les baies, les zones peu profondes des complexes récifo-lagonaires ou encore la frange externe des récifs barrière la journée pour le repos. La nuit, le dauphin à long bec s'alimente au large dans des secteurs d'environ 1000 m de profondeur. Cette espèce est présente dans toutes les eaux tropicales du monde (Norris *et al.*, 1994).

**Figure 2.5 :** Dauphin à long bec (*S. longirostris*).

Dans le sud-ouest de l'océan Indien, l'espèce est distribuée de l'Afrique du Sud à la Mer Rouge, incluant les îles du sud-ouest de l'océan Indien dont les Comores et Mayotte (Kiszka *et al.*, 2007a, 2009a). L'habitat du dauphin à long bec est très large, de quelques mètres de profondeur à environ 3000 m autour de certaines îles océaniques (Best, 2007). Cette espèce a tendance à former des groupes fidèles à certains sites, comme en zone insulaire où les individus ont des territoires limités au pourtour des îles (Orémus *et al.*, 2008).

Le dauphin à long bec a un régime alimentaire constitué de proies mésopélagiques de moins de 20 cm. Les familles de proies dominantes sont les Myctophidés, les Photichthydés pour les poissons et les Onychoteuthidés pour les céphalopodes. Les crustacés entrent régulièrement dans l'alimentation de cette espèce, en particulier les crevettes des genres *Sergia* et *Pasiphea* (Perrin *et al.*, 1973 ; Norris *et al.*, 1994). Les dauphins à long bec capturent leurs proies durant la nuit à des profondeurs variant entre quelques mètres et 400 mètres. La chasse s'effectue en coopération (notamment par paire) et préférentiellement dans les agrégations denses de proies (Benoit-Bird & Au, 2003). A Mayotte, les groupes de dauphins à long bec sont formés de 4 à 600 individus. La taille moyenne des groupes est d'environ 70 individus (Kiszka *et al.*, 2007). Le dauphin à long bec a surtout une structure sociale de type « fission-fusion », mais cette organisation tend à varier en fonction des zones et de l'isolement géographique. En effet, les groupes isolés tendent à former des associations très stables dans le temps (Karszmarski *et al.*, 2005).

#### 2.1.4.3 Le dauphin tacheté pantropical (*Stenella attenuata*)

Le dauphin tacheté pantropical est une espèce mesurant environ 220 cm qui peut atteindre 90 kg. La pigmentation est gris ardoisé sur le dos et plus claire sur les flancs à rosâtre sur le ventre. Les tâches sont blanches et de plus en plus nombreuses avec l'âge (les jeunes individus n'ont pas de tâches ; Figure 2.6). Le dauphin tacheté pantropical se répartit dans toutes les eaux tropicales et subtropicales du monde, à la fois près des côtes et en pleine mer (Best, 2007). Les formes côtières et océaniques de cette espèce sont morphologiquement distinctes. Cette espèce est largement répandue dans l'ensemble du sud-ouest de l'océan Indien (Kiszka *et al.*, 2009a).

**Figure 2.6 :** Dauphin tacheté pantropical (*S. attenuata*).

Le dauphin tacheté pantropical consomme essentiellement des poissons et des céphalopodes épi- à mésopélagiques. Les proies de surface sont surtout consommées le jour alors que les proies mésopélagiques sont consommées durant leurs remontées nycthémérales. A Mayotte, cette espèce a été très régulièrement observée de jour s'alimenter de poissons volants (Exoceatidae). Les groupes de dauphins tachetés pantropicaux peuvent atteindre le millier d'individus (à Mayotte seulement 300 individus au maximum, et 70 en moyenne). Cette espèce est très souvent associée au dauphin à long bec ainsi que d'autres espèces comme le thon jaune (*Thunnus albacares*) et plusieurs espèces d'oiseaux marins.

La structure sociale du dauphin tacheté pantropical n'est pas connue, mais les groupes semblent souvent ségrégés par classe d'âge et de sexe (groupes de femelles avec jeunes, groupes de subadultes, etc.).

### 2.1.4.4 Le péponocéphale (*Peponocephala electra*)

Le péponocéphale (ou dauphin d'Electre) est un delphinidé, de la sous-famille des globicéphalinés, qui peut atteindre 260 cm pour un poids de 180 kg (adulte). Le dimorphisme sexuel est peu prononcé. La pigmentation est noire et un peu plus claire sur le ventre, les lèvres sont blanchâtres (Figure 2.7). Le péponocéphale est un delphinidé océanique réparti dans toutes les eaux tropicales et subtropicales du monde (Jefferson *et al.*, 2008). Dans le sud-ouest de l'océan Indien, cette espèce est fréquente, notamment autour des îles océaniques où les côtes (ou les barrières récifales) sont proches du domaine océanique. Cette espèce est rencontrée essentiellement dans des eaux de plus de 500 m de profondeur, mais dans certaines zones comme à Mayotte, elle peut être observée au repos dans des eaux de 100 m de profondeur.

**Figure 2.7 :** Péponocéphale (*P. electra*).

Peu d'information existent sur l'écologie alimentaire du péponocéphale. Toutefois, les céphalopodes mésopélagiques (Ommastrephidae, Onychoteuthidae, Chirotheutidae, Mastigoteuthidae, Cranchidae) et dans une moindre mesure les poissons (Myctophidae, Paralepididae, Scopelarchidae) semblent constituer l'essentiel de l'alimentation de cette espèce (Brownell *et al.*, 2009). Le péponocéphale s'alimente essentiellement la nuit dans les premiers 700 mètres depuis la surface (Young, 1978).

Les groupes de péponocéphales peuvent atteindre un millier d'individus, mais comptent typiquement entre 200 et 600 animaux (Best, 2007 ; Kiszka *et al.*, 2007). Aucune information n'est disponible sur la structure sociale de cette espèce.

### 2.1.4.5 Le dauphin de Fraser (*Lagenodelphis hosei*)

Le dauphin de Fraser est un delphinidé océanique qui peut atteindre 260 cm pour un poids de 210 kg. La pigmentation est très variable en fonction de l'âge et du sexe (Figure 2.8). Le dos est grisâtre et le ventre blanchâtre à rosâtre. Les mâles adultes se caractérisent par une bande noire qui part de l'œil et qui aboutit à la région anale. Cette bande est grisâtre chez les femelles. L'espèce vit essentiellement loin des côtes dans les zones tropicales et subtropicales. Elle a été régulièrement observée dans le sud-ouest de l'océan Indien, notamment à La Réunion, à Madagascar mais également aux Comores et à Mayotte (Best, 2007 ; Kiszka *et al.*, 2007a, 2010).

**Figure 2.8 :** Dauphin de Fraser (mâle et femelle, respectivement ; *L. hosei*).

Le dauphin de Fraser est généralement observé au-delà du domaine néritique et du plateau continental, dans des eaux de plus de 500 m. Les études de contenus stomacaux de dauphins de Fraser indiquent que cette espèce se nourrit de poissons et de céphalopodes mésopélagiques de grande taille jusqu'à une profondeur de 600 m (Robison & Craddock, 1983; Dolar *et al.*, 2003). Il s'agirait essentiellement d'un prédateur nocturne, bien qu'observé en alimentation sur des proies de surface en pleine journée. Aucune information sur la structure sociale de cette espèce n'est disponible.

## 2.2 Approche méthodologique de l'étude de la ségrégation écologique

Les études sur la ségrégation écologique de communautés d'espèces, qu'elles soient terrestres ou marines, utilisent des techniques similaires. La plus ancienne est l'étude comparée des habitats préférentiels. Cette approche utilise des observations *in situ* et les corrèlent avec les variables de l'environnement, qu'elles soient physiographiques (profondeur, inclinaison de la pente sous-marine) ou biotiques (production primaire, distribution et densité des proies). Actuellement, la modélisation (modèles de présence ou de présence-absence ; ENFA[1], ACP[2] ou GLM/GAM[3], respectivement) est très couramment employée pour caractériser les habitats préférentiels (e.g. Cañadas *et al.*, 2002 ; Praca & Gannier, 2008). Un modèle d'habitat vise à établir une relation quantitative entre la distribution d'une espèce et un certain nombre de variables environnementales. Toutefois, la ségrégation des niches écologiques ne peut être étudiée en détail uniquement par la dimension de l'habitat. La niche alimentaire est un axe majeur de la niche écologique.

La méthode la plus ancienne et la plus couramment utilisée est l'étude comparée de l'alimentation par l'analyse des contenus stomacaux. Le calcul d'indices de chevauchement permet d'évaluer les interactions écologiques (le calcul des indices de Simpson et de Pianka, par exemple ; Dajoz, 2000). Chez les prédateurs marins, cette approche a été entreprise pour de nombreuses communautés comme les oiseaux marins subantarctiques (Ridoux, 1994), les grands poissons océaniques de l'océan Indien occidental (Potier *et al.*, 2004) ou encore la communauté de prédateurs supérieurs du golfe de Gascogne (Pusineri *et al.*, 2008). Cette méthode introduit un certain nombre de biais car les contenus stomacaux reflètent l'alimentation à très court terme (derniers repas). Par ailleurs, les différentes pièces utilisées pour l'identification de proies (bec de céphalopode, céphalothorax de crustacé ou otolite de poisson) s'érodent de manière différente lors de la digestion. D'autres approches à plus long terme peuvent alors être employées. Il s'agit des éléments traces (métaux lourds comme le mercure, le cadmium, par exemple), des polluants organiques persistants, des acides gras ou encore des isotopes stables. Les contaminants peuvent révéler la présence de groupes de prédateurs écologiquement distincts utilisant des ressources et des habitats différents, ceci

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[1] *Ecological Niche Factor Analysis* (Analyse Factorielle des Niches Ecologiques).

[2] Analyse en Composante Principale.

[3] Modèles Linéaire Généralisés/Modèles Additifs Généralisés.

étant lié à des différences de contamination des différents taxons et des habitats d'alimentation des prédateurs (Lahaye *et al.*, 2005 ; Borrell *et al.*, 2006). Les isotopes stables du carbone ($\delta^{13}C$) et de l'azote ($\delta^{15}N$) fournissent une bonne alternative à l'étude de l'écologie alimentaire et des relations trophiques au sein d'une communauté. Les rapports isotopiques du carbone et de l'azote d'un consommateur reflètent ceux de son alimentation (Hobson, 1999). Le $\delta^{15}N$ renseigne sur le niveau trophique (enrichissement d'environ 3 ‰ par niveau trophique) et le $\delta^{13}C$ renseigne sur les habitats d'alimentation (enrichissement de 1 ‰ par niveau trophique ; Hobson, 1999). L'étude des relations trophiques d'organismes de nombreuses communautés de prédateurs marins supérieurs a été étudiée, comme chez les pinnipèdes (Zhao *et al.*, 2004), les oiseaux marins (Cherel *et al.*, 2008), les grands poissons osseux (Ménard *et al.*, 2007), les requins (Domi *et al.*, 2005) ou encore les delphinidés (Gross *et al.*, 2009).

### 2.3 Analyse des données dans le cadre de la thèse

Dans le cadre de ce travail, plusieurs méthodes ont été combinées pour étudier la ségrégation écologique de la communauté de delphinidés tropicaux de Mayotte. Nous avons également étudié la structure de population à fine échelle et la ségrégation intra-spécifique chez le grand dauphin de l'Indo-Pacifique. Dans les deux cas, certaines analyses n'ont pu être réalisées comme l'étude des contenus stomacaux. Les échouages et les captures accidentelles sont très rares à Mayotte, ne permettant pas d'analyses détaillées de l'alimentation des différentes espèces.

Pour explorer la ségrégation écologique au niveau des trois axes de la niche écologique, trois méthodes ont été combinées :

- l'étude de l'habitat préférentiel des principales espèces et la comparaison des habitats en relation avec certaines variables physiographiques (profondeur, pente, distance à la côte et aux récifs coralliens). Une approche en considérant uniquement les données de présence a été privilégiée en raison de l'hétérogénéité de l'effort d'observation autour de Mayotte. Le détail des analyses est décrit dans la partie 4.
- l'étude du partage des ressources par l'analyse des signatures isotopiques du carbone et de l'azote ($\delta^{15}N$ et $\delta^{13}C$) dans la peau et le lard des dauphins. Pour cela et du fait de l'absence d'autres sources de matériel biologique, des biopsies ont été réalisées à l'aide d'une arbalète propulsant une fléchette munie d'un petit emporte-pièce (Figure 2.9). Le détail de la méthode de prélèvement et des analyses isotopiques est décrit

dans la partie 4, tandis que l'impact de ce mode d'échantillonnage sur les animaux est évalué en annexe 2.

- l'étude des variations temporelles des budgets d'activités (collectés à l'occasion de suivis focaux tout au long de la journée et en toute saison, Figure 2.9), de l'habitat et des signatures isotopiques des delphinidés. Cette approche a pu être entreprise du fait de la bonne accessibilité des principales espèces de la communauté de delphinidés de Mayotte permettant la mise en œuvre des méthodes de suivi focal (détail dans la partie 4).

Enfin, l'étude de la ségrégation à l'échelle intra-spécifique, de la structure de population à fine échelle et du fonctionnement social chez le grand dauphin de l'Indo-Pacifique (partie 6) a été étudiée par combinaison :

- d'analyses génétiques (structure de population, liens de parenté),
- de l'étude des associations préférentielles (qui révèlent la structure sociale),
- de l'étude du domaine vital et de l'habitat à l'échelle individuelle,
- et de l'étude de la ségrégation écologique, à la fois sur le plan de l'habitat mais aussi des ressources par l'analyse des signatures isotopiques du carbone et de l'azote ($\delta^{15}N$ et $\delta^{13}C$) dans la peau et le lard des dauphins.

Toutes les données ont été collectées toute l'année autour de Mayotte entre juillet 2004 et avril 2009. Des parcours côtiers non systématiques ont été réalisés avec de petites embarcations et les sessions de terrain consistaient à collecter :

- des séries d'observations de delphinidés (et autres cétacés) pouvant être pondérées avec l'effort d'observation,
- des données sur les caractéristiques des groupes (taille, composition, structure),
- des données comportementales pour l'étude des budgets d'activités,
- des biopsies de peau et de lard pour les analyses génétiques et isotopiques,
- des données de photo-identification, tout particulièrement pour le grand dauphin de l'Indo-Pacifique (étude de la structure sociale, du domaine vital, etc.).

**Figure 2.9 :** Prélèvement par biopsie (gauche) et suivi focal d’un groupe de dauphins (droite).

L’ensemble des détails méthodologiques est donné dans les différents articles, que ce soit pour la collecte ou pour l’analyse des données.

# Partie 3 :

# Diversité et structure de la communauté

# Structure de la communauté de cétacés odontocètes de Mayotte

## Résumé

Caractériser une communauté biologique est une étape importante pour la compréhension de la composition d'un écosystème, de sa dynamique et de son évolution. La description des communautés de cétacés tropicaux a peu été entreprise par le passé. Dans cette étude, nous présentons une description de la structure d'une communauté de cétacés odontocètes autour de l'île de Mayotte, dans le sud-ouest de l'océan Indien (45°10'E, 12°50'S). A partir de campagnes en mer à bord de petites embarcations conduites entre juillet 2004 et juin 2006, 16 espèces d'odontocètes ont été recensés. L'indice de diversité de Shannon était tout particulièrement élevé le long de la pente externe du récif barrière. La distribution spatiale des différentes espèces met en évidence l'existence de trois grandes catégories d'habitats pour les cétacés odontocètes autour de Mayotte : les eaux intérieures du lagon (*T. aduncus*, *S. chinensis*), les abords de la pente externe du récif barrière (*S. longirostris*, *S. attenuata*, *P. electra*) et les zones océaniques et de pente de plus de 500 mètres de profondeur (*M. densirostris*, par exemple). Les caractéristiques des groupes, comme leur taille, varient significativement en fonction des espèces. Les petits delphinidés océaniques ont les tailles de groupe plus importantes que les espèces strictement côtières ou que les espèces n'appartenant pas à la famille des delphinidés. D'après les résultats de l'étude, il semble que les eaux de la pente externe de la barrière récifale constituent un habitat privilégié pour les delphinidés tropicaux. Ceci met en évidence la dépendance de ces espèces aux complexes récifaux. Le nombre important d'espèces de delphinidés suggère l'existence de processus de ségrégation écologique qui doit être étudié à l'avenir.

# Structure of a toothed cetacean community around a tropical island (Mayotte Island, Mozambique Channel)

Jeremy Kiszka [1, 2, 4 *], Peter J. Ersts [3] & Vincent Ridoux [1]

[1] LIENSs (LIttoral, ENvironnement et Sociétés), UMR 6250, CNRS-Université de La Rochelle, 2, rue Olympe de Gouges, F-17000, La Rochelle, France.
[2] Direction de l'Environnement et du Développement Durable, Collectivité Départementale de Mayotte. BP 101 F-97600 Mamoudzou, Mayotte.
[3] Center for Biodiversity and Conservation, American Museum of Natural History, Central Park West at 79th Street, New York, New York, 10024 USA.
[4] Past affiliation: Observatoire des Mammifères Marins. Direction de l'Agriculture et de la Forêt & Office National de la Chasse et de la Faune Sauvage. BP 103, 97600 Mamoudzou, Mayotte.

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## Abstract

Characterizing biological communities is an important step to assess ecosystem composition, dynamics, and evolution. The description of tropical cetacean communities has been poorly investigated. Here we present a description of the structure of a toothed cetacean community around the island of Mayotte (SW Indian Ocean, 45°10'E, 12°50'S). From small boat-based surveys conducted from July 2004 to June 2006, 16 odontocete species were recorded. Index of diversity (Shannon-Weaver) is particularly high along the outer slope of the barrier reef. Patterns of spatial distribution underline the existence of three main cetacean habitat types: the inner lagoon (*T. aduncus*, *S. chinensis*), the outer reef slope (*S. longirostris*, *S. attenuata*, *P. electra*) and oceanic waters deeper than 500 m (*M. densirostris*, for example). Group characteristics are highly variable among species, with oceanic small delphinids having higher group sizes than strictly coastal and non-delphinid oceanic species. Based on our results, it is evident that the outer slope of the barrier reef is of primary importance in terms of density and diversity of odontocetes around Mayotte. These data also support the hypothesis that a number of cetacean species, especially several delphinid species, are dependant to coral reef complexes. The high number of species living in sympatry suggests some fine-scale niche segregation processes that need to be further assessed.

**Keywords:** cetaceans, odontocetes, community composition, distribution, encounter rates, barrier reef slope, Mayotte, Indian Ocean.

## Introduction

Characterizing biological communities is an important part of assessing ecosystem composition, dynamics, and evolution. A community can be defined as a collection of species that occur together in some common environment, or habitat, and that the organisms making up the community are somehow integrated or interact as a society (Chapman & Reiss, 1999). Distribution, diversity and group characteristics of cetacean communities have been described from polar to tropical waters in a variety of marine ecosystems (e.g., coastal, slope-associated and oceanic, etc.), including in the Antarctic (Thiele *et al.*, 2000), the Mediterranean Sea (Gannier, 2005), off the Bahamas (MacLeod *et al.*, 2004), the Gulf of Mexico (Maze-Foley & Mullin, 2006), the southwest Atlantic (Moreno *et al.*, 2005) and in French Polynesia (Gannier, 2000, 2002). These studies have been conducted at the scale of oceanic basins, regions and archipelagos and show that species partition their habitat according to a number of abiotic and biotic environmental variables, such as physiography and primary production. Most cetacean habitat studies find that depth is one of the primary environmental features explaining cetacean distribution (see for example Cañadas *et al*., 2002).

Few studies have examined cetacean community structure around tropical islands and atolls (MacLeod *et al.*, 2004; Anderson, 2005; Dulau-Drouot *et al.*, 2008; Hermans & Pistorius, 2008). In the waters surrounding Great Abaco Island, in the Bahamas, few cetacean species are encountered and the limited number of species at low abundance observed there has been attributed to the low-productive tropical waters (MacLeod *et al.*, 2004). In the western Indian Ocean, cetacean communities found at Aldabra atoll (southern Seychelles; Hermans & Pistorius, 2008), off the west coast La Réunion, in the Mascarenes (Dulau-Drouot *et al.*, 2008), and at a larger regional scale of the western Indian Ocean (Ballance & Pitman, 1998), have been described in terms of diversity and habitat. Around these western Indian Ocean islands, cetacean communities are largely dominated by small delphinids that are resident year-round with the spinner dolphin (*Stenella longirostris*) being the most common species (Kiszka *et al.*, 2009). The western Indian Ocean is also used by large mysticetes, especially by humpback whales (*Megaptera novaeangliae*) during the austral winter when breeding and calving occur (Dawbin, 1966).

When comparing communities from ocean basin or regional scales to local (insular or archipelago) scales, oceanic tropical islands appear to constitute areas of particular diversity and density of top predators, such as cetaceans (Gannier, 2000, 2002; Baird *et al.*, 2003). Similar to continental margins, where land plunges to the deep oceanic waters, insular slopes potentially provide more abundant resources and perform essential functions such as nutrient cycling (Levin & Dayton, 2009). Turbulence and vertical mixing in island channels are believed to create nutrient-rich conditions around archipelagos (Gilmartin & Revelante, 1974). The formation of these isolated nutrient-rich regions, especially in the oligotrophic regimes of the tropics where ocean productivity is generally low, is the primary reasons why islands and archipelagos can be “oases” of biodiversity. These oases are of critical importance for conservation and management actions that require examination over a range of spatial and temporal scales.

Around the Mozambique Channel island of Mayotte (in the eastern Comoros archipelago), a diverse cetacean community has been recorded (Kiszka *et al.*, 2007a). The island of Mayotte is characterised by diverse ecosystems in close proximity to each other, i.e. mangroves, fringing reefs, a large semi-closed lagoon, barrier and double barrier reef systems, and deep oceanic waters within a few kilometres from shore (Quod *et al.*, 2000). To date, 17 species of cetaceans have been recorded in the waters surrounding Mayotte (Kiszka *et al.*, 2007a). This community is mostly composed by delphinids but also includes large odontocetes (e.g., ziphiids, kogiids, physeterids), blue (*Balaenoptera musculus*) and humpback whales. Although some of the species recorded are rare, all of them (except humpback whales) are present year-round. As there is a growing need to identify critical areas for marine biodiversity, both locally and regionally, this paper provides much needed data describing the general structure of the odontocete community encountered around the island of Mayotte. We will present the diversity of species living in the surrounding waters of the island in relation to the main habitat types. The spatial distribution and encounter rates of the most common species will be also detailed.

## Materials and methods

### Study area

Mayotte (45$^{o}$10’E, 12$^{o}$50’S) is situated in the northern Mozambique Channel and is part of the Comoros archipelago (Figure 3.1). Mayotte is almost entirely surrounded by a 197 km long barrier reef, with a second double-barrier in the southwest and the immerged reef complex of Iris in the northwest. There are a series of deep passes through the reefs, some of which are the sites of old rivers (Quod *et al.*, 2000). The lagoon and surrounding reef complexes is 1,500 km² with an average depth of 20 m and a maximum depth of 80 m found in the western, older, region of the lagoon. Some 20 small islets are present in the lagoon, ranging from one to 242 ha, which are also surrounded by fringing reefs. Approximately 670 ha of mangrove forests occur around the main island, especially in protected bays (Quod *et al.*, 2000). The insular slope on the exterior of the barrier reef is very steep and contains many submarine canyons. Broad canyons with numerous volcanoes and landslides deeply incise the slope (Audru *et al.*, 2006).

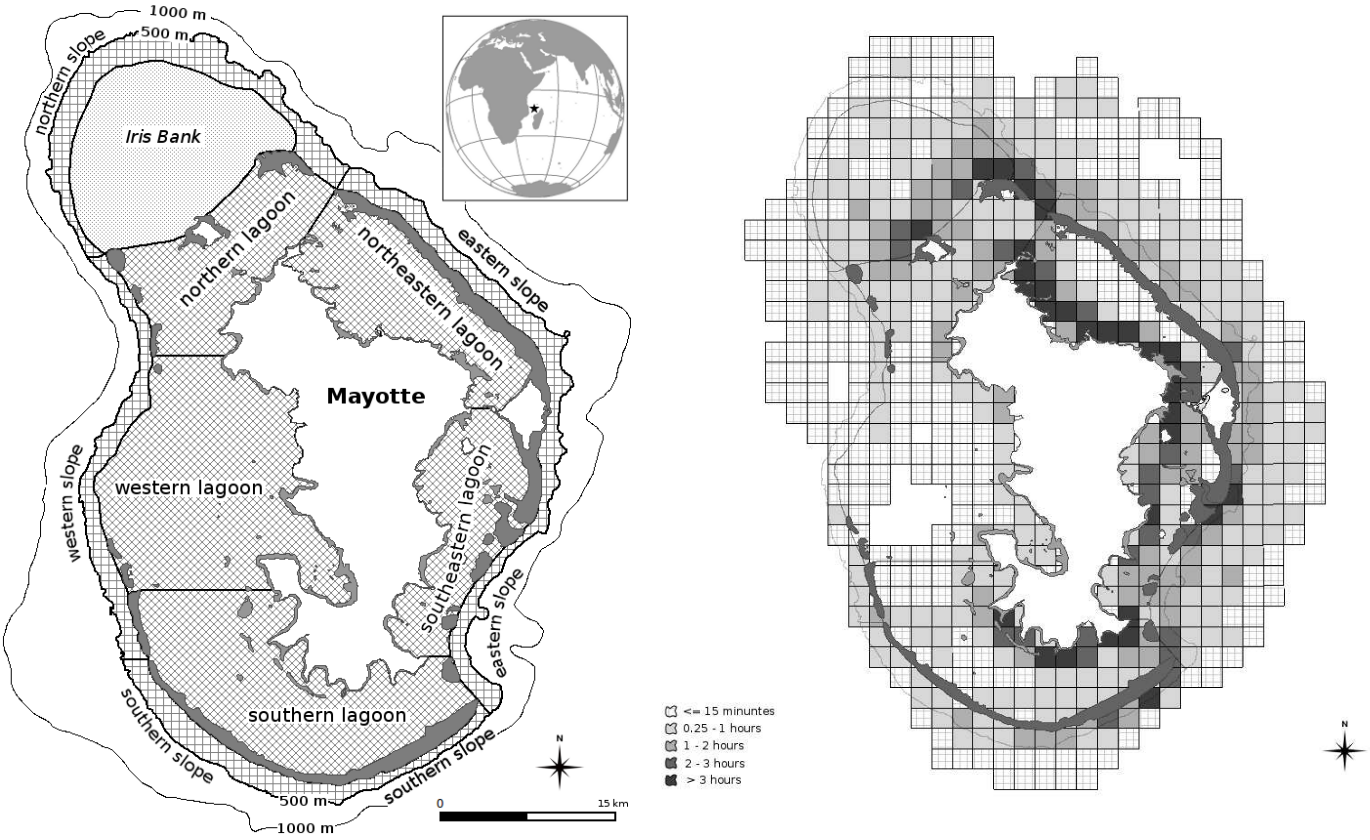

**Figure 3.1:** Sub-areas defined for encounter rate calculations around Mayotte and spatial representation of searching effort from July 2004 to June 2006.

Data collection

From July 2004 to June 2006, small boat based surveys were undertaken in the surrounding waters of Mayotte. Several types of boats were used: a 7 meter catamaran equipped with two, four-stroke, 60-hp outboard engines; a 7 meter boat equipped with two, two-stroke, 40-hp outboard engines; a 6.4 meter cabin boat equipped with one, four-stroke, and 150-hp outboard engine. Surveys were conducted throughout the study period during daylight hours between 07:00h and 18:00h in sea conditions not exceeding Beaufort 3. Survey vessels did not follow pre-defined transects but every attempt was made to sample each habitat type within the surrounding waters of Mayotte, i.e. coastal areas (mangrove fronts, fringing reef), lagoonal waters, barrier reef associated areas (inner and outer slopes) and oceanic/slope waters (> 500 m). Constant GPS logging was used to collect geographic positions every 5 seconds from departure to return to the harbour using a hand-GPS *Garmin Gecko*®. When cetaceans were encountered, standard sighting data were recorded; species, group size (maximum, minimum, best estimate) and geographic position were collected for all encounters. For small aggregations of cetaceans, group size was defined as the number of animals at the surface within five body lengths of each other (Smolker *et al*., 1992). Large aggregations of small delphinids often consisted of a super group, comprised of several smaller animal units or aggregations (typically 2 to 20), spaced several dozen meters apart, moving in the same direction and exhibiting similar patterns of behaviour. For these large aggregations, group size reflects the size of the super group not the individual aggregations.

Data analysis

Only data for odontocetes were used in this study. Eight geographic zones were defined around the island based on their general location and environmental characteristics (Figure 3.1, Table 3.2). These eight geographic zones were grouped into three broad habitat categories to assess cetacean diversity for each habitat type, 1) inner lagoon, 2) outer reef slope (depth < 500 m) and 3) oceanic waters (depth > 500 m). Encounter rate was defined as the number of sightings per unit of effort (N sightings/effort), expressed in hours. Diversity of species was measured through two measures: species richness (R) and the Shannon-Weaver index (S). Species richness (number of species) misses the information that some species are rare and others common. A community with “equitable” distribution of abundances is more diverse that a community with variable specific abundances (Begon *et al.*, 2009). The Shannon-Weaver index is one of several diversity indices used to measure diversity in categorical data. It is the information entropy of the distribution, treating species as symbols and their relative population sizes as the probability. This diversity measure came from information theory and measures the order (or disorder) observed within a particular system. In ecological studies, this order is characterized by the number of individuals observed for each species in the sample plot. It is calculated as follow:

$$H = -\sum_{i=1}^{S} Pi \ln Pi$$

where $Pi$ is the relative abundance of each species. Shannon-Weaver index was calculated for the whole study area and for each of the three broad habitat categories.

Values of the median, minimum, and interquartile ranges of depth are provided to describe bathymetric preferences for each species. Depth data were provided by *Service Hydrographique et Océanographique de la Marine*. Depth data were associated with each sighting location using an overlay technique in a GIS. GPS track data was downloaded, interpolated to provide a track point for each second and then post processed to isolate portions of track spent "on effort", which were subsequently used to calculate the effort within each 2 km square and geographic zone (Table 3.2, Figure 3.2).

**Results**

General

From July 2004 to June 2006, more than 441 hours were spent in "search mode" actively searching for marine mammals around Mayotte. Search effort did not vary across months and years (among four periods over the two years and the rain/dry season, H = 4.167; *df* = 3: *P* = 0.244). As the main harbour is located on the northeast coast, the observation effort was greater off the east coast, in the south and in the north. The western portion of the lagoon and deep oceanic waters were less surveyed (Table 3.1, Figure 3.1).

Melon-headed whales, pantropical spotted and spinner dolphins had the largest group sizes (mean=287.8, mean=70.9 and 72.8, respectively, Table 1), and were frequently encountered on the outer reef slope. Indo-Pacific humpback (mean=2.4) and bottlenose dolphins (mean=6.5), the most coastal species, had the smallest group size (Table 3.2).

Diversity and distribution

During this study, 16 odontocete species were recorded, including 11 *Delphinidae* belonging to 9 genera, two *Ziphiidae*, two *Kogidae* and one *Physeteridae* (Table 3.1). The Shannon-Weaver index of diversity is 1.76 for the whole study area, while it varied among geographic zones: 0.57 for the inner lagoon (4 species recorded), 1.31 for the outer reef slope (<500 m in depth, 5 species) and 0.62 for the oceanic waters (>500 m in depth, 12 species). Higher index for the outer reef slope area is due to balanced abundances of species. Conversely, in oceanic waters, high variability of abundances of species (reflected through group size) are less balanced (high group size in delphinids *vs*. low in the largest toothed whales), making the index decreasing. Spatial distribution of cetaceans encountered around Mayotte was highly variable. Spinner and pantropical spotted dolphins had similar distributions along the outer reef slope and on the Iris bank and were rarely observed inside the lagoon (Figure 3.2). Indo-Pacific bottlenose and humpback dolphins were primarily observed inside the lagoon. Indo-

Pacific bottlenose dolphins were also regularly observed on the Iris bank, in waters less than 40 m deep (Figure 3.3a, Table 3.3). Melon-headed whales were observed on the outer reef slope area and in the shallower waters of the Iris bank, but were never sighted inside the lagoon (Table 3.1 and 3.3, Figure 3.3b).

**Table 3.1:** Sighting (number, cumulated number of individuals) and group size characteristics of cetaceans encountered around Mayotte from July 2004 to June 2006.

| Species | N sightings | % sightings | N individuals (cumulate) | % cumulated individuals | Mean group size | Range | SD |
|---|---|---|---|---|---|---|---|
| *Stenella longirostris* | 177 | 48.5 | 9,242 | 59.7 | 72.8 | 3-500 | 87.1 |
| *Stenella attenuata* | 85 | 23.3 | 2,553 | 16.5 | 70.9 | 3-300 | 71.9 |
| *Tursiops aduncus* | 64 | 17.5 | 414 | 2.7 | 6.5 | 1-15 | 3.5 |
| *Peponocephala electra* | 9 | 2.5 | 2,590 | 16.7 | 287.8 | 140-450 | 84.2 |
| *Sousa chinensis* | 7 | 1.9 | 17 | 0.1 | 2.4 | 1-3 | 0.8 |
| *Mesoplodon densirostris* | 6 | 1.6 | 14 | 0.1 | 2.3 | 1-5 | 1.6 |
| *Grampus griseus* | 5 | 1.4 | 44 | 0.3 | 8.8 | 2-20 | 6.8 |
| *Tursiops truncatus* | 2 | 0.5 | 160 | 1 | 80 | 40-120 | - |
| *Pseudorca crassidens* | 2 | 0.5 | 250 | 1.6 | 125 | 100-150 | - |
| *Kogia sima* | 2 | 0.5 | 3 | 0.01 | 1.5 | 1-3 | - |
| *Kogia breviceps* | 1 | 0.3 | 6 | 0.03 | 6 | - | - |
| *Mesoplodon pacificus* | 1 | 0.3 | 1 | 0.006 | 1 | - | - |
| *Physeter macrocephalus* | 1 | 0.3 | 11 | 0.07 | 11 | - | - |
| *Globicephala macrorhynchus* | 1 | 0.3 | 60 | 0.4 | 60 | - | - |
| *Lagenodelphis hosei* | 1 | 0.3 | 120 | 0.8 | 120 | - | - |
| *Feresa attenuata* | 1 | 0.3 | 4 | 0.03 | 4 | - | - |
| TOTAL | 365 | 100 | 15,489 | 100 | 53.8 | 1-500 | |

The remaining delphinids were oceanic species observed further offshore, which included common bottlenose dolphin (mean depth at encounter, MDE=509 m), Risso's dolphin (MDE=1,150), Fraser's dolphin (MDE=336 m), false killer whale (MDE=1,168 m), short-finned pilot whale (MDE=996 m) and pygmy killer whale (MDE=1,593 m, Figure 3.3b). While rarely encountered, larger toothed whales, Blainville's beaked whale (Table 3), pygmy sperm whale (MDE=705 m), dwarf sperm whale (MDE=919 m) and Longman's beaked whale (MDE=1,945 m), were also observed in deep waters off the barrier reef over the slope (Figure 3.3c).

**Table 3.2:** Searching effort (in hours), number of sightings and encounter rates (ER) of cetaceans encountered around Mayotte from July 2004 to June 2006.

| Geographic Zone | Effort (hours) | *Tursiops/ Sousa* (ER) | *Stenella longirostris* (ER) | *Stenella attenuata* (ER) | *Peponoce. electra* (ER) | L. toothed whales (ER) | Other Delphinids (ER) |
|---|---|---|---|---|---|---|---|
| Eastern slope | 48.2 | 0 | 50<br>(1.04) | 19<br>(0.39) | 2<br>(0.04) | 0 | 0 |
| Iris | 46 | 10<br>(0.22) | 40<br>(0.87) | 20<br>(0.43) | 1<br>(0.02) | 0 | 0 |
| North-eastern lagoon | 75.7 | 12/3<br>(0.2) | 0 | 1<br>(0.01) | 0 | 0 | 0 |
| Northern slope | 14.4 | 0 | 6<br>(0.42) | 2<br>(0.14) | 0 | 0 | 1<br>(0.07) |
| Northern lagoon | 32.5 | 6<br>(0.18) | 13<br>(0.4) | 3<br>(0.09) | 0 | 0 | 0 |
| South-eastern lagoon | 52.6 | 12/2<br>(0.25) | 2<br>(0.04) | 2<br>(0.04) | 0 | 0 | 0 |
| Southern slope | 23.7 | 0/1<br>(0.04) | 46<br>(1.94) | 22<br>(0.93) | 0 | 0 | 0 |
| Southern lagoon | 56.8 | 16/1<br>(0.28) | 6<br>(0.11) | 2<br>(0.04) | 0 | 0 | 0 |
| Western slope | 4.8 | 0 | 1<br>(0.21) | 1<br>(0.21) | 1<br>(0.21) | 0 | 1<br>(0.21) |
| Western lagoon | 22 | 8<br>(0.36) | 2<br>(0.09) | 1<br>(0.05) | 0 | 0 | 0 |
| Total | 376.8 | 64/7<br>(0.18) | 166<br>(0.44) | 73<br>(0.19) | 4<br>(0.01) | 0 | 2<br>(0.01) |
| Entire survey area | 441.9 | 64/7<br>(0.16) | 177<br>(0.40) | 85<br>(0.19) | 9<br>(0.02) | 11<br>(0.02) | 12<br>(0.03) |

**Table 3.3:** Depth preferences of the most frequently sighted cetacean species around Mayotte from July 2004 to June 2006.

| Species | Mean | SD | Range | Median | Q1 | Q3 |
|---|---|---|---|---|---|---|
| *Stenella longirostris* | 123.7 | 187.3 | 3-1,335 | 54 | 25 | 128.5 |
| *Stenella attenuata* | 193.7 | 255.7 | 5-1,301 | 74 | 24 | 268.3 |
| *Tursiops aduncus* | 23 | 16 | 1-57 | 21 | 10 | 35 |
| *Peponocephala electra* | 383 | 286.4 | 20-845 | 400 | 118 | 560 |
| *Sousa chinensis* | 17 | 7.7 | 7-28 | 14 | 12 | 22.5 |
| *Grampus griseus* | 1,150 | 385 | 762-1,784 | 1 121 | 953 | 1,129 |
| *Mesoplodon densirostris* | 1,000 | 365.5 | 482-1,524 | 1 070 | 782.5 | 1,143.5 |

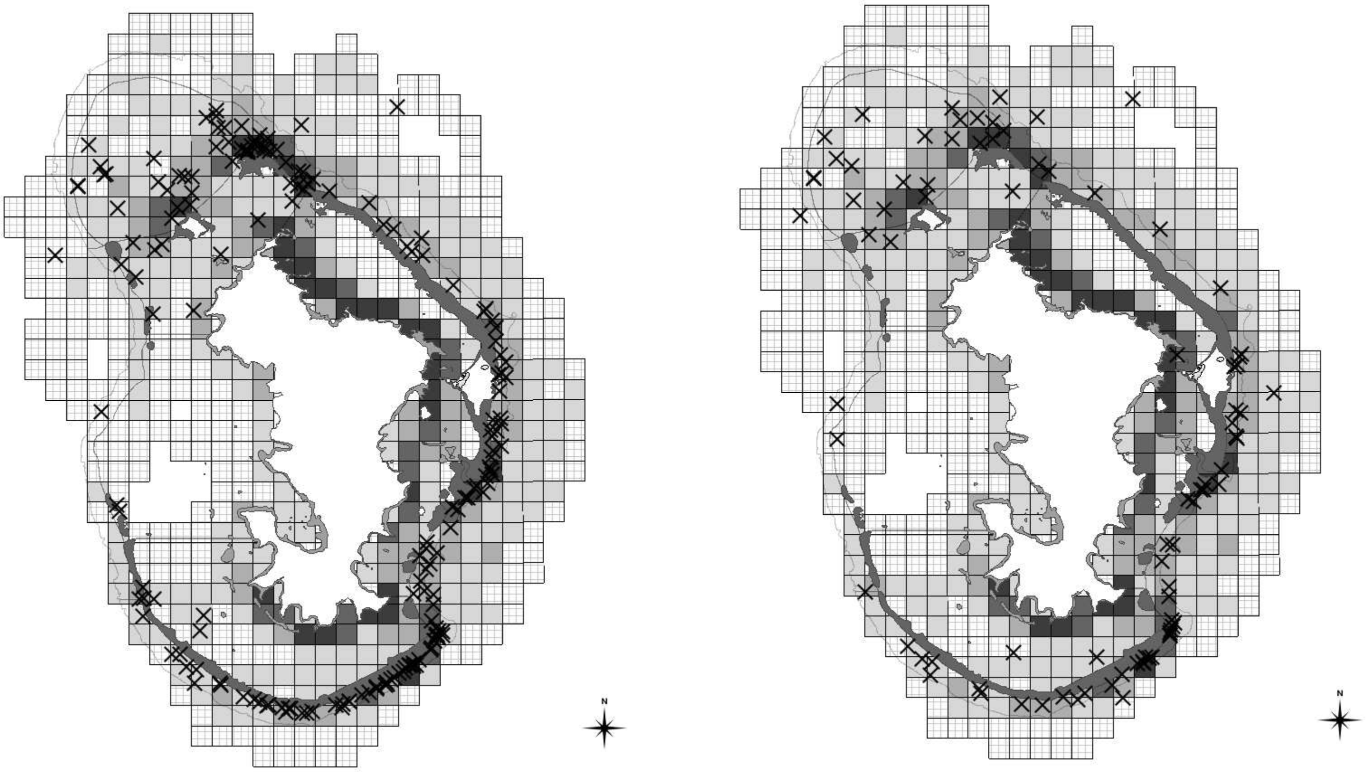

**Figure 3.2:** Spatial distribution of spinner dolphins (*Stenella longirostris*, left) and pantropical spotted dolphins (*Stenella attenuata*, right) in relation to effort encountered around Mayotte from July 2004 to June 2006.

### Encounter rates

Encounter rates were derived for the coastal species (Indo-Pacific bottlenose and humpback dolphins), the spinner dolphin, the pantropical spotted dolphin, the melon-headed whale, the oceanic delphinids, and the largest toothed whales (beaked and sperm whales) by geographic zone (Table 3.2). Search effort varied among geographic zones (Table 3.2). Nonetheless, when sightings are normalized for effort some trends appear, especially for the most common species. For coastal species the highest encounter rate was observed for the western portion of the lagoon (0.36 group/hour), in the south-eastern lagoon (0.25 group/hour) and on the Iris bank (0.22 group/hour). Spinner dolphins were encountered frequently on the eastern outer slope (1.04 group/hour), but even more frequently along the southern slope (1.94 group/hour). A similar trend can be observed for pantropical spotted dolphins for the later area (0.93 group/hour). Beaked whales were only encountered in waters deeper than 500 m and rarely observed.

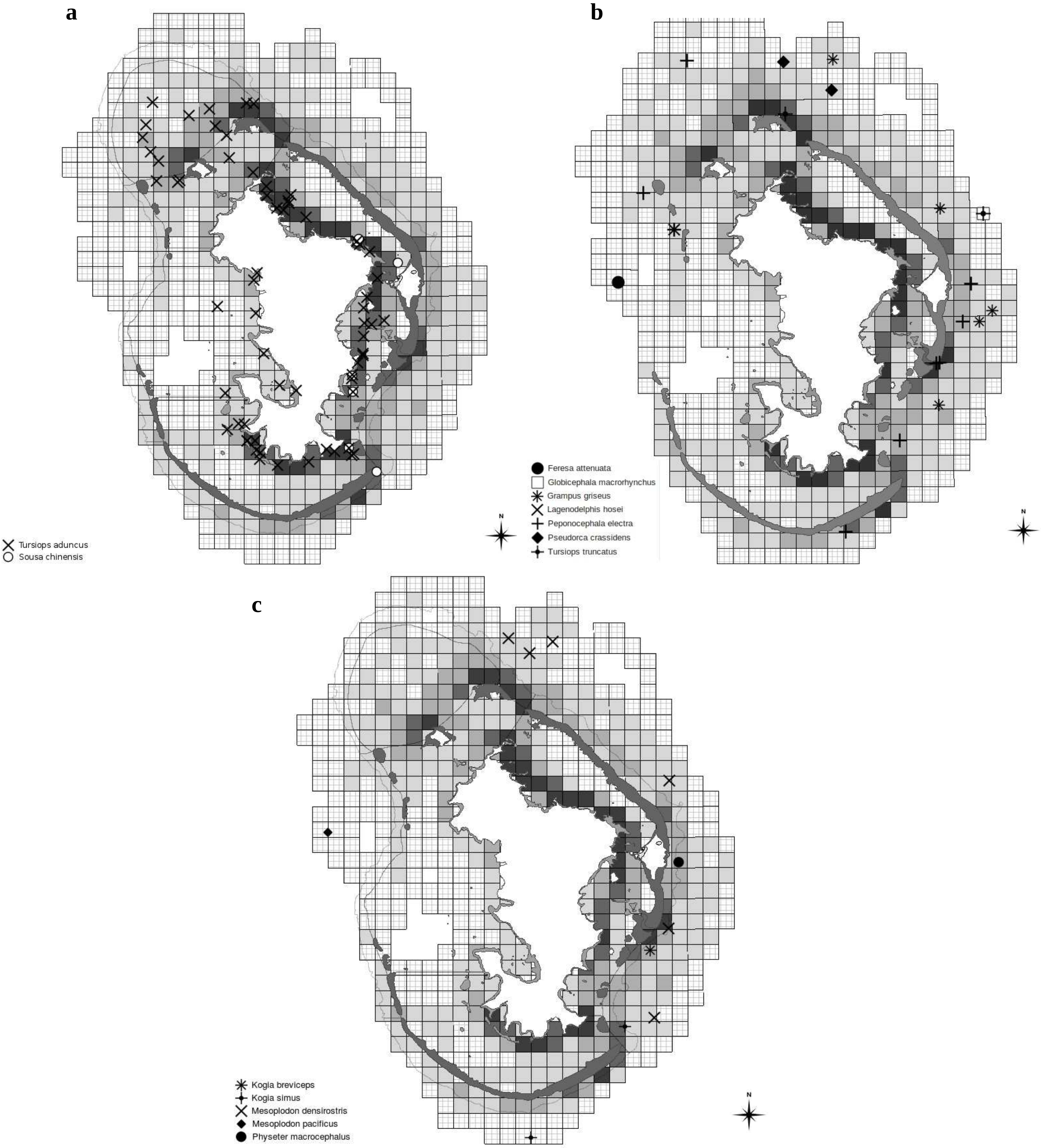

**Figure 3.3:** Spatial distribution of a- coastal dolphins (*Tursiops aduncus* and *Sousa chinensis*), b- oceanic delphinids and c- the largest toothed whales in relation to effort encountered around Mayotte from July 2004 to June 2006.

## Discussion

To date, at least 31 cetacean species have been recorded in the southwest Indian Ocean, including 23 odontocetes (Kiszka *et al.*, 2009a). The odontocete community around Mayotte has a number of notable characteristics. First, species richness within the area is high, especially in waters deeper than 500 meters (12 species recorded, *vs*. 5 in the outer reef slope area and 4 inside the lagoon). The Shannon-Weaver index was significantly lower in oceanic waters deeper than 500 meters and inside the lagoon due to the high variability of abundance among species. For example, in oceanic waters, delphinids have a significantly higher abundance than beaked whales and sperm whales. Conversely, on the outer reef slope, species richness is lower (five species) but abundance is more similar among species, making the outer reef slope community more diverse. A previous description of cetacean diversity around Mayotte documented the presence of 17 species including 15 odontocetes and possibly (no supporting photographic evidence), a ginkgo-toothed beaked whale (*Mesoplodon ginkgodens*) (Kiszka *et al.*, 2007a). This study did not confirm the presence of this later species, but added the pygmy sperm whale (*Kogia breviceps*) to the species list for Mayotte. In addition, killer whales (*Orcinus orca*) have been observed on multiple occasions by whale watching operators in the recent years (N. Bertrand/Sea Blue Safari, personal communication). The odontocete diversity around Mayotte is high, especially in comparison to other tropical islands and archipelagos such as La Réunion in the Mascarenes (eight odontocetes; Dulau-Drouot *et al.*, 2008), Great Abaco, in the northern Bahamas (seven odontocetes, MacLeod *et al.*, 2004), Aldabra, southern Seychelles (twelve odontocetes, Hermans & Pistorius, 2008), and the whole Hawaiian archipelago (fourteen odontocetes, Baird *et al.*, 2003). Some oceanic species have not yet been recorded around Mayotte, such as the Cuvier's beaked whale (*Ziphius cavirostris*), the rough-toothed dolphin (*Steno bredanensis*) or the striped dolphin (*Stenella coeruleoalba*), which may be due to the lower observation effort undertaken in offshore waters. Overall, the high diversity of odontocetes recorded around Mayotte may be linked to the diversity of habitat types encountered around this island, especially in comparison to other oceanic islands that do not have lagoon or/and extended coral complexes. However, it is still difficult to directly compare study areas, as the number of species recorded is also linked to the spatial and temporal distribution of effort.

In term of distribution, a detailed description of 4 delphinid distributions around Mayotte has been given by Gross *et al.* (2009). Our study confirms that around the island, the Indo-Pacific bottlenose dolphin has a coastal and shallow water distribution. The coastal range of this species has been documented in other areas of the southwest Indian Ocean, such as at La

Réunion (Dulau-Drouot *et al.*, 2008) and off the south coast of Zanzibar (Stensland *et al.*, 2006). Another species documented in our study is the Indo-Pacific humpback dolphin, but this species appears to be very rare and no detailed analysis of distribution and habitat characteristics has been possible. Along the outer reef slope, spinner and pantropical spotted dolphins had high encounter rates and this study suggest these are the most abundant cetacean species found around the island. In a previous study, a comparative habitat analysis confirmed that these two species overlap in their distribution as well as in their isotopic niches, which could indicate a possible competition between these sibling species (Gross *et al.*, 2009). In our study, bathymetric preferences were different between species. The spinner dolphin occurs in shallower waters than the pantropical spotted dolphin, which has been described previously in other insular populations from the region (Dulau-Drouot *et al.*, 2008). Habitat features of spinner dolphin around Mayotte are slightly different than in other areas. In French Polynesia, Hawaii or the Maldivian atolls, spinner dolphins enter atolls, sheltered bays and lagoons through reef channels in the morning and leave in the afternoon to feed overnight (Würsig *et al.*, 1994; Anderson, 2005; Gannier & Petiau, 2006). Around Mayotte, spinner dolphins predominantly inhabit the outer reef slope and have a greater depth range than is reported by other studies. In addition, spinner dolphin mean school size recorded (mean=72.8) in the waters of Mayotte was slightly higher than in other areas such as at La Réunion (mean=51.2) and in the Maldives (mean=58.2). The reasons why spinner dolphins do not regularly use lagoonal waters around Mayotte were not elucidated. Nevertheless, ideal habitat conditions are available in the lagoonal waters for spinner dolphins. While it is still speculative, the absence of spinner dolphins inside the lagoon may be the result of the presence of Indo-Pacific bottlenose dolphins, a larger possibly more dominant, territorial species. Pantropical spotted dolphins demonstrate a wide range of distribution and habitat characteristics around Mayotte, utilizing both shallow and oceanic waters along the outer reef slope. This species was most frequently observed close to reef on the outer reef slope. In Golfo Dulce, along the Pacific coast of Costa Rica, pantropical spotted dolphin occur in shallower waters (mean=92.7 m; Cubero-Pardo, 2007) while at La Réunion, in the Indian Ocean, spotted dolphins are only encountered in relatively deep waters (mean=881 m; Dulau-Drouot *et al.*, 2008).

Melon-headed whales have been reported at a number of island groups, including the Hawaii archipelago, the Philippines, French Polynesia and in the Indian Ocean, such as off the Maldives, La Réunion and the Comoros, including Mayotte (Gannier, 2000, 2002; Baird *et al.*, 2003; Anderson, 2005; Dolar *et al.*, 2006; Kiszka *et al.*, 2007a, 2010; Dulau-Drouot *et al.*, 2008; see for review Brownell *et al.*, 2009) and are generally accepted to have a global distribution preferring deep tropical and warm temperate waters (Perryman, 2002). In comparison to other areas such as Hawaii, La Réunion and the Gulf of Mexico, encounters of melon-headed whales around Mayotte occurred in shallower waters in the vicinity of the barrier reef where they were observed engaged in resting/socializing behaviour. This daylight behaviour, also observed in other areas throughout the species range (Brownell *et al.*, 2009), suggests that melon-headed whales use shallower waters to rest and socialize and feed in deeper waters (probably on the slope).

Several large oceanic delphinids (e.g. *Grampus griseus*, *Globicephala macrorhynchus*, *Pseudorca crassidens*), beaked whales (e.g. *Mesoplodon densirostris*) and sperm whales (*Kogia* spp. and *Physeter macrocephalus*) have also been encountered, but less frequently. These species have been observed throughout the southwest Indian Ocean (Leatherwood & Donovan, 1991; Kiszka *et al.*, 2009a). These species have a preference for slope and oceanic waters (Baird *et al.*, 2003; Whitehead, 2003; MacLeod & Zuur, 2005). However, the encounter rate for Blainville's beaked whales was particularly high around Mayotte (0.09 groups per hour in waters deeper than 500 m), which is similar to little Bahama bank, in the Caribbean (0.07 groups per hour, MacLeod & Zuur, 2005), and higher than the main Hawaiian Islands (0.012 groups per hour; R.W. Baird, personal communication). The number of beaked whale encounters around Mayotte could be attributed to the number of broad submarine canyons that deeply incise the outer slope, which may concentrate the main prey of these teuthophageous predators (MacLeod *et al.*, 2003; Audru *et al.*, 2006).

Based on our results, it is evident that the outer reef slope is of primary importance in terms of density and diversity of odontocetes around Mayotte. This particular habitat (or collection of habitats) provides resting and foraging areas for several species, such as spinner dolphins, pantropical spotted dolphins and melon-headed whales (Norris & Dohl, 1979; Würsig *et al.*, 1994; Brownell *et al.*, 2009). Many oceanic species also make regular incursions in these habitats and many of these species, such as short-finned pilot whales; have been observed in close proximity to the Mayotte's barrier reef while resting. The presence of shallow waters, providing protected areas with fewer predators in close proximity to oceanic foraging habitats may be the ideal combination that attracts so many cetaceans to Mayotte's waters. This uncommon assemblage of habitats in close proximity highlights the high conservation value of the outer reef slope, especially for cetaceans. It also indicates a probable dependence of cetaceans to coral reef systems, as major feeding and resting areas. The current decline of coral reefs, both at the global and regional scale of the western Indian Ocean (MacClanahan *et al.*, 2007) should be considered as a possible long-term loss of toothed cetacean habitat.

## Conclusion

The lagoon and adjacent outer slope waters of Mayotte support a high diversity of toothed cetaceans, particularly delphinids. This community includes coastal, semi-pelagic/oceanic and oceanic species. The high diversity of species combined with the sizes of aggregations underline the importance of Mayotte to cetaceans. It is also important to notice that several delphinids seem to greatly overlap in their distribution, especially in species living along the outer reef slope (confirmed in Gross *et al.*, 2009). As species should occupy its own niche, some fine scale segregation processes should occur, which need to be assessed through in depth habitat analyses. These results provide important, previously unavailable, descriptive information that is critical for conservation and management efforts. Human activities are rapidly growing in the coastal and lagoonal waters, especially regarding the increasing maritime traffic, fishing pressure and disturbances from commercial whale and dolphin watching activities. Further effort is needed to assess the spatial and temporal interactions between maritime human activities and cetaceans around this rapidly developing island.

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### Synthèse

La communauté de cétacés odontocetes de Mayotte présente des traits particuliers : une diversité importante, fortement influencée par la présence de nombreuses espèces de delphinidés. Les delphinidés occupent tous les grands types d'habitats marins présents autour de l'île : le lagon, la pente externe du récif barrière et la pente océanique (> 500 m). Le lagon est dominé par une espèce, le grand dauphin de l'Indo-Pacifique (*T. aduncus*). Une autre espèce est également présente mais de manière très marginale, le dauphin à bosse (*S. chinensis*). La pente externe de la barrière récifale est dominée par la présence de deux espèces : le dauphin à long bec (*S. longirostris*) d'une part, et le dauphin tacheté pantropical (*S. attenuata*) d'autre part. De manière régulière, plusieurs espèces océaniques effectuent des incursions à proximité de la pente externe du récif barrière comme le péponocéphale (*P. electra*) ou le dauphin de Fraser (*L. hosei*). Enfin, un ensemble diversifié d'espèces exclusivement océaniques occupe la frange océanique de la pente comme le dauphin de Risso (*G. griseus*) ou encore le pseudorque (*P. crassidens*).

L'étude met également en évidence que la pente externe de la barrière récifale est un habitat qui regroupe une densité et une diversité d'espèces de delphinidés particulièrement importante. Cette diversité et cette densité importantes sont liés à des facteurs écologiques sous-jacents, comme la disponibilité en habitats favorables pour le repos, l'alimentation ou encore la protection contre les prédateurs, par exemple. Cette étude descriptive de la communauté de cétacés odontocètes de Mayotte n'explore pas en détail les caractéristiques d'habitat et les modes d'utilisation des habitats et des ressources par les différentes espèces. Toutefois, il apparaît qu'un certain nombre d'espèces vivent en sympatrie directe, c'est à dire que leur distribution se chevauche. C'est tout particulièrement le cas chez les deux espèces du genre *Stenella*, et dans une moindre mesure avec le péponocéphale (espèce plus rare). Dans la mesure où les habitats marins de Mayotte sont très proches les uns des autres et que certains delphinidés ont une distribution similaire, il apparaît que des processus de ségrégation écologique à fine échelle doivent exister, permettant d'assurer la coexistence des différentes espèces.

La partie 4 explore donc la ségrégation écologique des principales espèces de delphinidés vivant autour de Mayotte à travers les trois dimensions majeures de la niche écologique : l'habitat, l'alimentation et le temps (variations temporelles de l'utilisation des habitats et des ressources).

# Partie 4 :

# Ségrégation écologique des delphinidés

# Ségrégation écologique de la communauté de delphinidés de Mayotte

## Résumé

L'étude de la ségrégation écologique au sein d'une communauté d'organismes partageant des traits de morphologie et de distribution spatiale peut être rendue complexe. Autour de l'île de Mayotte, une communauté diversifiée de delphinidé est présente tout au long de l'année dans une aire géographique relativement limitée. Au moins quatre espèces sont présentes : le grand dauphin de l'Indo-Pacifique (*Tursiops aduncus*), le dauphin à long bec (*Stenella longirostris*), le dauphin tacheté pantropical (*Stenella attenuata*) et le péponocéphale (*Peponocephala electra*). De plus, une autre espèce plus océanique fait régulièrement des incursions dans les eaux péri-insulaires de Mayotte, le dauphin de Fraser (*Lagenodelphis hosei*). Cette étude a pour objectif d'évaluer la ségrégation écologique des delphinidés vivant en sympatrie autour de Mayotte. Nous émettons l'hypothèse que les différentes espèces constituant la communauté ont des niches écologiques bien distinctes définies par les axes habitat, ressources et temps. Nous avons analysé l'habitat en relation avec les variables physiographiques, les budgets comportementaux et les signatures isotopiques du carbone et de l'azote dans des biopsies de peau et de lard des différentes espèces de dauphins. Cette étude confirme que l'habitat et les budgets comportementaux des espèces sont généralement différents. Chez les espèces où il existe un chevauchement des habitats (notamment chez les espèces vivants le long de la pente externe du récif barrière), les signatures isotopiques montrent que ces espèces ont au moins un niveau trophique ($\delta^{15}N$) ou des habitats d'alimentation ($\delta^{13}C$) différents. Ce travail met en évidence l'importance de combiner les méthodologies permettant d'explorer les mécanismes de partage des niches écologiques opérant le long des axes habitat, ressource et temps, notamment quand les espèces d'une communauté donnée ont une distribution et une morphologie similaires.

# Ecological niche segregation within a community of sympatric dolphins around a tropical island

Jeremy Kiszka [1,2], Ludivine Martinez [1], Benoit Simon-Bouhet [1], Claire Pusineri[3], Pierre Richard [1] & Vincent Ridoux [1]

[1] LIttoral ENvironnement et Sociétés (LIENSs), UMR 6250 CNRS-Université de la Rochelle, 2 rue Olympe de Gouges, 17000 La Rochelle, France.
[2] Direction de l'Environnement et du Développement Durable, Collectivité Départementale de Mayotte, BP 101, 97600 Mamoudzou, Mayotte, France.
[3] Office National de la Chasse et de la Faune Sauvage, Cellule Technique Océan Indien. BP 27, Coconi, Mayotte, France.

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## Abstract

Investigating ecological segregation among organisms of a given community may be challenging, especially when these organisms share similar patterns of distribution and similar size and morphology. Around the island of Mayotte, a diversified community of sympatric delphinids is present year round within a very restricted range. At least four species permanently co-occurs, which are the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*), the spinner dolphin (*Stenella longirostris*), the pantropical spotted dolphin (*Stenella attenuata*), the melon-headed whale (*Peponocephala electra*). In addition to those, the Fraser's dolphin (*Lagenodelphis hosei*) makes incursions into peri-insular waters as well. This study aims to assess niche segregation among this tropical dolphin community. We hypothesized that each species occupies is own distinct niche, defined by the axes habitat, resources and time. We analysed habitat in relation to physiography, behavioural budgets and C and N stable isotope signatures from skin and blubber samples for each species. The results confirm that habitat and behavioural budgets were relatively distinct among species, with few exceptions. However, in these species (living on the outer reef slope), when habitat and behaviour were not well discriminated, stable isotope analyses confirmed that species have different trophic levels (reflected through N signatures) and/or foraging habitat (reflected through C signatures). This study also shows that the use of multiple methodologies (habitat, behaviour and feeding ecology studies) are recommended to investigate ecological niche segregation, especially when looking at closely related species within a common restricted range.

**Keywords:** tropical dolphins, ecological niche, habitats, stable isotopes, carbon, nitrogen, south-west Indian Ocean, Mayotte.

## Introduction

Understanding niche segregation processes is critical in ecology, particularly when investigating the ecology of species communities. A community can be defined as a collection of species that occur together in a common environment, or habitat, the organisms making up the community being somehow integrated or interacting as a society (Chapman & Reiss, 1999). Each species has its own unique niche (Grinnell, 1924). The ecological niche is a complex set of variables structured along three main axes: habitat (influence of environmental variables), diet (diet composition, trophic level, prey quality) and time (use of habitat and resources according to time, such as season and time of day). Sympatric species with similar ecological requirements would compete for resources and their coexistence requires some degree of habitat and resource segregation (Pianka, 1974). Similar species that co-occur are thought to compete for resources unless they occupy different physical locations and/or feed on different prey. A shared resource in limited supply will bring about competition between members of the same species (intra-specific competition) or between individuals of different species (inter-specific competition) (Roughgarden, 1976). Intra-specific competition may be expressed by sex or age related difference in habitat and resource use and have consequences on social structures. Inter-species competition can take various forms, including direct interference (aggressive behaviour) and exploitation-competition, in which individuals indirectly interact for resources (Begon *et al.*, 1986).

Investigating segregation processes within communities of organisms having similar size and morphology has been particularly challenging. In such communities, niche partitioning is difficult to assess as they can occur over small spatial and temporal scales. For example, in species with similar morphology (e.g. body size, jaw/beak shape, etc.), feeding niches are distinct even when feeding occurs in both species within the same area (MacArthur, 1958). In top marine predators having high trophic position, niche segregation has been investigated in a number of taxa, including large teleost fish (Potier *et al.*, 2004; Ménard *et al.*, 2007), sharks (Estrada *et al.*, 2003; Domi *et al.*, 2005; Papastamatiou *et al.*, 2006), seabirds (Ridoux, 1994; Cherel *et al*., 2008; Jaeger, 2009), marine mammals (Das *et al.*, 2003; Whitehead *et al.*, 2003; Praca & Gannier, 2008) including delphinids (Pusineri *et al.*, 2008; Gross *et al.*, 2009). Methods used to discriminate niches are variable, from stomach content analyses to habitat modelling. For example, niche partitioning has been assessed in polar communities using stable isotope analyses of C and N, such as in Antarctic pinnipeds, showing clear ecological segregation between species (Zhao *et al.*, 2004). Conversely, in tropical sympatric seabirds, important overlap of feeding niches has been found, which may be interpreted by the low productivity of tropical oligotrophic waters, leading these predators to share same feeding resources that are not quantitatively limited (Cherel *et al.*, 2008). In the tropical cetacean community of the Bahamas, it has been shown that the ecological niches of four cetacean species (including delphinids and medium-sized whales) do not overlap. Other cetacean species are observed in the area only during the season when prey abundance is sufficiently high to support their presence, while they are competitively excluded for the rest of the year (MacLeod *et al*., 2004).

Around the tropical island of Mayotte (Comoros, SW Indian Ocean), a great diversity of cetaceans may be found within a limited geographical range, i.e. at least 19 species within an area of 2,500 km² (Kiszka *et al.*, 2007a). In this area, high cetacean diversity may be interpreted by the presence of a wide range of marine habitats within close proximity to one another: turbid mangrove fronts, fringing reef systems, clear lagoon areas, barrier and double barrier reef-associated habitats, a steep insular slope and deep oceanic waters. In some locations around Mayotte lagoon, water depth reaches more than 1,000 m less than 3 km away from the barrier reef. The permanent presence of odontocetes within a restricted range suggests that fine-scale mechanisms allow for the partitioning of habitats and/or resources. The five commonest dolphin species there have a size ranging from 1.80 m spinner dolphin (*Stenella longirostris*, the smallest) to the 2.80 m melon-headed whale (*Peponocephala electra*, the largest). Other species include the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*), the pantropical spotted dolphin (*Stenella attenuata*) and the Fraser’s dolphin (*Lagenodelphis hosei*). A preliminary study of the tropical delphinid community around the island of Mayotte has shown that the ecological niches of the delphinid occurring were, at least partially, overlapping (Gross *et al.*, 2009). Using sighting data related to environmental variables and stable isotope analyses from biopsy samples, it was shown that the Indo-Pacific bottlenose dolphin has a coastal/lagonal distribution, while the spinner dolphin, the melon-headed whale and the pantropical spotted dolphin have similar habitat characteristics, along the outer reef slope. Stable isotope analyses from a small amount of biopsy samples allowed discriminating all species of the community, except the two congeneric “sibling” dolphins of the genus *Stenella*, having similar morphological characteristics and frequently forming inter-species aggregations. Methodological constraints and limited sample size are likely to explain the absence of measurable differences between species. Therefore, the present work aims to characterize habitat and resource partitioning among delphinids living in sympatry around the island of Mayotte from multiple lines of evidence, along the axes of habitat, diet (more particularly trophic level and foraging habitat) and time (season and time of day, Table 4.1).

Delphinids around Mayotte should have distinct ecological niches, defined by habitat, behavioural budgets and isotopic niches; therefore we hypothesize that for any given pair of species, statistical difference should be found for at least one of the variables tested.

We will investigate habitat in relation to environmental variables, activity budgets and their variability among species and according to time, as well as stable isotope analyses ($\delta^{13}C$ and $\delta^{15}N$) from biopsy samples. We also assessed seasonal variations of habitat preferences, behavioural budgets and stable isotope signatures, as seasonality may be a major factor segregating species among them.

**Table 4.1:** Methodologies used for the exploration of the three main dimensions of the ecological niche in the present study.

| | **Niche dimensions** | | |
|---|---|---|---|
| ***Variables tested*** | ***Habitats*** | ***Resources*** | ***Time*** |
| **Distribution and associated habitat characteristics** | Habitat defined on physiographic aspects (and seasonal variation of) | | |
| **Activity budget** | | | Daily activity rhythm (and seasonal variation of) |
| **N isotopic signature** | | Trophic level (and seasonal variation of) | |
| **C isotopic signature** | Habitat along a coastal-oceanic gradient (and seasonal variation of) | | |

## Materials and methods

### Study area

Mayotte (45°10’E, 12°50’S) is located in the north-eastern Mozambique Channel, and is part of the Comoros archipelago. The island is surrounded by a 197 km long barrier reef, with a second double-barrier in the southwest and the immerged reef complex of Iris in the northwest. The lagoon and surrounding reef complexes are 1,500 km² with an average depth of 20 m and a maximum depth of 80 m found in the western, older, region of the lagoon (Quod *et al.*, 2000). The insular slope on the exterior of the barrier reef is very steep and contains many submarine canyons and volcanoes (Audru *et al.*, 2006). The island of Mayotte is characterized by the presence of high cetacean diversity (19 species including 12 delphinids; Kiszka *et al*., 2007a). The most common species are the spinner dolphin (*Stenella longirostris*), the pantropical spotted dolphin (*Stenella attenuata*), the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) and the melon-headed whale (*Peponocephala electra*); these are resident year-round (Kiszka *et al*., 2007a). Preliminary abundance estimates obtained from aerial surveys suggest a total number of 41 Indo-Pacific bottlenose dolphins (CI 95%, 30 – 67), 703 spinner dolphins (CI 95%, 643 – 1,046) and 375 pantropical spotted dolphins (CI 95%, 342 – 557) (Pusineri *et al.*, 2009).

### Data and sample collection

From July 2004 to April 2009, small boat based surveys were undertaken around Mayotte. Several types of boats were used to collect data: a 7-m catamaran equipped with two, four-stroke, 60-hp outboard engines; a 7-m boat equipped with two, two-stroke, 40-hp outboard engines; a 6.4-m cabin cruiser equipped with one, four-stroke, 150-hp outboard engine; and a 10.8-m cabin cruiser equipped with two, four-stroke, 115-hp outboard engines. Surveys were conducted throughout the study period during daylight hours between 07:00 h and 18:00 h in sea conditions not exceeding Beaufort 3. Survey vessels did not follow pre-defined transects but every attempt was made to sample the whole daylight period as well as each habitat type within the surrounding waters of Mayotte, *i.e.* coastal areas, lagonal waters, barrier reef associated areas (inner and outer slopes) and oceanic or slope waters (>500 m). When delphinids were encountered, standard sighting data were recorded: species, group size (maximum, minimum, best estimate), geographic position and behavioural activity. The predominant activity was defined as the behavioural state in which most animals (> 50%) of the group were involved at each instantaneous sampling. Typically, more than 90% of the animals in a group were engaged in the same activity.

In order to measure behaviour of the focal dolphins and determine their behavioural budgets, focal group follows were used (Mann, 1999). While one of the preferred option in behaviour sampling is to follow a focal individual (Mann, 1999), this method was not suitable for large aggregations of oceanic dolphins. In addition, following groups, rather than individuals, is more suitable for behavioural studies as appropriate conditions for individual sampling are rare in diving cetaceans (Whitehead, 2004). Individual follows were possible in the easily identifiable Indo-Pacific bottlenose dolphins (not on each occasions as some individuals were not identifiable), but for comparative purposes, we used a focal group protocol, which has been used in other studies on similar models (Neumann & Orams, 2006). The encountered group was approached slowly (typically at 2-3 knots), from the side and rear, with the vessel moving in the same direction as the animals. Groups were scanned, including all individuals, to prevent attention being drawn to only specific individuals or behaviours (Mann, 1999). During focal follows, dolphin behaviour was recorded every 5 minutes. Five categories of behavioural states were defined: milling, resting, travelling, feeding/foraging (hereafter foraging), and socializing as defined in previous studies (e.g. Norris & Dohl, 1979; Bearzi, 2005a; Neumann & Orams, 2006; Degrati *et al.*, 2008). Feeding was characterised by loose to disperse group formations and dolphins were observed swimming in circles, and pursuing fishes (prey observed at the surface). Preys were frequently seen at the surface during foraging activity. In bottlenose dolphins, large preys were frequently exhibited by the animals at the surface. Travelling consisted of persistent and directional movements of all the individuals of a group. Milling was characterised by non-directional movements of the dolphin, with frequent changes in heading. Socialising consisted in frequent interactions between individuals in the form of body contacts, with high-speed movements, frequent changes in direction and aerial displays. Resting was characterised by low level of activity, with groups in tight formations, with little evidence of forward propulsion. Surfacings are slow and relatively predictable.

For stable isotope analyses, biopsy attempts were made when groups and individuals were easily approachable and when conditions were optimal (Beaufort < 2, dolphins closely approaching the boat). Optimal weather conditions allowed stability of the research boat and better chances to sample the animals successfully and safely. Biopsies were collected by using a crossbow (BARNETT Veloci-Speed® Class, 68-kg draw weight) with Finn Larsen (Ceta-Dart, Copenhagen, Denmark) bolts and tips (dart 25-mm long, 5-mm-diameter). A conical plastic stopper caused the bolt to rebound after the impact with the dolphin. The dolphins were hit below the dorsal fin when sufficiently close (3-10 m) to the research boat. Approaches of focal groups/individuals were made under power at speeds of 1-4 knots. Blubber and skin biopsy samples were preserved individually in 90% ethanol before shipping and subsequent analysis. Biopsy sampling was conducted under French scientific permit #78/DAF/2004 (September 10, 2004) and permit #032/DAF/SEF/2008 (May 16, 2008) after examination of the project by *Conseil National de Protection de la Nature*.

Muscle samples from several fish species were also collected for stable isotope analyses, especially to investigate trophic interactions between delphinids and potential dolphin preys as well as fish species with clear ecological profiles (see below). Fish specimens were collected in a local fish market. Fish muscle samples were sampled in April 2009 and preserved in ethanol before subsequent analyses. The fish species selected were pelagic, demersal and benthic species from reef associated habitats, *i.e.* from various environments in the lagoon and surrounding waters, and different trophic levels (herbivorous, planctonophageous and piscivorous): *Hemiramphus far*, epipelagic, inhabiting waters near reef systems and feeding on the pelagic zooplankton; *Mulloidichthys vanicolensis*, demersal on seaward reefs, feeding on small worms and crustaceans; *Siganus argenteus*, demersal, inhabiting coastal and inner reef slopes and feeding on algae; *Scarus russelii*, demersal, inhabiting shallow coastal reef and feeding on algae by grazing on coral bubble and *Caranx melampygus*, demersal and pelagic predator feeding on small schooling fishes (Froese & Pauly, 2010). Two species were sampled because they regularly enter into the diet of the Indo-Pacific bottlenose dolphin: *Hemiramphus far* and *Caranx melampygus* (J. Kiszka & C. Pusineri, personal observations).

### Habitat analyses

We constituted a database in which every dolphin observation was associated with the physiographic characteristics (distance from the coast, distance from the nearest reefs, depth and slope of seafloor) corresponding to the GPS (Global Positioning System) fixes of the observation. Bathymetric data were obtained from *Service Hydrographique et Océanographique de la Marine* (SHOM). Interpolation of bathymetry data, needed to generate depth and slope data for each sighting, was undertaken with the extension Spatial Analyst by kriging transformation of the raster file into an interpolated data file. The distance data were obtained using GIS (Geographic Information System) software ArcView (ArcGIS 8.3) by ESRI (Environmental Systems Research Institute). We represented the distribution of the four dolphin species investigated in relation to the environmental predictors using kernel density plots to view the distribution of species. In order to differentiate species in relation to habitat characteristics, we used Multidimensional Scaling (MDS). Metric Multidimensional scaling (MDS) takes a set of dissimilarities and returns a set of points such that the distances between the points are approximately equal to the dissimilarities. It displays the structure of distance-like data as a geometrical picture (Gower, 1966). In other words, the purpose of MDS is to provide a visual representation of the pattern of proximities (*i.e.* similarities or distances) among a set of objects. This multivariate analysis was used in order to discriminate species in their habitat preferences. Presence-absence models were not used due to heterogeneous sampling of the study area.

In order to complement this multivariate approach, univariate non-parametric pairwise Wilcoxon tests were used to compare species distribution for each environmental variables.

Seasonal differences of habitat preferences were investigated using Mann-Whitney U-tests for each species, in relation to the four environmental co-variates that were used. Two seasons were considered: rain/summer (November – April) and dry/winter seasons (May – October). Analyses were performed using Rv2.10.0 (R Development Core Team, 2010).

### Behavioural budget analyses

To analyse diel patterns of behaviour, we defined three time-blocks: morning (before 10:00 h), noon (between 10:01 h and 14:00 h) and evening (after 14:01 h). Seasons considered were identical than for the habitat analyses (dry/rain season). Diurnal and seasonal patterns were investigated by assigning a behavioural sequence to a time block or a season. Contingency table analyses were used in order to compare behavioural budgets among species. Nonparametric tests were selected because assumptions regarding normality and homogeneity of variance were not met. Kruskal-Wallis tests were also used to investigate the effect of habitat (especially depth and distance from coast) on behavioural budgets.

### Stable isotope analyses

Blubber and skin were separated for each dolphin biopsy sample. Fish muscle tissues were used for stable isotope analyses. The ethanol was evaporated at 45°C over 48 h and the samples were ground and freeze-dried (Hobson *et al.*, 1997). Because lipids are depleted in $\delta^{13}C$, they were extracted to avoid a bias in the isotopic signature of $\delta^{13}C$ (De Niro & Epstein, 1978; Tieszen *et al.*, 1983). This was done by shaking (1 h at room temperature) in cyclohexane ($C_6H_{12}$), and subsequent centrifugation prior to analysis. After drying, small sub-samples (0.35 to 0.45 mg ± 0.001 mg) were prepared for analysis. Stable isotope measurements were performed with a continuous-flow isotope-ratio mass spectrometer (Delta V Advantage, Thermo Scientific, Germany) coupled to an elemental analyser (Flash EA1112 Thermo Scientific, Italy). Results are expressed in δ notation relative to PeeDee Belemnite and atmospheric $N_2$ for $\delta^{13}C$ and $\delta^{15}N$, respectively, according to the equation:

$$\delta X = \left[ \frac{R_{sample}}{R_{s\tan dard}} - 1 \right] \times 1000$$

Where X is $^{13}C$ or $^{15}N$ and R is the isotope ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicated that measurement errors were <0.1‰ for $\delta^{13}C$ and $\delta^{15}N$. Percent C and N elemental composition of tissues were obtained using the elemental analyzer and used to calculate the sample C:N ratio, indicating good lipid removal efficiency when <4. Differences of stable isotopes signatures of $\delta^{15}$N and $\delta^{13}$C among species were tested using non-parametric Kruskal-Wallis and Mann Whitney U-tests. Seasonal variations were investigated using Mann-Whitney U tests. Like for seasonal variations of habitat preferences, the two seasons considered were rain (November – April) and dry seasons (May – October).

## Results

### Field effort and data collected

From July 2004 to April 2009, data were collected during 224 boat-based surveys. A total of 355 sightings of the targeted species were collected (92% of cetacean encounters around Mayotte), *i.e.* 195 for *Stenella longirostris*, 95 for *Tursiops aduncus*, 53 for *Stenella attenuata* and 12 for *P. electra*. The spatial distribution of observation effort and initial encounters is presented in Figures 4.1a and b. Overall, spatial coverage of effort was heterogeneous, but covered all available habitats around the island, both inside and outside the lagoon.

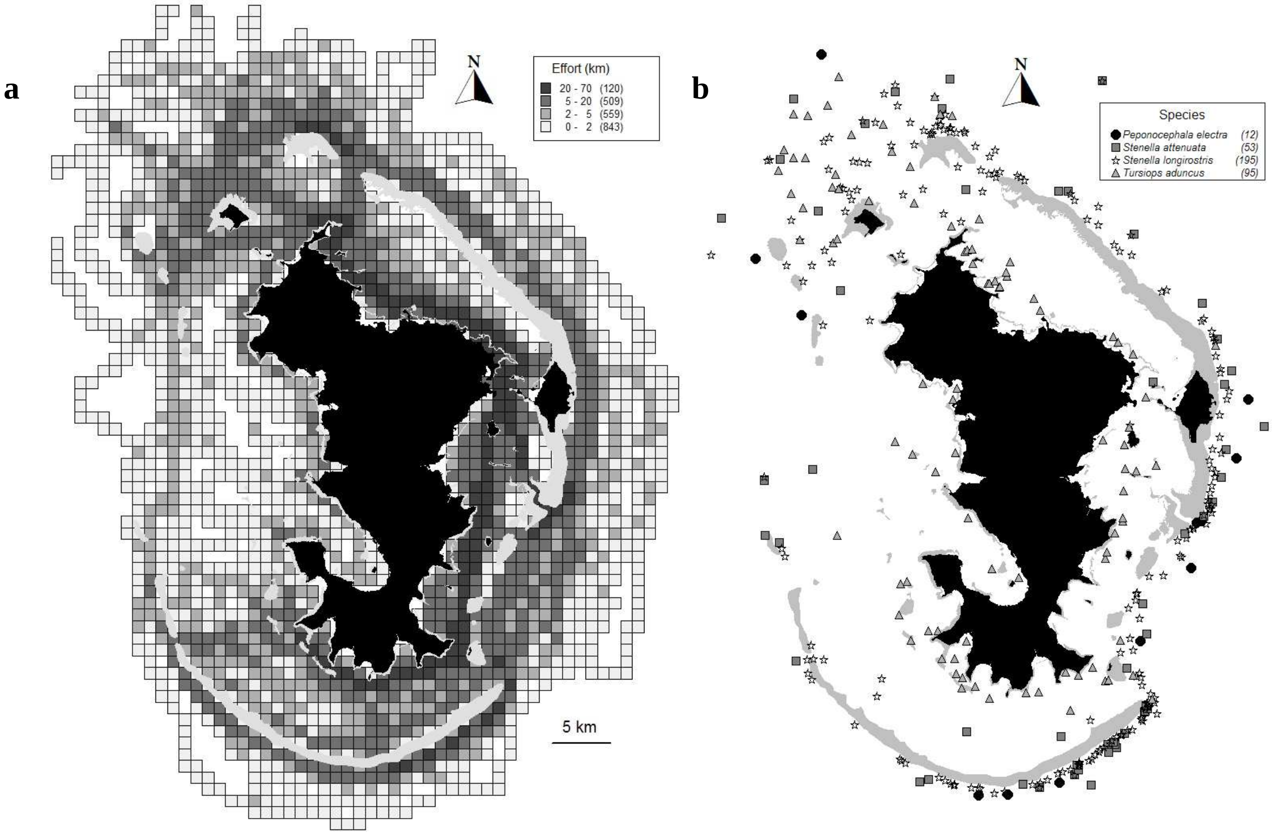

**Figure 4.1:** Spatial distribution of effort (per 1km cell) and distribution of dolphin sightings around Mayotte from July 2004 to April 2009.

We collected biopsy samples from the four focal species from December 2004 to April 2009 (*Stenella longirostris*, n=28; *Stenella attenuata*, n=22; *Tursiops aduncus*, n=28 and *Peponocephala electra*, n=20) and from another delphinid species, the Fraser's dolphin (*Lagenodelphis hosei*, n=7), during a single and unique encounter (in association with a group of melon-headed whales) in January 2005. Seasonal distribution of sighting data and biopsy samples was balanced, allowing analyses of seasonal patterns of variation of habitat and stable isotope signatures (Figure 4.2). For fish and stable isotope analyses in muscle samples, sample size was

distributed al follows: *Hemiramphus far* (n = 5); *Mulloidichthys vanicolensis* (n = 5); *Siganus argenteus* (n = 5); *Scarus russelii* (n = 5) and *Caranx melampygus* (n = 2).

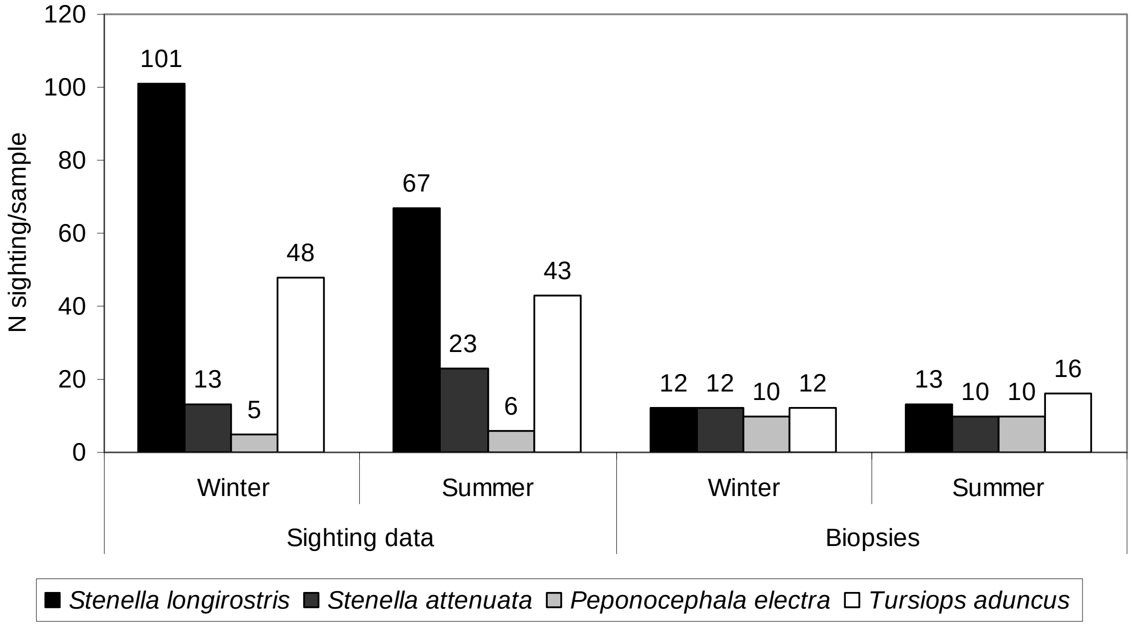

**Figure 4.2:** Seasonal distribution (winter/dry season: May to October; summer/rain season: November to April) of sighting data and biopsy samples collected from December 2004 to April 2009.

Focal follows were performed on 33 groups of spinner dolphins (total time spent = 37.1 hours: n = 466 behavioural sequences), 28 groups of Indo-Pacific bottlenose dolphins (total time spent = 25.5 hours; n = 413 behavioural sequences) and 12 groups of pantropical spotted dolphins (total time spent = 16.3 hours; n = 193 behavioural sequences). The melon-headed whale was not included in the behavioural budget analysis as sample size was too small (4 focal follows).

Habitat differentiation

Table 4.2 presents distribution of the four species investigated in relation to environmental predictors. Table 4.3 presents correlation between variables. Only two variables were significantly auto correlated: distance from the coast and depth ($P$ = 0.019). Density plots show that the four species are not well differentiated, except for two variables: depth and distance from coast (Figure 4.3). For these variables, the Indo-Pacific bottlenose dolphin occurs significantly closer to the shore and in shallower waters, whereas the three other species are not well discriminated.

**Table 4.2:** Distribution of the delphinids in relation to physiographic variables.

| Species | *Stenella longirostris* | *Stenella attenuata* | *Tursiops aduncus* | *Peponocephala electra* |
|---|---|---|---|---|
| **Depth (m)** | | | | |
| Mean | 220.7 | 301.4 | 47.9 | 486.5 |
| Median | 230.5 | 276.4 | 32 | 462.2 |
| SD | 175.9 | 277.2 | 70.2 | 244.1 |
| Q1 | 71.7 | 44.9 | 19.7 | 274.9 |
| Q3 | 285.7 | 370.4 | 45.1 | 666.2 |
| **Slope (deg.)** | | | | |
| Mean | 9.5 | 9.7 | 2.1 | 13.6 |
| Median | 0 | 0 | 0 | 0 |
| SD | 17.9 | 19.7 | 6.7 | 20.4 |
| Q1 | 0 | 0 | 0 | 0 |
| Q3 | 7.9 | 2.9 | 0.8 | 39.8 |
| **Distance coast (m.)** | | | | |
| Mean | 5258.8 | 6295.3 | 2001.8 | 6665.6 |
| Median | 5068.3 | 5771.8 | 996.2 | 7086.4 |
| SD | 2763.5 | 3331.2 | 2169.8 | 2130.7 |
| Q1 | 3216.6 | 3921.7 | 487.6 | 5369.9 |
| Q3 | 7191.7 | 8602.8 | 2778.5 | 8520.4 |
| **Distance reef (m.)** | | | | |
| Mean | 1059.7 | 2011.8 | 1363 | 2452.1 |
| Median | 700.4 | 1210.0 | 509.2 | 1363.3 |
| SD | 1144.8 | 1999.5 | 2071.8 | 3014.8 |
| Q1 | 478 | 722 | 268.7 | 927.6 |
| Q3 | 1320.6 | 2701.9 | 1474.1 | 2563.8 |

**Table 4.3:** Correlation between variables (p-values. Pearson's correlations).

| | Distance coast | Distance reef | Slope | Depth |
|---|---|---|---|---|
| **Distance coast** | - | 0.27 | -0.13 | 0.01 |
| **Distance reef** | 0.27 | - | 0.13 | 0.34 |
| **Slope** | -0.13 | 0.13 | - | 0.24 |
| **Depth** | 0.01 | 0.34 | 0.24 | - |

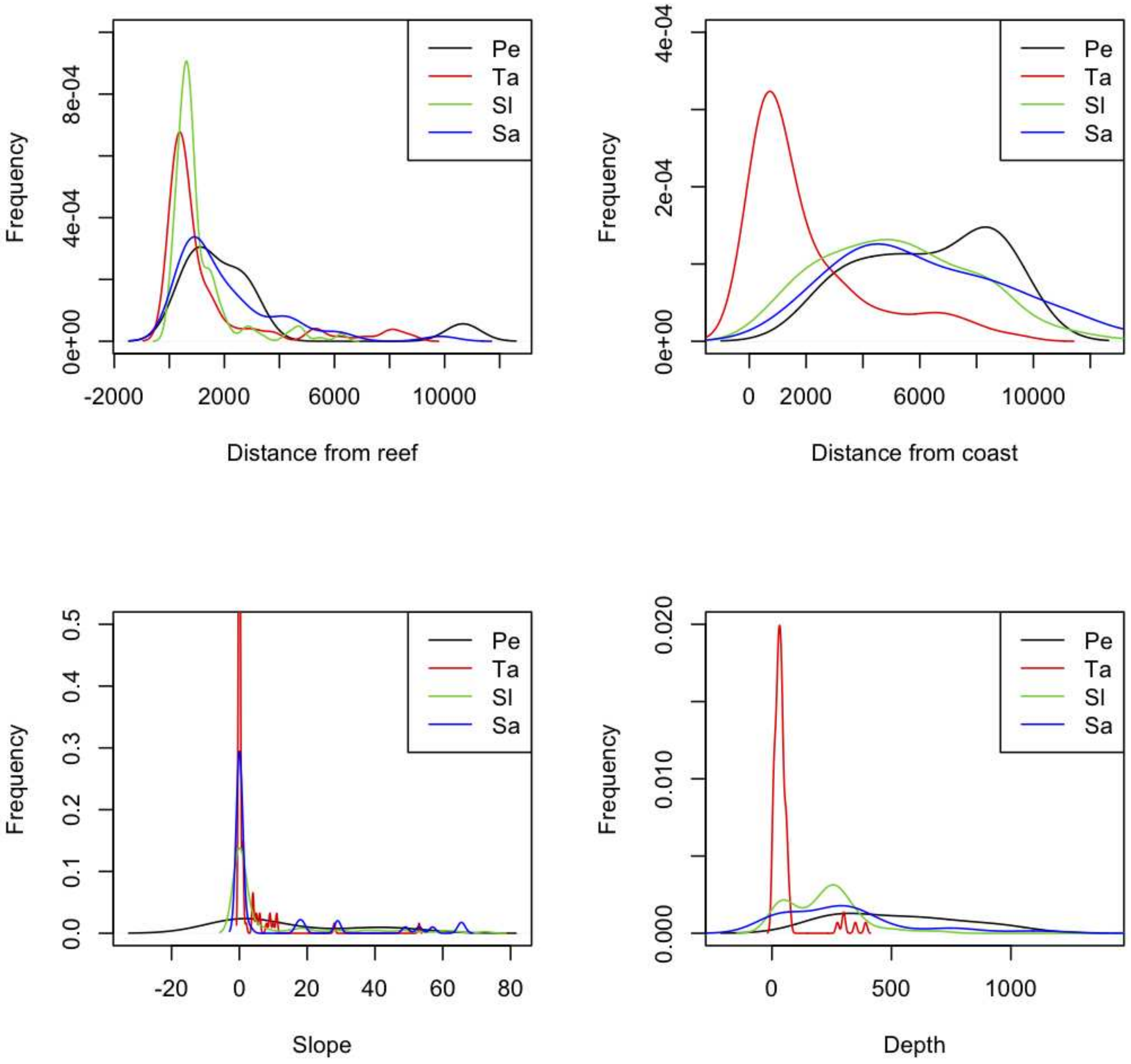

**Figure 4.3:** Density plot of sightings of dolphins around Mayotte in relation to physiographical variables: depth (meters), slope (degree), distance from coast (meters) and distance from nearest reefs (meters).

For the MDS, axes 1 and 2 explained 78.4% and 21.2% of the variance, respectively (Figure 4.4). The plot slightly discriminated the Indo-Pacific bottlenose dolphin, but segregation among the other three species appeared relatively weak. The pairwise comparison of species distribution for each variable provided more significant results. For depth, the three species occurring essentially outside the lagoon (*S. longirostris*, *S. attenuata* and *P. electra*) could not be discriminated ($P > 0.05$), while the *T. aduncus* significantly differed from the three others (all $P < 0.001$). Slope did not segregate any species. The variable "distance from the coast" significantly segregated *T. aduncus* from the three other species (all $P < 0.0001$). The variable "distance from the nearest reef" was significantly discriminant among the oceanic species: *S. longirostris* with *S. attenuata* ($P = 0.002$), *S. longirostris* with *P. electra* ($P = 0.03$). For all variables, *P. electra* and *S. attenuata* were never discriminated ($P > 0.05$). In all delphinid species, no seasonal variation of habitat preferences was observed, for any variable (all $P > 0.05$).

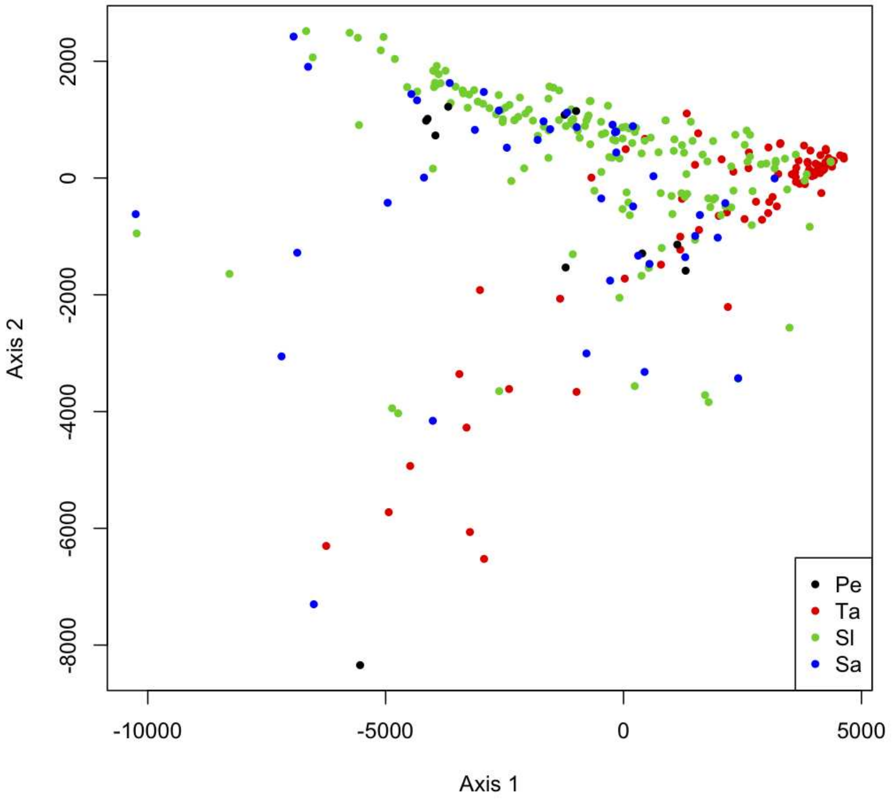

**Figure 4.4:** Metric Multi-Dimensional Scaling plot of delphinid habitat in relation to physiographical variables around Mayotte.

### Overall behavioural budgets

As we used four types of vessel for collecting behavioural data, we tested for a potential boat effect on the data but failed to find a significant difference ($\chi^2 = 3.238$, $df = 4$; $P = 0.569$); therefore, subsequent analyses presented here used a pooled data set. In Indo-Pacific bottlenose dolphins, the most frequent activities recorded were milling (32%), travelling (22%) and foraging (16%, Figure 4.5). A quite similar pattern was also observed in the pantropical spotted dolphin, with travelling being the prevalent activity (32%), followed by milling (22%) and foraging (18%). In the spinner dolphin, socialising was the most commonly recorded behaviour (28%), followed by travelling (26%) and milling (22%, Figure 5). Foraging behaviour was not observed in the spinner dolphin. Among the three species, significant differences in activity budgets were found ($\chi^2 = 177.33$; $df = 12$; $P < 0.0001$). These differences were confirmed when performing pairwise comparisons: *T. aduncus* vs. *S. longirostris* ($\chi^2 = 137.50$; $df = 6$; $P < 0.0001$), *T. aduncus* vs. *S. attenuata* ($\chi^2 = 53.42$; $df = 6$; $P < 0.001$) and *S. longirostris* vs. *S. attenuata* ($\chi^2 = 109.18$; $df = 6$; $P < 0.0001$).

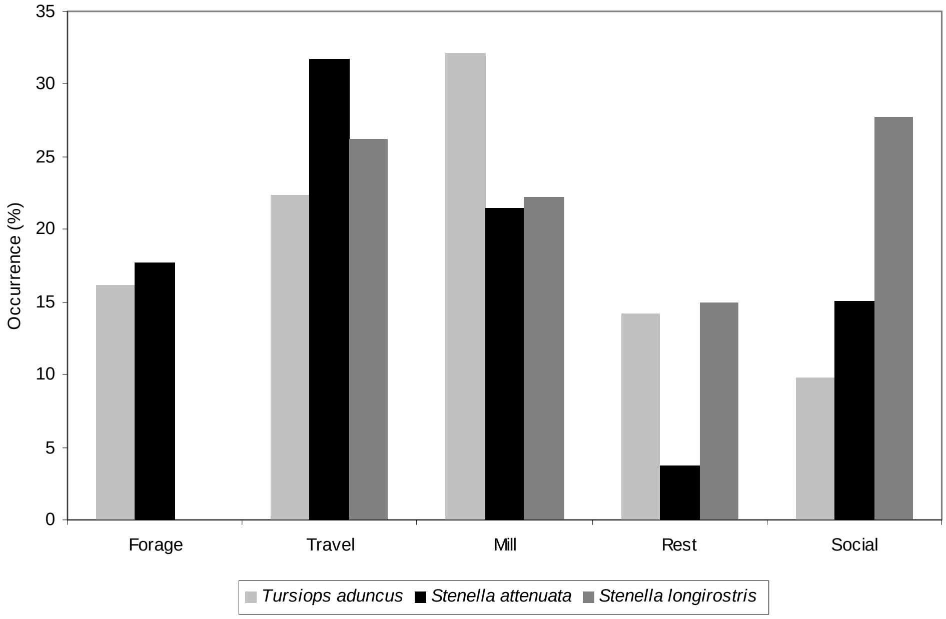

**Figure 4.5:** Overall activity budgets for Indo-Pacific bottlenose dolphins, pantropical spotted dolphins and spinner dolphins around Mayotte from 2004 to 2009.

### Temporal variation of activity budgets

For all species, no significant variations of activity patterns were observed among seasons (KW, $P > 0.05$). Contrastingly, behaviour patterns varied significantly according to time of day for Indo-Pacific bottlenose dolphin ($\chi^2 = 48$; $df = 5$; $P < 0.001$), spinner dolphin ($\chi^2 = 13$;

*df* = 5; *P* = 0.002) and pantropical spotted dolphin ($\chi^2$ = 11; *df* = 5; *P* = 0.009) (Figure 4.6, a to c). In Indo-Pacific bottlenose dolphins, foraging activities were prevalent during the morning and decreased throughout the day, whereas socializing was more frequent in the afternoon. In spinner dolphins, travelling activities increased along the day and social activities were more observed in the morning and the afternoon, whereas resting behaviour was more predominant around noon time. Finally, in pantropical spotted dolphins, feeding behaviour prevailed during the afternoon, along with travelling.

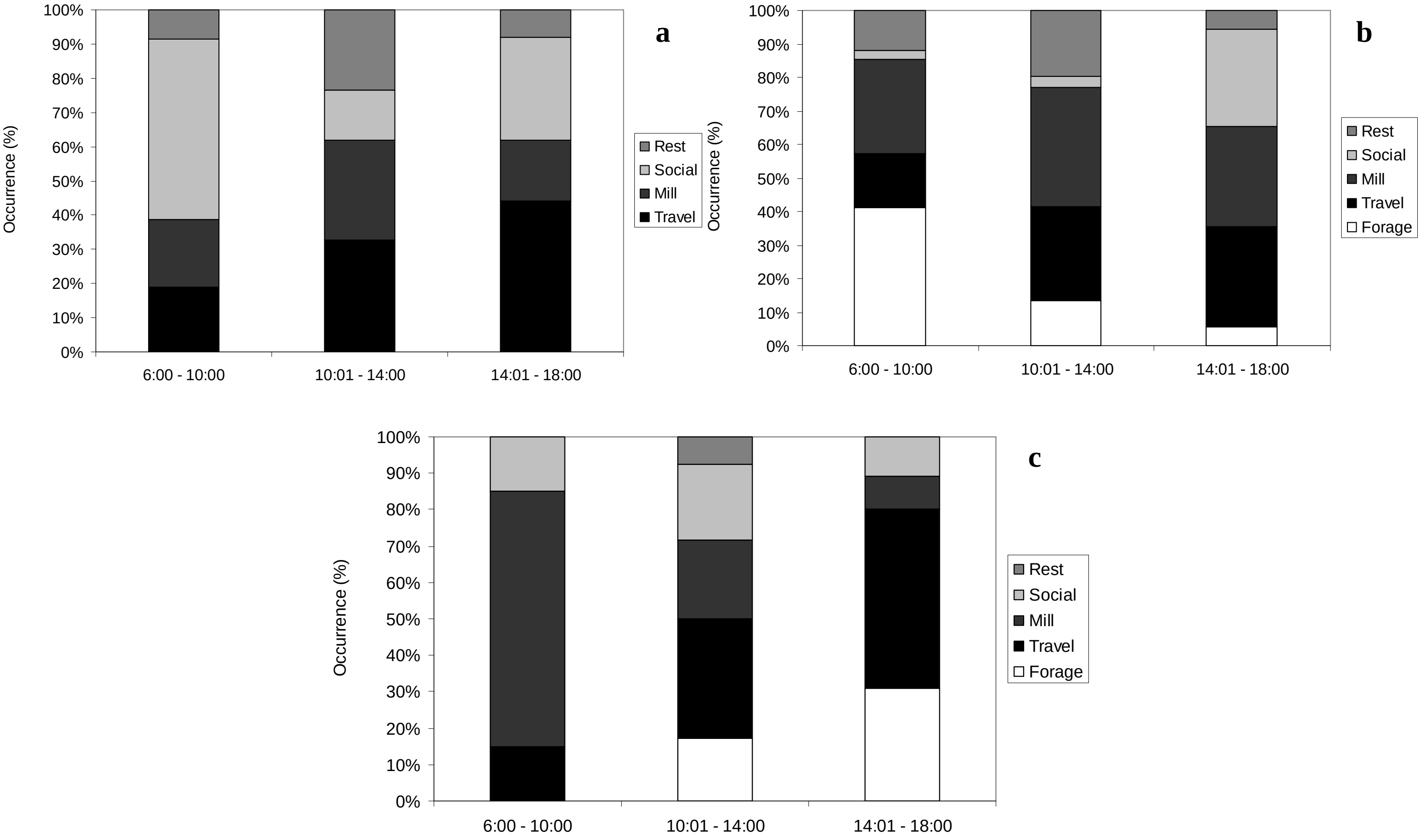

**Figure 4.6:** Within day variations of behavioural budget in spinner dolphin (a), Indo-Pacific bottlenose dolphin (b) and pantropical spotted dolphin (c) around Mayotte from 2004 to 2009.

Activity budgets did not vary with water depth in Indo-Pacific bottlenose dolphin (H = 2.060; *df* = 4; *P* = 0.725), spinner dolphin (H = 5.621; *df* = 4; *P* = 0.229) and pantropical spotted dolphin (H = 8.049; *df* = 4; *P* = 0.09). However, activity budget varied with distance from the coast for Indo-Pacific bottlenose dolphin (H = 9.542; *df* = 4; *P* = 0.04; especially increasing foraging activity closer to shore), although not for either spinner (H = 3.251; *df* = 4; *P* = 0.517) or pantropical spotted dolphins (H = 4.201; *df* = 4; *P* = 0.379). Feeding activities of the Indo-Pacific bottlenose dolphin increased with decreasing distance from coast.

Stable isotope analyses

Stable isotope values of delphinids and fish are significantly different, as shown in figure 4.7. The most apparent pattern is the higher trophic level of delphinids, reflected by higher $\delta^{15}N$ values. In addition, $\delta^{13}C$ signatures in delphinids are lower than in fish.

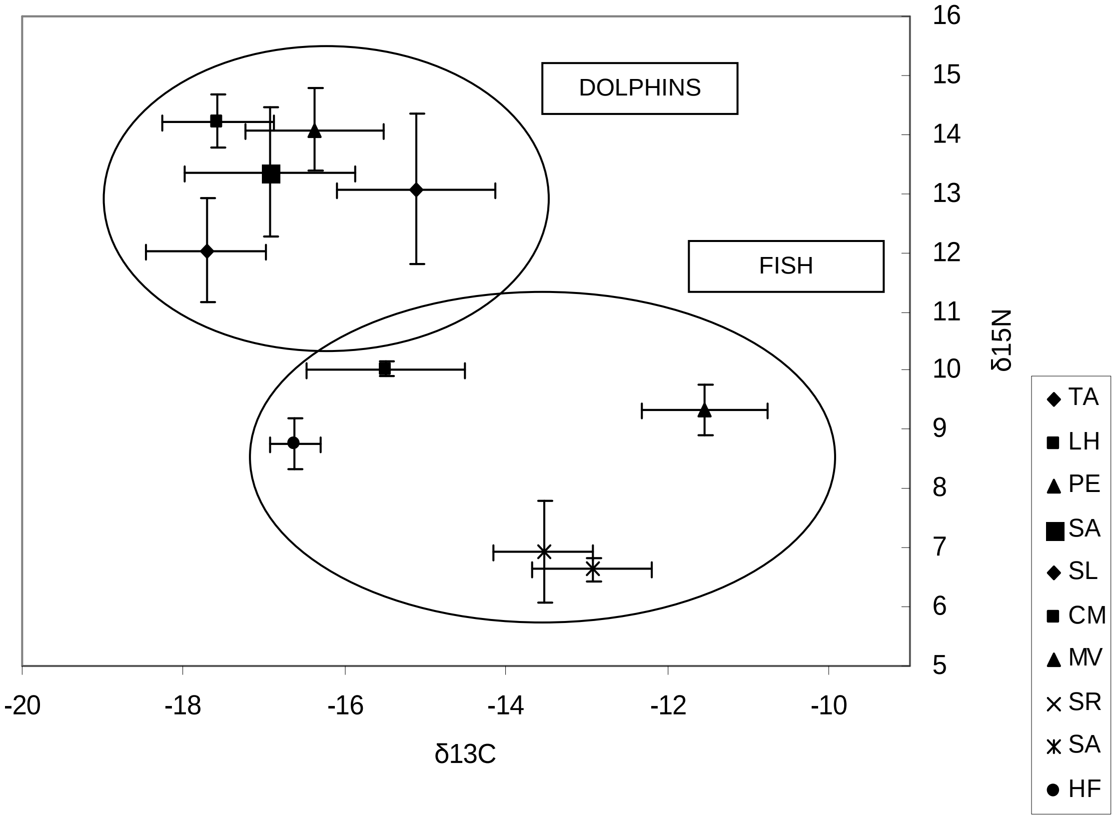

**Figure 4.7:** Mean (and SD) stable isotope values in dolphin skin and fish muscle ($\delta^{13}C$ and $\delta^{15}N$ in ‰). Legend: TA: *Tursiops aduncus*, LH: *Lagenodelphis hosei*, PE: *Peponocephala electra*, SA: *Stenella attenuata*, SL: *Stenella longirostris*, CM: *Caranx melampygus*, MV: *Mulloidichthys vanicolensis*, SR: *Scarus russelii*, SA: *Siganus argenteus*, HF: *Hemiramphus far*.

In delphinids, stable isotope ratios were lower in blubber than in skin. However, the pattern of differences observed between species was similar in both tissues (Figure 4.8 and 4.9). The Fraser’s dolphin shows a high marginality in comparison to the other species, with significantly higher $\delta^{15}N$ values in the blubber (Figure 4.8). However, for skin values, overlap was observed with the melon-headed (Table 4.4). Overall, among species, differences in carbon and nitrogen in the skin were significant for $\delta^{15}$N (H = 33.6; *df* = 2; *P* < 0.0001) and $\delta^{13}$C (H = 53.6; *df* = 1; *P* < 0.0001). For blubber, significant differences were also found for $\delta^{15}$N (H = 49.7; *df* = 1; *P* < 0.0001) and $\delta^{13}$C (H = 63; *df* = 1; *P* < 0.0001). A similar statistical difference among species for blubber tissue was found, even when excluding the Fraser's dolphin, very different to the four other species (H = 34; *df* = 2; *P* < 0.0001 for $\delta^{15}$N and H = 60; *df* = 2; *P* < 0.0001 for $\delta^{13}$C). The Indo-Pacific bottlenose dolphin had the greatest $\delta^{13}$C values, while the lowest values were observed in the Fraser's dolphin and in the two species of the genus *Stenella*. The melon-headed whale had intermediate values of $\delta^{13}$C, both for skin and blubber (Figures 4.8 and 4.9). When looking at pairwise comparisons of $\delta^{15}$N and $\delta^{13}$C values in blubber and skin tissues, however, some degrees of overlap can be observed (Table 4.4). From skin samples, $\delta^{15}$N signatures were significantly different among species, except between *S. attenuata* and *T. aduncus,* as well as between *L. hosei* and *P. electra* (U-tests; *P* > 0.05). For $\delta^{13}$C values, overlap was evident between *L. hosei* and the two species of the genus *Stenella.* Finally, for blubber tissue, $\delta^{15}$N values were significantly different among species, except for *S. attenuata* and *P. electra* and between *S. attenuata* and *T. aduncus.* $\delta^{13}$C values showed the highest degrees of overlap, particularly between *S. longirostris* and *S. attenuata*, between *S. attenuata* and *L. hosei*, as well as between *L. hosei* and *P. electra* (U-tests; *P* > 0.05; Table 4). Stable isotope values from fish samples were useful in order to provide a context to interpret values in delphinids. Among fish, significant differences were observed for $\delta^{13}$C (H = 11.2; *df* = 4; *P* = 0.02) and $\delta^{15}$N (H = 11.6; *df* = 4; *P* = 0.01). *Siganus argenteus* and *Scarus russelii* (herbivores) have the lowest trophic position ($\delta^{15}$N), while *Caranx melampygus,* the most predatory species, has the highest trophic level ($\delta^{15}$N). Their foraging habitats are also well discriminated, with *Mulloidichthys vanicolensis* having the highest $\delta^{13}$C values and *Caranx melampygus* with *Hemiramphus far* the lowest (Figure 4.7). These latter are about 0.5-1.5 ‰ $\delta^{13}$C and 3-4 ‰ $\delta^{15}$N lower than *T. aduncus*.

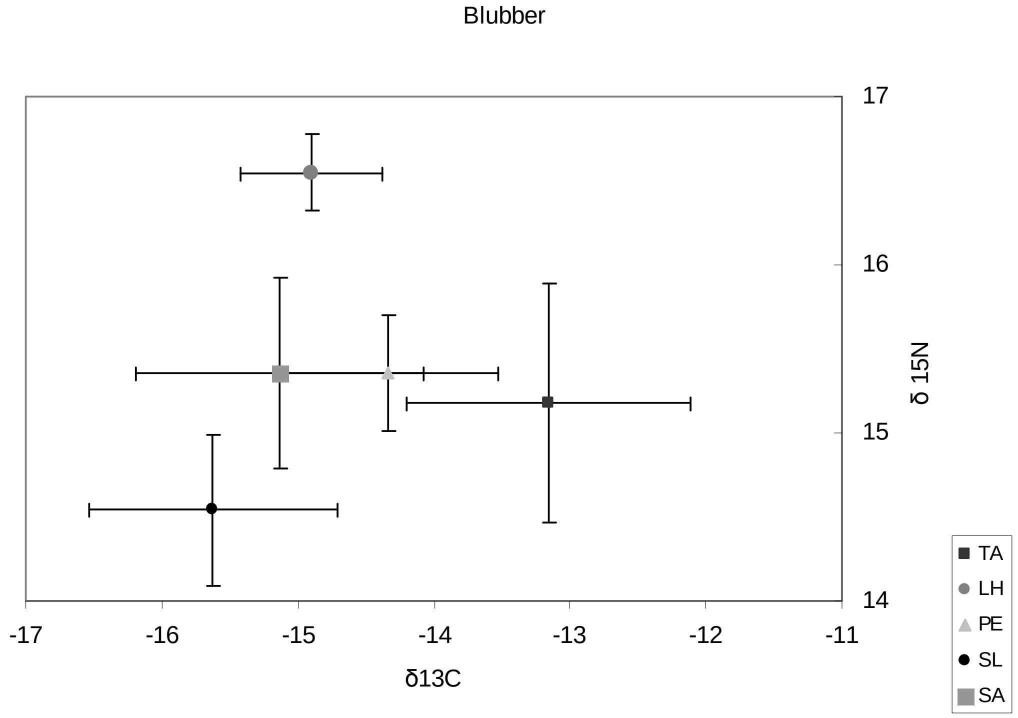

**Figure 4.8:** Mean (and SD) stable isotope values in dolphin blubber.

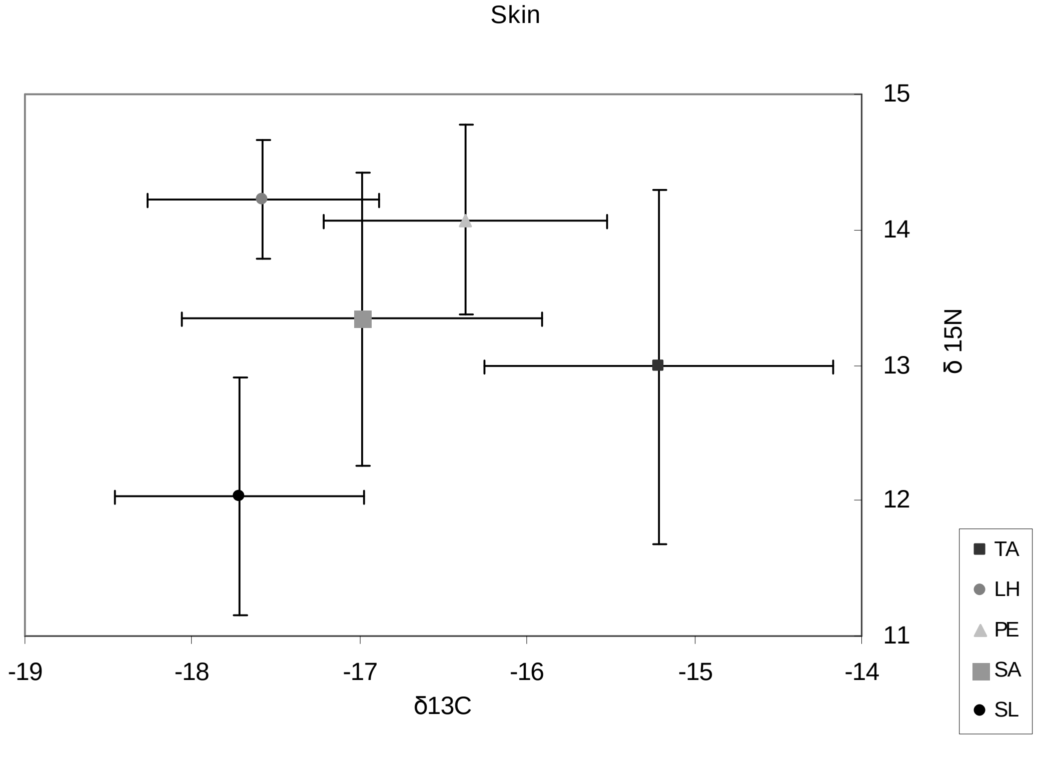

**Figure 4.9:** Mean (and SD) stable isotope values in dolphin skin.

Seasonal variations of stable isotope signatures were observed in both species for skin and blubber tissues (Table 4.5). In the two species of the genus *Stenella* and the melon-headed whale, $\delta^{13}$C values were more negative during the rain season. A reverse situation was observed in *T. aduncus* during the rain season; $\delta^{15}$N values were decreasing for *Stenella* dolphins and *P. electra*, while increased in *T. aduncus*. However, while (sometimes) statistically significant in some cases, seasonal variations appear to be relatively limited.

**Table 4.4:** Pairwise Mann-Whitney U test p values for each pairs of delphinid species in carbon and nitrogen in skin and blubber. Values in bold are statistically significant.

| **SKIN** | | | | |
|---|---|---|---|---|
| **Nitrogen** | *Lagenodelphis hosei* | *Peponocephala electra* | *Stenella attenuata* | *Stenella longirostris* |
| *Tursiops aduncus* | **0.01** | **0.001** | 0.125 | **0.0001** |
| *Stenella longirostris* | **0.0001** | **0.000** | **0.00001** | |
| *Stenella attenuata* | **0.01** | **0.009** | | |
| *Peponocephala electra* | 0.232 | | | |
| **Carbon** | | | | |
| *Tursiops aduncus* | **0.00001** | **0.00001** | **0.000** | **0.000** |
| *Stenella longirostris* | 0.339 | **0.000006** | **0.02** | |
| *Stenella attenuata* | 0.157 | **0.008** | | |
| *Peponocephala electra* | **0.008** | | | |
| **BLUBBER** | | | | |
| **Nitrogen** | | | | |
| *Tursiops aduncus* | **0.0000835** | **0.022** | 0.08 | **0.000742** |
| *Stenella longirostris* | **0.000083** | **0.000** | **0.000004** | |
| *Stenella attenuata* | **0.0001** | 0.485 | | |
| *Peponocephala electra* | **0.0001** | | | |
| **Carbon** | | | | |
| *Tursiops aduncus* | **0.0002** | **0.000001** | **0.000** | **0.000** |
| *Stenella longirostris* | **0.02** | **0.00001** | 0.182 | |
| *Stenella attenuata* | 0.242 | **0.003** | | |
| *Peponocephala electra* | 0.112 | | | |

**Table 4.5:** Pairwise Mann-Whitney U test p values for seasonal differences of stable isotope signatures for each species and type of tissue.

| Species/Season | Blubber | Skin |
|---|---|---|
| ***Tursiops aduncus*** | | |
| Dry season | **Significant for N (+)** | **Significant for N (+)** |
| Rain season | Not significant for C | Not significant for C |
| ***Peponocephala electra*** | | |
| Dry season | Not significant for N | Not significant for N |
| Rain season | Not significant for C | **Significant for C (-)** |
| ***Stenella attenuata*** | | |
| Dry season | Not significant for N | Not significant for N |
| Rain season | **Significant for C (-)** | **Significant for C (-)** |
| ***Stenella longirostris*** | | |
| Dry season | Not significant for N | **Significant for N (+)** |
| Rain season | Not significant for C | Not significant for C |

## Discussion

### General

This study represents a detailed study on habitat and resource segregation among tropical dolphins around Mayotte, in the southwest Indian Ocean. It integrates several methods implemented over four years, with varying temporal resolutions: from instantaneous sighting data and behavioural observations collected during daylight hours to stable isotope analyses in skin that represents the foraging niche over days or in the blubber which integrates stable isotope signatures over months (Abend & Smith, 1995). The indicators were selected for their ability to document the main dimensions of the ecological niche along which segregation might occur: physiographic characteristics describe the spatial dimension of the ecological niche, carbon isotopic signature focuses on the coastal-offshore gradient of the foraging niche, nitrogen isotopic signature expresses the resource dimension of the niche, and the daily activity budget deals with temporal dimension.

Overall, the main finding of this work is that none of the indicators of trophic niche dimensions, examined solely, reveals complete ecological segregation amongst the four species studied, but the combination of all indicators do (Table 4.6). Hence, physiographic characteristics of habitats used by the dolphins during daylight, when visual observations were possible, only allow the Indo-pacific bottlenose dolphin to be differentiated from the others. Carbon isotope signatures allow the melon-headed whale to be separated from the

*Stenella* dolphins. Finally nitrogen isotopic signature and activity budget identify differences between spinner and pantropical spotted dolphins.

**Table 4.6:** Summary of results obtained for the four indicators of ecological niche dimensions among the Mayotte delphinid community. Different letters denote species that segregate for the indicator being considered.

| **Indicators of niche dimensions** | *Tursiops aduncus* | *Stenella attenuata* | *Stenella longirostris* | *Peponocephala electra* |
|---|---|---|---|---|
| Physiographic characteristics | A | B | | |
| Carbon isotopic values | A | B | | C |
| Nitrogen isotopic values | A | | B | C |
| Daily activity rhythm | A | B | C | Not investigated |

Identifying the limitations of the study is necessary for delineating its validity range. Most daily field trips were undertaken from Mayotte main harbour located on the east coast of the island and were limited to daylight hours. Hence, effort was concentrated in the lagoon and the vicinity of outer slope of barrier reef, within the 1000 m isobath, and nocturnal distribution and activity could not be documented. The resource dimension of the niche was documented in a very integrated way, as C and N isotopic contents of a predator express foraging habitat and trophic level but not diet *per se*, which is only documented by sporadic direct observations when no biological material is available. Also, in stable isotopes analyses, as in most studies relying on the use of ecological tracers transmitted via food (e.g. fatty acids, contaminants, heavy metals), only differences in stable isotope contents are really informative, whereas similarities may result from a variety of prey combinations. Finally, behavioural budget data is limited by our capacity to infer dolphin underwater activity from surface events. In particular, foraging, which is the key activity to consider when investigating segregation mechanisms, can either be associated to no or barely visible surface events or to explicit and often highly dynamic ones. Nonetheless, in a multifaceted approach as the one followed here, the limitations of each indicator tend to be compensated by the others. For instance, stable isotope analyses reveal foraging habitat and trophic level of prey eaten day and night over the past few days or months, which is extremely useful to disentangle the inherent ambiguities of observations limited to daylight hours. Conversely, behavioural data can help identify differences in foraging strategies that cannot be found in stable isotope analyses.

The ecological significance of these indicators will now be interpreted sequentially from those related to the spatial, the resource and finally the temporal dimensions of the ecological niche.

### Spatial segregation inferred from direct observations and $\delta^{13}C$ signatures

This study confirms that *T. aduncus* is associated to coastal, shallow water and reef habitats. Its ecological niche clearly differs spatially from the other species of the community. Coastal foraging habitats are confirmed by high $\delta^{13}C$ value indicating a benthic carbon source that is primarily available in coastal environments (Hobson, 1999). Preference for coastal habitat is reported throughout species range, a preference shared with the Indo-pacific humpback dolphin, *Sousa chinensis,* which is present in very low numbers around Mayotte, and therefore could not be considered in this work.

*S. longirostris* and *S. attenuata* co-occur in waters along the outer slope of the barrier reef around Mayotte. They overlap extensively, but the latter tends to occur in deeper waters, located further offshore. Low $\delta^{13}C$ values found in both species, with extensive overlap, are in line with foraging habitats located outside the lagoon at epipelagic depths; this interpretation is reinforced by the overlap also found between the two *Stenella* and the Fraser's dolphin, a typically oceanic dolphin. The pattern observed around Mayotte has also been reported from other insular populations, such as off La Réunion where spotted dolphins occur in deeper, more offshore waters than spinners do (Dulau-Drouot *et al.*, 2008). These two species are not restricted to peri-insular waters; instead vast populations of the two species also dwell in the open ocean (Wade & Gerrodette 1992; Ballance & Pitman, 1998). In this situation, extensive overlap in preferred habitat is also observed, as reported from the western South Atlantic and the eastern tropical Pacific (Polachek, 1987; Moreno *et al.*, 2005).

For melon-headed whale, a fairly limited number of sightings were collected, allowing only a partial description of its habitat preferences. Nevertheless, habitat physiographic characteristics of *P. electra* as documented in this work were significantly different from *S. longirostris*, but could not be differentiated from *S. attenuata*. The melon-headed whale has a more oceanic distribution than the other species (Brownell *et al.*, 2009) and it is unknown whether the groups seen around Mayotte are mostly oceanic dwellers that occasionally visit peri-insular waters or if they display some group-specific preference for the peri-insular slope, a habitat that they could exploit around all islands, reefs and seamounts from off the northern end of Madagascar to Grande Comore (western Comoros archipelago). Quite interestingly,

$\delta^{13}C$ values measured in the melon-headed whale are intermediate between the epi- to mesopelagic *Stenella* and Fraser's dolphins and the coastal dwelling Indo-pacific bottlenose dolphin, rather than being identical to the *Stenella* carbon isotopic content as could be expected from the similarity found in physiographic characteristics. This would suggest spatial segregation along a vertical axis, with melon-headed whales foraging deeper and hence closer to benthic carbon sources than *Stenella* spp. do.

### Resource partitioning inferred from $\delta^{15}N$ signatures

Nitrogen isotopic signatures are the main source of information on resource utilization by dolphins in Mayotte. Direct evidences of resource use are limited to some anecdotal observations of prey hunt or capture by *T. aduncus* and *S. attenuata* (Kiszka and Pusineri, unpublished observations). Carbon isotopic signatures of fish collected in the lagoon also convey some contextual information on plausible prey for the more coastal dolphins. Finally, when comparing trophic levels inferred from $\delta^{15}N$ signatures one should only consider in the comparison dolphin species with overlapping $\delta^{13}C$ signatures, i.e. living in the same habitat, because reference levels of $\delta^{15}N$ in oceanic vs. lagoon habitats are unknown.

Indo-pacific bottlenose dolphins isotopic content can be compared to the isotopic signature of putative prey fish collected in the lagoon. The herbivorous fish *Siganus argenteus* and *Scarus russelii* have $\delta^{13}C$ values 2-4 ‰ higher than *T. aduncus,* and would therefore unlikely be important components of its diet. In contrast, blue trevally *Caranx melampygus* and blackbarred halfbeak *Hemiramphus far* display carbon and nitrogen signatures about 0.5-1.5 ‰ and 3-4 ‰ lower respectively than *T. aduncus*; such differences fit well with an enrichment of one trophic level. Therefore, these two predatory fish would be plausible major prey for *T. aduncus*. Anecdotal direct observations in Mayotte are in line with this interpretation even if other fishes, like the mullet *Mulloidichthys vanicolensis,* were also observed being preyed upon (Kiszka and Pusineri, unpublished observations). Our result is also consistent with existing information on the diet of the Indo-Pacific bottlenose dolphin in the region (Zanzibar, Tanzania), suggesting this species forage on a large number of prey species, especially reef fish (Amir *et al.*, 2005). Elsewhere, *T. aduncus* is known to feed on fish species that do not aggregate in large schools (Mann *et al.*, 2000).

The two *Stenella* have largely overlapping ranges of both physiographic habitats and carbon isotopic contents, even if *S. attenuata* is seen a bit farther offshore and is nonetheless slightly carbon-enriched (higher $\delta^{13}C$ ratios). According to $\delta^{15}N$ values, pantropical spotted dolphins are on average *c.* 1.5‰ higher than spinner dolphins, *i.e.* half a trophic level, which would express some degree of niche segregation between the two species. In addition to this, *S. attenuata* seems to have a wider niche breadth than *S. longirostris*. Pantropical spotted dolphins have been frequently observed feeding close to the barrier reef where their prey aggregate (fishes of the genus Exocoetidae; Kiszka and Pusineri, unpublished observations), in agreement with their slightly higher $\delta^{13}C$ signature. Fine-scale processes allowing niche differentiation between the two *Stenella* species have also been found in other regions, such as in the eastern tropical Pacific (Perrin *et al.*, 1973). Spinner dolphins there are reported to feed at night upon scattering–layer organisms, *i.e.* on vertically migrating mesopelagic fishes, cephalopods and crustaceans, caught in the upper 200 m and occasionally as deep as 400 m (Perrin *et al.*, 1973; Norris *et al.*, 1994; Dolar *et al.*, 2003). Conversely, pantropical spotted dolphins would feed day and night on epipelagic fishes and cephalopods (Perrin *et al.*, 1973).

Melon-headed whales were observed in much the same habitats as pantropical spotted dolphins, but comparatively higher $\delta^{13}C$ values suggested vertical segregation could occur. Nitrogen isotopic content further suggests a slightly higher trophic level (about 1/3 trophic level). Earlier works report mesopelagic fishes and cephalopods, supposedly preyed upon in the upper 700 meters, as the main component of its diet (Young, 1978; Brownell *et al.*, 2009). An element of comparison is provided by the Fraser's dolphin, which was added to the study in an attempt to provide isotopic reference for a true oceanic predator; in addition to this, the species is frequently observed forming mixed group with melon-headed whale (Jefferson & Barros, 1997; Kiszka *et al.*, 2007a; Dulau-Drouot *et al.*, 2008). Not surprisingly, Fraser's dolphins display the second lowest $\delta^{13}C$ values, in agreement with their oceanic lifestyle, and the highest $\delta^{15}N$ values, that fit well with the higher trophic level, likely associated with its preference for larger prey already reported elsewhere (Dolar *et al.*, 2003). Studies of stomach contents from the Pacific suggest this species feeds on relatively large mesopelagic fish and cephalopods from near the surface to probably as deep as 600 meters (Robison & Craddock, 1983; Dolar *et al.*, 2003). In Mayotte, Fraser's dolphins and melon-headed whales, although generally seen associated, do not overlap in their isotopic niches, the latter being more $\delta^{13}C$ enriched than the former, which could be interpreted as feeding a deeper food source, possibly associated to peri-insular slopes, whereas the Fraser's dolphin would rely on large epi- to-mesopelagic truly oceanic prey. These two species might associate for other reasons than foraging, such as social advantage or vigilance against predators.

### Temporal segregation inferred from seasonal patterns and activity budgets

Our study did not reveal seasonal variations of occurrence or habitat preferences as based on the analyses of visual observations; this could be linked to the absence of seasonal variability in tropical environments (Cherel *et al.*, 2008). On the other hand, stable isotope signatures displayed significant differences between dry and rain seasons in all species. Oceanic species, *i.e.* spinner, pantropical spotted dolphins and melon-headed whales, had similar variations. Conversely, the Indo-Pacific bottlenose dolphin had opposite variations. This later species only forage in the lagoon, and, during the rain season, $\delta^{13}C$ signatures is higher which could be linked to increasing hydrodynamic activity and remobilisation of benthic sources of carbon in the lagoon. It is therefore suggested that all species have the same habitat use year-round, but isotopic content can vary seasonally as a result of hydro-climatic processes.

At a finer time scale, segregation mechanisms could rely on differential daily activity budget between species; this aspect was investigated in the bottlenose and the two *Stenella* dolphins, but not in the melon-headed whale. Foraging activities of *Tursiops aduncus* were observed throughout the day, but more frequently in the morning, closer to shore. A similar pattern was observed in common bottlenose dolphins (*Tursiops truncatus*) in Florida (Shane, 1990). Pantropical spotted dolphins feed during daylight, with an increase in feeding activity along the day. Nocturnal feeding is not excluded for these two species but could not be accessed directly. Spinner dolphins would only feed at night as foraging was never observed during daylight hours. Behavioural ecology of spinner and pantropical spotted dolphins around Mayotte is similar than in other areas, including around Hawaii and in the oceanic eastern tropical Pacific (Perrin *et al.*, 1973; Norris *et al.*, 1994). Our results underline a clear pattern of niche segregation along the time dimension, at least during the day.

### Final comments

Three main dimensions define the ecological niche of a species: habitat, diet and time. Our study integrated these three axes to investigate ecological niche segregation among the delphinid community found around Mayotte. Habitat has been assessed through the investigation of the relationships between delphinid distribution and environmental variables (particularly physiography). Trophic level and foraging habitat have been assessed indirectly, through the use of stable isotopes of N and C respectively (De Niro & Epstein, 1978; Kelly, 2000). Finally, the temporal component of the ecological niche has been integrated through the study of behavioural budgets, especially their diurnal variations that may potentially segregate species' ecological niche. The use of multiple approaches (habitat, behaviour and feeding ecology studies) was most useful to investigate ecological niche segregation, especially when looking at closely related species within a common restricted range. The conceptual scheme of resource partitioning inferred from these measurements proposes that:

1 - Indo-Pacific bottlenose dolphin is mostly confined to inner reef sometimes very coastal habitats, where it feeds diurnally (possibly nocturnally as well, although this could not be documented), with daily routines that would follow variation in prey catchability during the day, e.g. mullets being often caught close to the coast in the morning, and *Caranx melampygus* and *Hemiramphus far* the rest of the day across the lagoon;

2 – Spinner dolphin lives in outer reef habitats and would forage only nocturnally on small mesopelagic prey;

3 – Pantropical spotted dolphin also lives in outer reef habitats, that largely overlap with the spinner’s, but would feed at least partly diurnally and at dawn on epipelagic prey, that include flying fish caught closer to the barrier reef;

4 – Melon-headed whale is seen in the same habitat to pantropical spotted dolphins, but would forage deeper over the peri-insular slope.

This ecological segregation is more significant than in other communities, such as in some epipelagic seabirds (Ridoux, 1994; Cherel *et al.*, 2008). Conversely, in diving predators such as large pelagic fish and dolphins, ecological niche segregation is clearly distinguishable (e.g. Potier *et al.*, 2004; Ménard *et al.*, 2007; Praca & Gannier, 2008). This could be related to the low spatial structure of marine ecosystems in tropical and oligotrophic areas. Conversely, clear isotopic and resource-related gradients can be found in subpolar and polar environments over large spatial scale (Jaeger, 2009) as well as vertically (including in the tropics), at a small spatial scale in the water column (this study). This vertical gradient is accessible to fish and dolphins, and not in epipelagic seabirds.

Improvement in our understanding of resource partitioning mechanisms among Mayotte delphinids may be obtained in several directions: - investigating acoustically dolphins’ nocturnal distribution and activity; - documenting the regional isoscape by analyzing carbon and nitrogen isotopic composition in particles or filter-feeders collected along a coastal-offshore gradient and along a vertical gradient as well; - investigating residency patterns of dolphin groups living around Mayotte by using photo-identification or individual telemetry approaches, in order to establish whether they are genuinely associated to these peri-insular structures, or have a more oceanic lifestyle, occasionally approaching islands.

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**Synthèse**

Cette étude détaille le partage des habitats et des ressources chez les delphinidés vivant en sympatrie autour de Mayotte. Elle combine l'analyse comparée des habitats préférentiels, des signatures isotopiques du carbone et de l'azote et les variations temporelles de l'utilisation de l'espace et des ressources. Ces indicateurs furent utilisés dans la mesure où ils documentent les trois principales dimensions de la niche écologique. Le résultat principal de ce travail est qu'aucun indicateur pris de manière indépendante ne permet d'établir une ségrégation écologique complète chez les espèces étudiées, alors que l'utilisation combinée de ces indicateurs le permet. L'habitat des delphinidés de Mayotte a été étudié en mettant en relation leur distribution avec les variables physiographiques. Le niveau trophique et les habitats d'alimentation ont été étudiés de manière indirecte par analyse des signatures isotopiques de l'azote et du carbone, respectivement. La dimension temporelle a été étudiée par l'analyse des variations diurnes et saisonnière des budgets d'activité, mais également de l'habitat et des signatures isotopiques. Le modèle conceptuel du partage des habitats et des ressources des delphinidés de Mayotte est le suivant :

- Le grand dauphin de l'Indo-Pacifique a un habitat côtier à l'intérieur du lagon et dans les zones peu profondes des bancs récifaux. Il s'alimente surtout le jour, notamment en début de journée sur des proies à la distribution prévisible et de manière opportuniste sur d'autres proies durant le reste de la journée.
- Le dauphin à long bec se distribue essentiellement le long de la pente externe du récif barrière, s'alimente la nuit sur des proies mésopélagiques.
- Le dauphin tacheté pantropical se distribue également le long de la pente externe du récif barrière (son habitat se chevauche donc partiellement avec celui du dauphin à long bec) et se nourrit la journée (probablement aussi la nuit) sur des proies épipélagiques, incluant les poissons volants présents à proximité de la barrière récifale.
- Le péponocéphale a un habitat proche des autres espèces du genre *Stenella* (notamment du dauphin tacheté pantropical) mais se nourrit la nuit sur des proies mésopélagiques mais d'un niveau trophique supérieur au dauphin à long bec et probablement plus profondément que ce dernier.

Toutefois, il est possible d'observer à Mayotte des associations poly-spécifiques (ou interspécifiques), notamment entre les deux espèces jumelles (le dauphin à long bec et le dauphin tacheté pantropical). Cette situation semble de prime abord en contradiction avec la théorie des niches. Pour cela, la nature de ces associations a été étudiée et est présentée dans le chapitre suivant (partie 5). Il est documenté que ces associations poly-spécifiques peuvent avoir trois significations écologiques principales : l'optimisation de la recherche de nourriture et de la capture des proies, la lutte contre les prédateurs et le renforcement des activités de socialisation. L'étude précédente nous a démontré que le dauphin à long bec et le dauphin tacheté pantropical n'occupaient pas les mêmes niches alimentaires, ce qui semble exclure l'hypothèse de la formation d'associations pour des raisons liées à l'utilisation des ressources. Toutefois, ces associations poly-spécifiques sont fréquentes et le chapitre suivant explore les trois hypothèses (qui ne sont pas mutuellement exclusives) pouvant motiver leur formation.

# Partie 5 :

# Signification écologique des associations poly-spécifiques

# Signification écologique de la formation des associations poly-spécifiques chez les espèces jumelles : *Stenella longirostris* et *Stenella attenuata*

## Résumé

Les associations poly-spécifiques sont des regroupements temporaires d'individus de différentes espèces qui ont une durée de plusieurs minutes à plusieurs années. Trois principales origines fonctionnelles de ces associations ont été documentées jusqu'à présent : la lutte contre les prédateurs, l'optimisation de la recherche alimentaire et de la capture des proies et les avantages sociaux. Les associations poly-spécifiques chez les mammifères et les delphinidés en particulier sont très fréquentes en milieux sauvage. A travers la présente étude, nous avons tenté d'interpréter l'origine de la formation d'associations poly-spécifiques entre deux espèces sympatriques et jumelles de delphinidés : le dauphin à long bec (*Stenella longirostris*) et le dauphin tacheté pantropical (*Stenella attenuata*) des eaux de Mayotte (sud-ouest de l'océan Indien). Nous avons déterminé si ces associations étaient formées pour la lutte contre les prédateurs, l'optimisation de la recherche alimentaire et de la capture des proies et les avantages sociaux. Nous avons utilisé des données d'observation collectées entre 2004 et 2009 dans les eaux de Mayotte tout au long de l'année. Un total de 67 associations poly-spécifiques a été collecté sur un total de 315 observations de deux espèces. Aucune variation saisonnière de l'occurrence des associations n'a été détectée. Les activités comportementales des groupes mono et poly-spécifiques étaient significativement différentes. La prospection alimentaire n'a jamais été observée chez les groupes mono-spécifiques de dauphins à long bec mais cette activité fut observée fréquemment chez les groupes mono-spécifiques de dauphins tachetés. Chez les deux espèces, la taille des groupes était plus importante chez les groupes en association. Enfin, les dauphins à long bec étaient observés dans des eaux plus profondes quand ces derniers étaient observés en association avec les dauphins tachetés. Ceci suggère que les associations poly-spécifiques sont formées pour la lutte contre les prédateurs. Aucune preuve d'association pour la pratique de comportements sociaux n'a été collectée, mais cette possibilité n'est pas rejetée du fait que les interactions sociales échappent pour la plupart aux observations faites depuis la surface. Nous proposons donc que les dauphins à long bec s'associent aux dauphins tachetés pour la lutte contre les prédateurs, notamment lorsqu'ils transitent entre les zones de repos.

# What drives sibling tropical dolphins to form mixed-species associations around Mayotte Island, southwest Indian Ocean?

Jeremy Kiszka [1, 2, *], Claire Pusineri [3] & Vincent Ridoux [1]

[1] LIENSs (LIttoral, ENvironnement et Sociétés), UMR 6250, CNRS-Université de La Rochelle, 2, rue Olympe de Gouges, F-17000, La Rochelle, France.

[2] Direction de l'Environnement et du Développement Durable, Collectivité Départementale de Mayotte. BP 101 F-97600 Mamoudzou, Mayotte.

[3] Office National de la Chasse et de la Faune Sauvage, cellule technique Océan Indien.

**En préparation**

## Abstract

Mixed-species associations are temporary aggregations of individuals of different species involved in similar activities for periods of variable duration, from minutes to days and even years. Three functional explanations to the formation of such associations are foraging, anti predator and social advantages. Mixed-species groups in mammals and delphinids in particular are frequent in the wild. Here we aimed to understand the ecological significance of mixed-species group formation in two sibling tropical delphinids: the spinner dolphin (*Stenella longirostris*), and the pantropical spotted dolphin (*Stenella attenuata*) in waters surrounding the island of Mayotte (Mozambique Channel, southwest Indian Ocean). We determined whether these associations occurred for anti predator, foraging and social advantages. We used sighting data collected from 2004 to 2009 year-round. A total of 67 mixed-species groups of spinner and pantropical spotted dolphins were encountered around Mayotte out of a total of 315 observations of either species (21% of the recorded groups). No daily or seasonal variability of the occurrence of associations were detected. Behavioural activities of single- and mixed-species groups differed significantly. Foraging was never observed in spinner dolphin but only observed in single-species groups of pantropical spotted dolphins. Both species were seen in larger groups when associated. Finally, when in association, spinner dolphins used deeper waters than in single-species groups. These elements suggest that mixed-species groups are formed for anti predator advantage, probably in favour of spinner dolphins. No evidence of association for social advantage was observed but this is not excluded to occur. Therefore, we suggest that spinner dolphins associate with spotted dolphins when transiting between resting areas.

**Keywords:** mixed-species associations, spinner dolphin, *Stenella longirostris*, pantropical spotted dolphin, *Stenella attenuata*, anti predator advantage.

## Introduction

Mixed-species associations have been described in many animal species, including birds, fishes and mammals (Terborgh, 1990). In mammals, they have been particularly reported in ungulates, primates and cetaceans. These mixed-species associations are also called interspecific, polyspecific or heterospecific groups (Stensland *et al.*, 2003). Mixed-species associations are temporary aggregations of individuals of different species involved in similar activities for periods of variable duration, from minutes to days and even years. These associations range from congeneric to non-congeneric species and occur across a wide range of taxa (Stensland *et al.*, 2003). Inter-species associations should be distinguished from aggregations occurring by chance, when two or more species move around independently and mix by responding in a similar way to environmental stimuli (such as a common resource or habitat, Waser, 1982; Stensland *et al.*, 2003). In this case, associations may not have a functional explanation. It is generally accepted that mixed-species associations occur as they provide evolutionary benefit over populations or species that do not mix (Whitesides, 1989; Heymann & Buchanan-Smith, 2000).

Three main functional explanations to the formation of mixed-species associations have been given: foraging, anti predator and social advantages. According to the foraging advantage hypothesis, mixed groups may locate and utilize resource more efficiently than in single species groups. According to the anti predator hypothesis, mixed groups could reduce predation due to their larger group size than single species groups, and detect and deter predators. Another functional explanation of mixed-species groups, the social hypothesis, may provide to mixed-species groups social or reproductive advantages, such as exploitation of larger home ranges, use of different habitats, and practice of social behaviour (Stensland *et al.*, 2003). Mixed-species associations may also constitute a survival strategy for population at very low density (Frantzis & Herzing, 2002).

The function of mixed-species groups in delphinids is not well understood but has been previously documented in various places. For example, common (*Delphinus delphis*), striped (*Stenella coeruleoalba*) and Atlantic spotted dolphins (*Stenella frontalis*) form mixed-species aggregations in the Azores for foraging advantage (Quérouil *et al.*, 2008). As functional hypotheses are not mutually exclusive, two (or more) species might associated for both anti predator and foraging advantages, as suggested in common bottlenose dolphins (*Tursiops truncatus*) and short-finned pilot whales (*Globicephala macrorhynchus*) in the Pacific (Scott & Chivers, 1990).

Inter-species associations between spinner (*Stenella longirostris*) and pantropical spotted dolphins (hereafter spotted dolphins, *Stenella attenuata*) have been documented in the eastern tropical Pacific and western Indian Ocean (Norris & Dohl, 1979; Ballance & Pitman, 1998). In the eastern tropical Pacific, it has been speculated that spinner and spotted dolphins form mixed-species association for anti predator advantages (Norris & Dohl, 1979). Indeed, spinner dolphin may seek the schools of spotted dolphins for refuge during rest in offshore waters. Spinner dolphins are night-time feeders while spotted dolphins would feed primarily during the day (Perrin *et al.*, 1973; Norris & Dohl, 1979; Norris *et al.*, 1994). Associations between these two species may be not food-related as their diets significantly differ (Perrin *et al.*, 1973). Spinner dolphin, while resting during the day, would seek out alert spotted dolphins in order to get protection against predators. This strategy is also supported by behavioural studies of insular spinner dolphins around Hawaii, as they rest during the day in shallow waters with open sandy bottoms where predators are easily detected (Norris & Dohl, 1979; Norris *et al.*, 1994). In the open ocean, where spinner and spotted dolphins occur in sympatry and frequently in association, no safe resting areas are available.

Around the island of Mayotte (Comoros, Mozambique Channel), spinner dolphins and spotted dolphins occur in such close sympatry along the outer slope of the barrier reef that identifying mechanisms allowing ecological partitioning between the two species was challenging (Gross *et al.*, 2009; Kiszka *et al.*, submitted). Hence, habitat partitioning could not be demonstrated from the analyses of either physiographic characteristics associated to day-time visual observations or from $\delta^{13}C$ signatures in skin and blubber biopsies, but some degree of ecological partitioning was found in terms of trophic levels as revealed by $\delta^{15}N$ signatures. Such associations have been rarely documented around islands but they sometimes occur, such as off Oahu where social interactions between the two species have been observed (Hawaii; Psarakos *et al.*, 2003), but very little is known of insular populations of spotted and spinner dolphins, particularly in the Indian Ocean.

Here we firstly aimed to characterize mixed-species associations in terms of occurrence, group size and habitats, as compared to single species group characteristics and secondly to determine whether mixed-species associations likely occurred for anti predator, foraging and social advantages on the basis of the examination of activity budgets. Group size would increase when mixed-species groups are formed, and further, individual vigilance would decrease as a result of the anti-predator advantage of the larger mixed-species group (Cords, 1987; FitzGibbon, 1990; Bshary & Noë, 1997; Hardie & Buchanan-Smith, 1997). Hence, if mixed-species dolphin groups are formed for anti-predator benefits, we would expect that group sizes of mixed-species groups would be larger than single species groups. Finally, if spinner dolphins use the higher vigilance of spotted dolphins while resting, we could observe a higher occurrence of resting behaviour in spinner dolphins when associated to spotted dolphins. On another hand if mixed-species groups would be related to enhanced social opportunities, one should observe a higher proportion of social activities in the activity budget of mixed-species groups than in single-species ones. Similarly, if these associations would provide foraging benefits to either species involved, one should observe more foraging activities in mixed-species groups than in single-species groups.

## Materials and methods

### Study area

Mayotte (45°10'E, 12°50'S) is located in the northern Mozambique Channel, in the Comoros archipelago. The island is almost entirely surrounded by a 197 km long barrier reef. The lagoon and surrounding reef complexes is 1,500 km² with an average depth of 20 m and a maximum depth of 80 m found in the western lagoon. The peri-insular slope off the barrier reef is very steep and contains many submarine canyons and volcanoes. Mayotte is characterized by the presence of high delphinid diversity (12 species; Kiszka *et al.*, 2007). The most common and abundant species are the spinner dolphin (*Stenella longirostris*) and the spotted dolphin (*Stenella attenuata*) (Kiszka *et al.*, 2007). Preliminary abundance estimates obtained from aerial surveys suggest a total number of 703 spinner dolphins (CI 95%, 643 – 1,046) and 375 spotted dolphins (CI 95%, 342 – 557) (Pusineri *et al.*, 2009).

### Data collection

From July 2004 to April 2009, small boat based surveys were undertaken around Mayotte. Surveys were conducted throughout the study period during daylight hours between 07:00 h and 18:00 h in sea conditions not exceeding Beaufort 3. Survey vessels did not follow pre-defined transects but every attempt was made to sample the whole daylight periods as well as each habitat type within the surrounding waters of Mayotte. When dolphins were encountered, standard sighting data were recorded: species, and for each species, group size (maximum, minimum, best estimate), geographic position and behavioural activity. Group size was defined as the number of animals at the surface within five body lengths of each other (Smolker *et al.*, 1992). However, in spinner and pantropical spotted dolphins, groups also consisted in super groups, including several tight aggregations (typically 2 to 10), spaced of a few tens of meters, moving in the same direction and exhibiting similar patterns of behaviour.

The predominant activity was defined as the behavioural state in which most animals (> 50%) of the group were involved at each instantaneous sampling. Typically, more than 90% of the animals in a group were engaged in the same activity. Five categories of behavioural states were defined: milling, resting, travelling, feeding/foraging (hereafter foraging), and socializing as defined in previous studies (e.g. Norris & Dohl, 1979; Bearzi, 2005; Neumann & Orams, 2006; Degrati *et al.*, 2008). Feeding was characterised by loose to disperse group formations and dolphins were observed swimming in circles, and pursuing fishes (preys observed at the surface). Preys were frequently seen at the surface during foraging activity. Travelling consisted of persistent and directional movements of all the individuals of a group. Milling was characterised by non-directional movements of the dolphin, with frequent changes in heading. Socialising consisted in frequent interactions between individuals in the form of body contacts, with high-speed movements, frequent changes in direction and aerial displays. Resting was characterised by low level of activity, with groups in tight formations, with little evidence of forward propulsion. Surfacings are slow and relatively predictable. A mixed-species group was defined as a group that included at least one individual of both species. We considered that the two species were in association when they were observed during more than 15 minutes, moving in the same direction and exhibiting similar patterns of activity. Then, the association was not considered as occurring by chance in our dataset.

### Data analysis

In order to interpret the formation of mixed-species groups, we tested whether the behavioural activities of spinner and spotted dolphins were different when in association *vs* not. We compared the frequencies of activities between single and mixed-species groups using a contingency table analysis (row *vs.* column). We tested if spinner and spotted dolphins had different group size in single *vs* mixed-species aggregations as well as if habitat characteristics (especially related to depth of encounter) were different between the two species when observed in mixed-species groups or not. Non parametric tests were selected because assumptions regarding normality and homogeneity of variance were not met. We compared the frequencies of activities between single and mixed-species groups using a contingency table analysis. Statistical analyses were made in Microsoft Excel with the significance level set at $\alpha$=0.05.

## Results

### Occurrence of mixed-species groups

From July 2004 to March 2009, data were collected during 224 daily small boat-based surveys. A total of 67 sightings of mixed-species associations of spinner and spotted dolphins were recorded. Single species groups were encountered on 195 occasions for *S. longirostris* and on 53 occasions for *S. attenuata.* Mixed-species groups represented 21% of the total recorded groups. No daily (Kruskal-Wallis test: $H_2$=3.714, $P > 0.05$) nor seasonal (Kruskal-Wallis test: $H_3$=3.837, $P > 0.05$) variability of the occurrence of mixed-species groups were detected.

### Group composition and size

When associated, spinner and spotted dolphins where observed in similar proportion (mean=50%), from 7 to 97% for spinner dolphins and from 3 to 93% for spotted dolphins. No difference of group size was observed between spinner and spotted dolphin when associated with each other ($P > 0.05$). In single-species groups, group size of spinner and spotted dolphins were not statistically significant ($P > 0.05$). However, there was a significant difference in group size between single- and mixed-species groups (Kruskal-Wallis test: $H_2$=87.73, $P < 0.001$), as both spinner and spotted dolphins were present in larger aggregations when associated ($P < 0.001$ for both species; Figure 5.1).

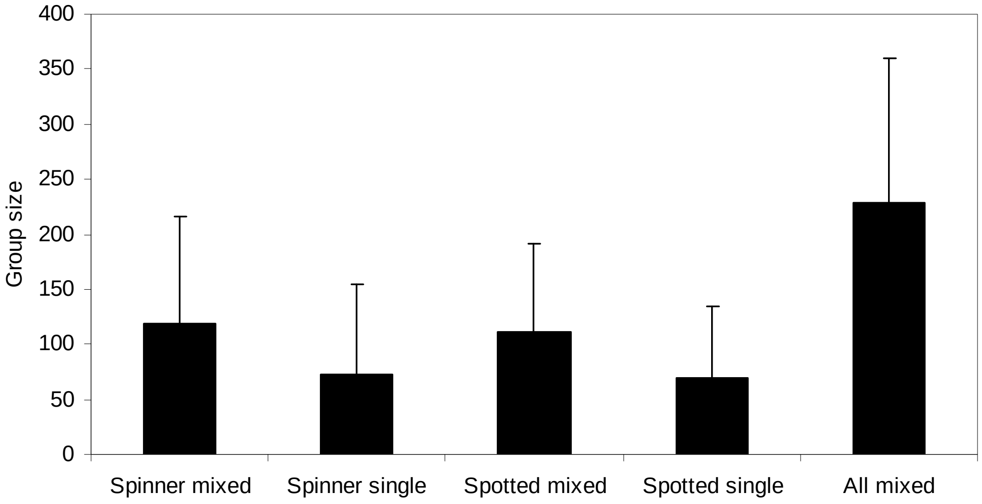

**Figure 5.1:** Mean group size (with Standard Deviation) of single and mixed-species groups of spinner dolphins and pantropical spotted dolphins around Mayotte from 2004 to 2009.

### Depth

There was a significant difference of depth preferences between mixed-species groups and single-species groups of spinner dolphins ($U$ = 4340; $P$ = 0.02). Indeed, when associated to spotted dolphins, spinner dolphins occurred in deeper waters (*S. longirostris* non-associated: mean=219.9, SD=175.2; *S. longirostris* associated: mean=267.3; SD=202.5). Spotted dolphins were seen in similar depths either when associated or not ($U$ = 1327; $P$ = 0.49; Figure 5.2).

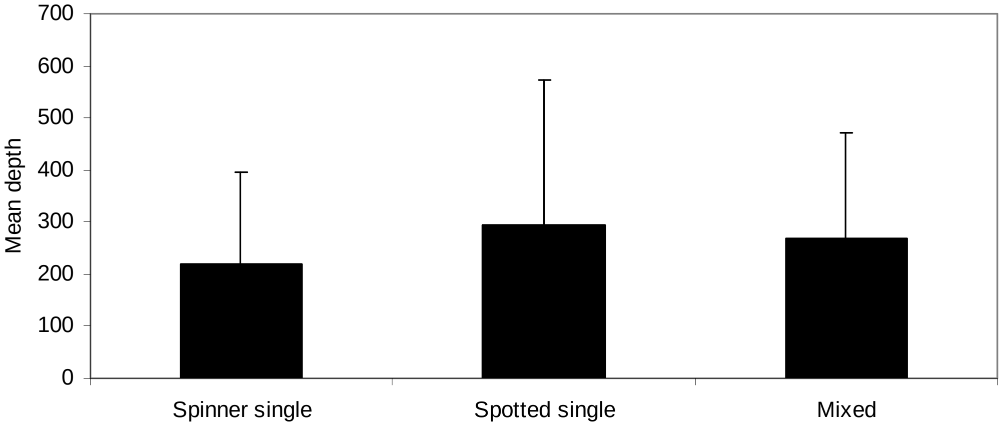

**Figure 5.2:** Mean depth (with Standard Deviation) of single and mixed-species groups of spinner dolphins and pantropical spotted dolphins around Mayotte from 2004 to 2009.

### Activities

The behavioural activities of single and mixed-species groups of spinner and spotted dolphins were significantly different ($\chi^2$ = 26.4, $df$ = 6; $P$ < 0.001). The spotted dolphin was the only species seen foraging in monospecific groups, while no foraging events were observed when this species was in association with spinner dolphins (Figure 5.3).

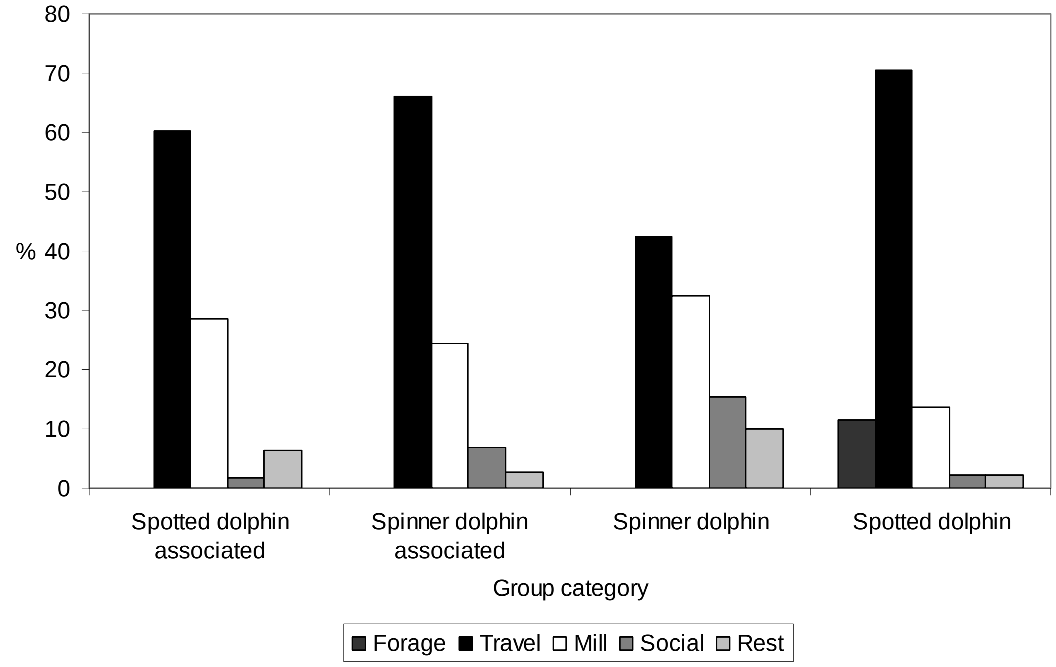

**Figure 5.3:** Occurrence of behavioural states observed in single and mixed-species groups of spinner dolphins and pantropical spotted dolphins around Mayotte from 2004 to 2009.

When in association with spotted dolphins, spinner dolphins increased their travel activity and decreased their social and resting behaviours. No direct interactions between spinner and spotted dolphins were observed across the study period.

## Discussion

Spinner and spotted dolphin formed frequent mixed-species groups around the island of Mayotte. Spotted dolphins were also more frequently encountered in association with spinner dolphins than in single species groups. Group sizes were larger and travelling was a more predominant activity in mixed-species groups than in single-species groups of either spinner or spotted dolphins. In addition to this, water depth used by mixed-species groups was deeper than of spinner dolphin single-species groups and could not be differentiated from spotted dolphin single-species groups. Behavioural activities other than travelling and milling were marginally represented and in particular foraging behaviours were absent. Conversely, single-species groups of spotted dolphins were frequently seen foraging, but not spinner dolphin single-species groups.

The inherent difficulty of this type of investigation is the lack of reference situation that precludes a proper experimental approach that would allow a clear testing of whether observed associations between spinner and spotted dolphins result from deliberate decisions or random events. Other limitations are common to all studies of delphinid activity budgets and include mostly limited sample size and the difficulty to infer underwater activities from surface observations only. Nonetheless, the present study provides new insights on the characteristics and circumstances in which mixed-species associations of small delphinids occur.

The present observation excludes the foraging advantage hypothesis, as this activity was absent from behaviours recorded for mixed-species aggregations. Moreover, previous studies on the comparative feeding ecology of spotted dolphins and spinner dolphins, such as in the oceanic eastern tropical Pacific or around Mayotte, showed that the two species use distinct feeding niches (Perrin *et al.*, 1973; Kiszka *et al.*, submitted) and therefore are unlikely to forage jointly. Among the five activity categories, travelling and to a lesser extend milling were markedly higher in mixed-species groups than in single species ones. In addition to this, the depth range at which most of these associations occur is higher than for spinner dolphin single-species groups. Therefore we propose as an explanatory hypothesis that, around Mayotte, spinner dolphins that usually rest in shallow waters during the day would associate with spotted dolphins when moving offshore between resting sites. Hence, the multi-species aggregation observed between spotted and spinner dolphins would represent some anti-predator benefits for the spinner dolphin. Group sizes support this explanatory hypothesis. Group sizes of mixed groups were significantly larger than in single-species groups. This suggests that one or both of the two species may decrease individual vigilance as a result of anti-predator advantage of the larger mixed-species group. It seems that the benefits would rather be for the spinner dolphin than for the spotted dolphin. Indeed, this species is smaller, and probably less alert during the day (at least during the morning as spinners do forage at night offshore; Norris *et al.*, 1994), and the presence of spotted dolphin may decrease predation risk for spinner dolphins.

It has not been possible to get information on the density of large predatory sharks around Mayotte, and relate this information with the presence of single and mixed species groups of spinner and spotted dolphins. Nonetheless, large species that are known to prey upon small delphinids are tiger shark (*Galeocerdo cuvier*), hammerhead sharks (*Sphyrna* spp.), the short-fin mako shark (*Isurus oxyrinchus*), the bull shark (*Carcharhinus leucas*) or the oceanic whitetip shark (*Carcharhinus longimanus*), also recorded around Mayotte (Heithaus, 2001; Jamon *et al.*, 2010). Several cases of severe injuries made by sharks on dolphins were observed around Mayotte, especially in coastal bottlenose dolphins (*Tursiops* aduncus, Kiszka *et al.*, 2008). This highlights the importance of the predation risk for dolphins in this area.

In previous works, it has been hypothesised that oceanic populations of spinner and spotted dolphins were seen in association for anti predator advantage because of the higher predation risk in offshore waters of the eastern tropical Pacific (Norris & Dohl, 1979). However, several large predatory sharks are abundant in shallow waters (over seagrass beds and coral reefs), such as the tiger shark in Shark bay (e.g. Heithaus & Dill, 2002). Spinner dolphins may also face predation risk around this insular/reef associated environment, where sharks may be abundant. Interestingly, around Réunion Island, in the Mascarenes, spinner dolphin frequently associates with another delphinid species, the Indo-Pacific bottlenose dolphin, which occurs in coastal waters. Associations between spinner and bottlenose dolphins around Réunion Island may be due to the closer proximity of spinner and bottlenose dolphin habitat as there is no lagoon around Réunion (Dulau-Drouot *et al.*, 2008). Conversely, around Mayotte, spinner dolphins live outside the lagoon while bottlenose dolphin occurs inside. Spinner dolphins live in direct sympatry with spotted dolphins, which could influence inter-species association rates between these two species. No interactions between spinner and spotted dolphins were observed in mixed-species groups around Mayotte. Hence, it is difficult to speculate on the social advantage hypothesis. Indeed, male spotted dolphins (either in alliance formation or not) may experiment herding smaller and weaker female spinner dolphins (like bottlenose dolphins do with young female of Atlantic spotted dolphins, *Stenella frontalis* in the Bahamas; Herzing & Johnson, 1997). In the future, they may become more successful in herding females of their own species and increase their reproductive success. However, we did not observe any inter-species interactions (direct contacts, pursuits, etc.) between spinner and spotted dolphins around Mayotte. However, spinner dolphins may use larger home ranges and different habitat when in association with spotted dolphins. It also confirms that spinner dolphins may benefit from the association with spotted dolphins.

### Conclusion

Spinner dolphins seem to associate with spotted dolphins for anti predator advantage, but the social advantage hypothesis is not excluded. When associated, spinner dolphins use deeper waters where spotted dolphins preferentially occur, which may constitute a strategy to detect and deter predators such as large sharks. When seen in association, spotted dolphins are not seen foraging and spinner dolphins are mostly observed travelling. Therefore, we suggest that spinner dolphins associate with spotted dolphins when transiting between resting areas.

**Synthèse**

Les associations poly-spécifiques entre dauphins à long bec et dauphins tachetés sont fréquentes à Mayotte. Il semble que l'origine de la formation de ces associations soit la lutte contre les prédateurs, qui serait surtout bénéfique pour le dauphin à long bec, notamment lorsque celui-ci se déplace entre ses zones de repos. Toutefois, la formation d'associations pour certains avantages sociaux n'est pas exclue puisque certains comportements, notamment ceux se produisant sous l'eau, ne peuvent être observés depuis un bateau.

Cette étude illustre également que les niches écologiques de ces deux espèces sont bien distinctes et que la formation d'associations, même si elle et temporaire, permet à ces deux espèces de tirer un profit, en l'occurrence celui de la diminution des interactions avec les prédateurs (même si ce profit semble davantage profitable au dauphin à long bec). L'étude confirme également la nécessité d'intégrer la composante comportementale dans l'analyse des niches écologiques à l'échelle d'une communauté, soit un quatrième axe (ou dimension) de la niche écologique.

L'étude suivante permet d'explorer la ségrégation des niches à l'échelle intra-spécifique. Cette approche a été envisagée chez l'espèce qui constitue un modèle facile d'accès, facilement identifiable et dont la faible taille de population permet d'analyser l'écologie à une échelle individuelle : le grand dauphin de l'Indo-Pacifique (*T. aduncus*). L'approche envisagée consistera en l'étude de la structure de population à fine échelle autour de Mayotte et ce à des échelles emboitées : de la structure génétique (long terme) à la ségrégation individuelle pour l'occupation de l'espace (court terme). L'analyse de l'habitat et du domaine vital individuels et des signatures isotopiques du carbone et de l'azote permettront de définir si des communautés de grands dauphins se partagent l'espace et les ressources, respectivement. Ces communautés sont des ensembles d'individus (et non d'espèces) partageant un même territoire et interagissant sur le plan social. Ils sont donc susceptibles de former des groupes dont les individus sont préférentiellement associés voire génétiquement distincts.

# Partie 6 :

# Structure de population à fine échelle et ségrégation intra-spécifique

# Structure de population à fine échelle et ségrégation intra-spécifique chez le grand dauphin de l'Indo-Pacifique *Tursiops aduncus*

## Résumé

Le grand dauphin (*Tursiops* sp.) est un petit cétacé qui au sein d'une population donnée peut constituer des communautés, constituée par des individus s'associant préférentiellement et partageant un domaine vital commun. Autour de l'île de Mayotte (45º10'E/12º50'S) vit une population d'environ 100 grands dauphins de l'Indo-Pacifique (*Tursiops aduncus*). Nous avons étudié la structure de cette population à fine échelle et les processus de ségrégation intra spécifique. Nous avons déterminé si la population de grands dauphins de Mayotte formait des communautés. Différents outils analytiques ayant des résolutions temporelles variables ont été employés. Des campagnes à bords d'embarcations légères ont été réalisées entre 2004 et 2008 pour collecter des données de photo identification et des biopsies cutanées. Des analyses de l'ADN mitochondrial (254 paires de base de la région du gène du cytochrome b) et 14 marqueurs microsatellites ont été utilisés pour examiner la structure génétique de la population. Les analyses n'ont pas révélé de polymorphisme et la présence d'un unique groupe panmictique à l'équilibre de Hardy Weinberg. Les données de photo identification ont été utilisées pour étudier la fidélité au site, calculer la taille du domaine vital grâce à la méthode des Polygones Convexes Minimum (MCP) et évaluer les préférences individuelles en relation avec la physiographie. Les analyses du domaine vital et de l'habitat des grands dauphins de l'Indo-Pacifique montrent la présence d'au moins deux communautés de grands dauphins dans le lagon de Mayotte. Des analyses des isotopes stables du carbone ($\delta^{13}C$ reflétant les habitats d'alimentation) et de l'azote ($\delta^{15}N$ reflétant le niveau trophique) ont été réalisées dans les tissus de peau et de lard collectés par biopsies. L'objectif était de détecter des différences interindividuelles de l'alimentation et de l'habitat. La variabilité des signatures isotopiques était importante mais aucune structure au sein de la population ne fut découverte. Enfin, l'étude du fonctionnement social à travers les associations a confirmé l'existence de deux communautés de grands dauphins autour de Mayotte, dont les membres ne sont pas apparentés.

# Fine scale population structure and intra-species segregation of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in a tropical lagoon

Jeremy Kiszka [1, 2 *], Benoit Simon-Bouhet [1], Caroline Gastebois [1], Claire Pusineri [3], Vanessa Becquet [1] & Vincent Ridoux [1]

[1] LIENSs (LIttoral, ENvironnement et Sociétés), UMR 6250, CNRS-Université de La Rochelle, 2, rue Olympe de Gouges, F-17000, La Rochelle, France.

[2] Direction de l'Environnement et du Développement Durable, Collectivité Départementale de Mayotte. BP 101 F-97600 Mamoudzou, Mayotte.

[3] Office National de la Chasse et de la Faune Sauvage, cellule technique Océan Indien, Mayotte.

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## Abstract

Bottlenose dolphins (*Tursiops* sp.) are coastal cetaceans in which a given population may segregate into communities, defined by common patterns of home range and association. Around the island of Mayotte (45°10'E/12°50'S), there is a population of about 100 Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). We investigated the fine-scale population structure and patterns of within-species segregation of this species around Mayotte. We assessed population structure and the existence of bottlenose dolphin communities. We combined several tools with various temporal scales in order to achieve this. Photo-identification data and biopsy samples were collected during small-boat dedicated surveys from 2004 to 2008. Genetic analyses using mtDNA (254 bp region of the cytochrome b gene) and 14 microsatellite markers were performed to examine the genetic structure of the population. The analyses revealed no mitochondrial polymorphism and the presence of a single population at Hardy-Weinberg equilibrium. Photo-identification data were used to assess patterns of site fidelity, calculate individual home range size using Minimum Convex Polygons (MCP), as well as individual habitat preferences (related to physiography). Home range analysis revealed the presence of at least two communities of Indo-Pacific bottlenose dolphins around Mayotte, based on their individual habitat preferences, home range size and location. Stable isotope analyses of $\delta^{13}C$ (feeding habitats) and $\delta^{15}N$ (trophic level) were performed by using skin and blubber samples to detect potential intra-species segregation of the diet. $\delta^{13}C$ and $\delta^{15}N$ values were highly variable among individuals and no structure across the population was detected. Finally, association indices were calculated, confirming the presence of at least two bottlenose dolphin communities around Mayotte, with no kinship among members.

**Keywords:** Indo-Pacific bottlenose dolphin, *Tursiops aduncus*, population structure, social structure, association patterns, community structure, stable isotopes, home range.

## Introduction

Understanding population structure requires a number of information, including rates of genetic flow and patterns of genetic structure. The genetic structure of marine populations is driven by a number of processes, such as water currents, sea floor topography, water temperature, life history and behaviour (e.g. Fullard *et al.*, 2000; Fontaine *et al.*, 2007). For wide-ranging animals such as cetaceans, significant genetic population structure may be found over large spatial scales, such as in north Atlantic common dolphins (*Delphinus delphis*; Mirimin *et al.*, 2009) or southern Hemisphere humpback whales (*Megaptera novaeangliae*; Rosenbaum *et al.*, 2009). At the local scale (an archipelago, a gulf), some fine-scale mechanisms of genetic structure may occur, particularly in resident species such as in the French Polynesian spinner dolphin (*Stenella longirostris*; Oremus *et al.*, 2007) or the Gulf of Mexico common bottlenose dolphin (*Tursiops truncatus*; Sellas *et al.*, 2005). In these cases, population structure is likely to be driven by habitat characteristics, especially depth that partition home ranges and populations (*e.g.* inshore *vs*. offshore populations, populations differentiated among islands). At the life-scale of individuals (or a few generations), population structure may also occur, which cannot be highlighted through genetic analyses. This finer-scale structure is likely to be driven by differential patterns of habitat and resource use. For example, in the north-east Atlantic, the common dolphin forms a unique panmictic population (Mirimin *et al.*, 2009). However, based on ecological indices (heavy metals, stable isotopes, fatty acid, stomach contents), three management units have been recently defined and these units would have to be managed separately regarding current threats, especially bycatch (Caurant *et al.*, 2009). These population segments use distinct ecological niches (Lahaye *et al.*, 2005; Pusineri *et al.*, 2007; Meynier *et al.*, 2008). It clearly underlines the importance of scales (temporal and spatial) to assess population structure, and the necessity to combine methodologies spanning these temporal scales in order to answer questions related to population structure.

The bottlenose dolphin (*Tursiops* sp.) is the most common, widely distributed and accessible small cetacean represented by two separate species the common bottlenose dolphin *T. truncatus* and the Indo-Pacific bottlenose dolphin *T. aduncus*. This genus constitutes an excellent biological model of coastal top marine predator, with a high conservation value, and is also considered as a good indicator of marine ecosystem health (Wells *et al.*, 2004). The coastal distribution of bottlenose dolphins makes this species particularly vulnerable to human activities, such as boat traffic and overfishing, and many local populations are currently endangered (Bearzi *et al.*, 2006; Bejder *et al.*, 2006). In many bottlenose dolphin populations, studies have been undertaken on population structure, particularly for management purposes, including along the Atlantic coast of the USA, in the Gulf of Mexico and in Europe (e.g. Sellas *et al.*, 2005; Borrell *et al.*, 2006; Urian *et al.*, 2009). In a number of populations, it has been shown that bottlenose dolphins may form communities (Wells, 1986; Rossbach & Herzing, 1999; Chilvers & Corkeron, 2001; Urian *et al.*, 2009). A community refers to an assemblage of interacting individuals within the species. A community is not a closed demographic unit, and community structure is defined by associations among dolphins that show long-term patterns of site fidelity (Wells, 1986; Wells *et al.*, 1987; Connor *et al.*, 2000). Despite the fluidity of bottlenose dolphin societies, characterised by a fission-fusion social structure (Connor *et al.*, 2000), communities, defined by shared patterns of residency and associations, may occur (Wells, 1986). The origin of community formation has been poorly investigated in the literature, but ecological needs and need of habitat and resource partitioning may well explain the fragmentation of a population into communities. Individuals within a species have similar requirements for survival, growth and reproduction. However, their needs for resources may exceed the immediate supply. The individuals then compete for resources (Begon *et al.*, 1986). The formation of communities would contribute to share habitat and resources for individuals, and then reduce competition.

The Indo-Pacific bottlenose dolphin (*Tursiops aduncus*), one of the two recognised bottlenose dolphin species in the world, occurs in coastal waters of the Indo-Pacific region, from eastern Africa, to the west and southwest Pacific (Jefferson *et al.*, 2008). This species also occurs around isolated oceanic islands, such as in the western Indian Ocean, in the Mascarenes, Seychelles and Comoros (Kiszka *et al.*, 2009a). Around the island of Mayotte (45°10'E, 12°50'S), a population of about 100 Indo-Pacific bottlenose dolphins occurs in the lagoon and adjacent reef banks. In this study, we aimed to assess the fine scale population structure of Indo-Pacific bottlenose dolphins living in the surrounding waters of Mayotte, mostly in the lagoon and adjacent reef banks (Kiszka *et al.*, 2007; Gross *et al.*, 2009). We tested if community exists around the island by examining ranging and association patterns of individuals. As a preliminary step, for a full understanding of population structure, we assessed the global pattern of genetic structure and site fidelity of bottlenose dolphins to verify that the population was resident. We also aimed to explore the origin of community formation. We hypothesised that the origin of community formation is based on one main factor, the ecological constraint (niche partitioning). In order to explore the existence of ecological segregation processes occurring at within the species or population, we used stable isotope signatures of $\delta^{13}C$ and $\delta^{15}N$ in skin and blubber from biopsy samples. The carbon and nitrogen isotope ratios of a consumer reflect those of its diet. Both isotopes help elucidate trophic relations and habitat use, and may be used to assess niche partitioning, including at sub-species level (Hobson, 1999). Finally, as ecological constraints are probably significant factors shaping social interactions (Lusseau *et al.*, 2003), we assessed patterns of social structure and kinship of Indo-Pacific bottlenose dolphins around Mayotte. We tested the hypothesis that community formation would genetically structure communities and that an effect of differential ranging and association patterns among communities would have an influence on spatial genetic structure. Even if bottlenose dolphins mostly exhibit a fission-fusion social structure (Connor *et al.*, 2000), matrilineal society may possibly occur mainly due to particular environmental conditions, such as geographic isolation (Lusseau *et al.*, 2003). In order to investigate the fine scale population structure of Indo-Pacific bottlenose dolphins around Mayotte, we combined photo-identification data (residency, individual home range and association patterns) and biopsy sampling (genetic and stable isotope analyses) conducted year-round from 2004 to 2008.

## Materials and methods

### Study area

Mayotte is located in the northern Mozambique Channel and is part of the Comoros archipelago. The island is almost entirely surrounded by a 197 km long barrier reef, with a second double-barrier in the southwest and the *Iris* immerged reef complex in the northwest. There are a series of deep passes through the reefs, some of which being the sites of old rivers. The lagoon and surrounding reef complexes is 1,500 km² with an average depth of 20 m and a maximum depth of 80 m found in the western, older, region of the lagoon (Quod *et al.*, 2000). The insular slope on the exterior of the barrier reef is very steep and contains many submarine canyons.

### Data collection

From July 2004 to October 2008, small-boat based surveys were undertaken around the island of Mayotte. Surveys were conducted throughout the study period during daylight hours between 07:00 h and 18:00 h in sea conditions not exceeding Beaufort 3. Survey vessels did not follow pre-defined transects but every attempt was made to sample each habitat type within the surrounding waters of Mayotte, i.e. coastal areas (mangrove fronts, fringing reef), lagonal waters and barrier reef associated areas. Constant GPS logging was collected every 5 seconds from departure to return to the harbour using a hand-GPS Garmin Gecko®. When bottlenose dolphins and other cetaceans were encountered, standard sighting data were recorded: group size (maximum, minimum, best estimate), geographic position (latitude, longitude), behaviour (milling, travelling, foraging, socializing) and group classification on the basis of relative size of individuals (adults, immatures, calves) (Shane, 1990). Group size was defined as the number of animals at the surface within five body lengths of each other (Smolker *et al.*, 1992). Standard photo-identification technique was used to identify individual dolphins using patterns of notches and scars on the dorsal fin (Würsig & Würsig, 1977; Scott *et al.*, 1990). This non-invasive method has been extensively used to investigate demographic parameters, movements, home range and social structure of delphinids, especially the bottlenose dolphin (Würsig & Würsig, 1977; Würsig & Jefferson, 1990; Bejder *et al.*, 1998; Ingram & Rogan, 2002; Möller *et al.*, 2006). In our case, this method has only been used in adult individuals, having sufficient distinguishable features on the dorsal fin. On average, 67% of dolphins we photographed around Mayotte were considered marked.

Stable isotope and genetic analyses were performed using skin and blubber samples. Biopsy attempts were made opportunistically, when groups and individuals were easily approachable and when conditions were optimal (Beaufort < 2, dolphins closely approaching the boat). Optimal weather conditions allowed stability of the research boat and better chances to sample the animals successfully and safely. Biopsies were collected by using a crossbow (BARNETT Veloci-Speed® Class, 68-kg draw weight) with Finn Larsen (Ceta-Dart, Copenhagen, Denmark) bolts and tips (dart 25-mm long, 5-mm-diameter). A conical plastic stopper caused the bolt to rebound after the impact with the dolphin. The dolphins were hit below the dorsal fin when sufficiently close (3-10 m) to the research boat. Approaches of focal groups/individuals were made under power at speeds of 1-4 knots. Blubber and skin biopsy samples were preserved individually in 90% ethanol before shipping and subsequent analysis. Biopsy sampling was conducted under French scientific permits #78/DAF/2004 (September 10, 2004) and #032/DAF/SEF/2008 (May 16, 2008) after examination of the project by *Conseil National de Protection de la Nature*. Tissue samples (i.e. skin and blubber) were stored in 95% ethanol until DNA extractions and stable isotopes analyzes.

### Residency index

An important step of this work was to determine the residency of Indo-Pacific bottlenose dolphins around Mayotte. Using photo-identification data, a residency index (RI) was calculated following Karczmarski (1999). This index relates the total number of sightings of an individual to the total number of months in which this particular individual was seen:

$$RI = S \times M/100$$

Where RI= residence index, S = total number of sightings of an individual, and M = total number of months in which this particular individual was seen.

DNA extraction, PCR, sequencing and genotyping

Total DNA was extracted from skin samples using the Nucleospin® Tissue Kit (Macherey Nagel). The manufacturer protocol was slightly modified as follows: the recommended lysis time was extended to 30 hours under permanent agitation and 10 minutes grinding step using a teflon pestle was added after 5 hours of enzymatic digestion.

A 254 base pairs fragment of the mitochondrial cytochrome b gene was amplified using the protocol and PCR primers described in Jayasankar *et al.* (2008) The sequencing was performed by Genoscreen corporation (Campus Pasteur - 1 rue du Professeur Calmette - 59 000 Lille - France) using an ABI PRISM® 3730 XL automated DNA Sequencer (Perkin-Elmer Applied Biosystems, Foster City, CA). Sequence data were aligned using ClustalX (Thompson *et al.,* 1994) and ambiguities were manually checked comparing each sequence with its complementary fragment using BioEdit (Hall, 1999).

In addition to mitochondrial analyses, 14 tetranucleotide microsatellite markers were used out of the set of 18 markers designed by Nater *et al.* (2009). Amplifications were carried out following the protocol and using the primers described in Nater *et al.* (2009). PCR products were screened on 6.5% polyacrylamide gels using a Li-Cor NEN Global IR2 DNA sequencer. Allele sizes were determined using a known DNA sequence with the SAGA-GT software (v3.1: Automated microsatellite Analysis Software, LI-COR Biosciences).

Patterns of population structure

Clustering methods based on Bayesian computations (*i.e.* Monte Carlo Markov Chains, MCMC) were performed using the software Structure v2.3.1 (Pritchard *et al*., 2000; Falush *et al*., 2003). In order to identify potential barriers to gene flow, the number of groups to test (*K*) has to be fixed. Then, the software computes the probabilities for each individual of the dataset to belong to each of the simulated group at Hardy-Weinberg equilibrium. We tested values of *K* ranging from 1 to 10. For each *K*, ten simulations were conducted in order to compute the inter-simulation variability and for each simulation, the likelihood of the multilocus dataset given *K* (i.e. $Pr(X|K)$) was computed. The most likely value for *K* is the one maximising $Pr(X|K)$ and minimizing the inter-simulation variability. A model with population admixture was used and the parameters of the MCMC were set as follows: burn-in = 50 000 steps, length of the Markov Chain = 200 000 steps.

The identification of sex has been determined opportunistically for several identified individuals. This has been achieved through *in situ* underwater observations and photography of the uro-genital area.

### Communities existence: ranging pattern analysis

We used the minimum convex polygon method (MCP; Mohr, 1947), to estimate home range area. This is the oldest and most commonly used method to estimate home range in the literature, allowing ready comparisons with other studies (White & Garrott, 1990). It encloses all data points by connecting the outer locations in such a way as to create a convex polygon. This method is completely non parametric and easy to construct. However, in certain situations, it may be uninformative as areas of high utilization have same values as areas of low utilization. It is also sensitive to sample size and to outliers and it ignores boundaries that exclude animal movement within the home range (Mohr, 1947). In our case, we estimated individual home range for animals with 3 or more sightings. Due to these restrictions and our limited dataset, absolute home range estimate was not our primary objective, but rather compare home range size and location among individuals in order to identify potential differences among them. MCP method was used rather than kernel home range estimator due to its lesser sensitivity to sample size in estimating home range. In addition, in a previous work on common bottlenose dolphins (*T. truncatus*) from Florida, no significant difference of home range size was found between the two estimators (Urian *et al.*, 2009). Individual habitat preferences were also calculated for individuals with more than 3 sightings. We constituted a database in which every individual dolphin sighting was associated with the physiographic characteristics (distance to the coast, to the fringing reef, to the barrier reef and depth) corresponding to the GPS (Global Positioning System) fixes of the observations. For each individual, minimum, maximum, standard deviation and mean values for each variables were calculated. The distance data were obtained using Geographic Information System (GIS) software MAPINFO PROFESSIONAL 6.5. Bathymetric data were obtained from *Service Hydrographique et Océanographique de la Marine* (SHOM) and were included in the GIS procedure, and maps and MCPs were drawn in R v2.11.1 using packages Maps, Mapdata, Argosfilter and Aspace (Becker & Wilks, 2009, 2010; Bui *et al.*, 2009; Freitas, 2010).

### Trophic segregation using stable isotope analyses

Stable isotope analyses were used to assess segregation patterns of bottlenose dolphins around Mayotte based on their foraging habitat (reflected through $\delta^{13}C$) and trophic level (reflected through $\delta^{15}N$). For dolphin biopsies, blubber and skin were separated for each sample. The ethanol was evaporated at 45°C over 48 h and the samples were ground and freeze-dried (Hobson *et al*., 1997). Because lipids are depleted in $\delta^{13}C$, they were extracted to avoid a bias in the isotopic signature of $\delta^{13}C$ (De Niro & Epstein, 1978; Tieszen *et al*., 1983). This was done by shaking (1 h at room temperature) in cyclohexane ($C_6H_{12}$), and subsequent centrifugation prior to analysis. After drying, small sub-samples (0.35 to 0.45 mg $\pm$ 0.001 mg) were prepared for analysis. Stable isotope measurements were performed with a continuous-flow isotope-ratio mass spectrometer (Delta V Advantage, Thermo Scientific, Germany) coupled to an elemental analyser (Flash EA1112 Thermo Scientific, Italy). Results are expressed in δ notation relative to PeeDee Belemnite and atmospheric $N_2$ for $\delta^{13}C$ and $\delta^{15}N$, respectively, according to the equation:

$$\delta X = \left[ \frac{R_{sample}}{R_{s\tan dard}} - 1 \right] \times 1000$$

Where X is $^{13}C$ or $^{15}N$ and R is the isotope ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicated that measurement errors were <0.1‰ for $\delta^{13}C$ and $\delta^{15}N$. Percent C and N elemental composition of tissues were obtained using the elemental analyzer and used to calculate the sample C:N ratio, indicating good lipid removal efficiency when <4.

### Social structure analysis: associations and kinship

In order to assess the social structure of bottlenose dolphins around Mayotte, we combined association and kinship analyses. This approach was used in order to verify that bottlenose dolphins around Mayotte formed a “fission-fusion” society. This approach also allowed assessing whether communities tend to be genetically structured or not.

Pairwise association of social animals may be tested using various indices. The most commonly used is the Half-Weight index (HWI), also called coefficient of association (CoA) (Cairns & Schwager, 1987). We used R v 2.11.1 (R Development Core Team, 2010) to calculate HWI (Whitehead, 2006). Individuals were considered as associated if found together in a group where they are no more distant than 100 m of each other, moving in the same direction and engaged in similar behaviour (Shane, 1990). Dolphins that were individually identified on at least three occasions were selected for calculating pairwise association using the HWI. Associations were calculated as follows: association between two individuals A and B = $2N_{ab}/N_a+N_b$, in which $N_{ab}$ is the number of times A and B were found together in the same group, and $N_a$ and $N_b$ are the total number of groups for A and B (Cairns & Schwager, 1987). HWI index ranges from 0 (two dolphins never seen together in a group) to 1 (two dolphins always seen together). In order to determine whether associations were different from random, we built an association matrix from calculated HWI. The null hypothesis is that individuals have no preferences for social partners, with the alternative that there are preferred and/or avoided associations between some pairs of individuals (Whitehead, 2008). To account for demographic effects (Manly, 1995; Bejder, *et al.*, 1998), pairwise associations were tested for departures from randomness using a permutation procedure (i.e. 5,000 permutations) implemented in Rv2.11.1 (R Development Core Team, 2010).

For each pair of individuals, genetic relatedness was estimated by the number of identical alleles over the 14 bi-allelic microsatellite markers. Thus, the pairwise genetic similarity index between two individuals varied from 0 (no allele in common) to 28 (all alleles in common).

For sake of comparison, pairwise HWI and pairwise genetic distances were used to build two UPGMA trees (Unweighed Pair Group Method with Arithmetic Mean) in R v2.11.1 (R Development Core Team, 2010).

### Community definition

In order to identify communities, we used data from individuals sighted at least on 3 occasions (only one sighting per day). On the basis of MCP maps, an empirical ranging category has been assigned for each individual to detect the existence of communities within Mayotte’ Indo-Pacific bottlenose dolphins. To support this empirical clustering, we used a Principal Component Analysis (PCA, function dudi.pca implemented in the package ade4; Dray & Dufour, 2007) integrating, for each individual, mean depth preferences, mean distance from the coast, mean distance from the barrier reef, home range size (in km²) and mean latitude and longitude to distinguish groups with varying habitat characteristics and home range.

## Results

Survey effort and sightings

From July 2004 to October 2008, data were collected during 196 independent boat-based surveys (time spent on the water = 1,375 hours; daily mean = 6.1 h; SD = 1.5 h; median = 6.4 h). A total of 91 sightings of bottlenose dolphins were collected (21% of cetacean encounters around Mayotte). Spatial distribution of observation effort covers the interior waters of the lagoon and surrounding deeper waters, outside the barrier reef. Most of the effort has been spent along the east coast, in the north and in the south. The west has been less surveyed. Bottlenose dolphins were essentially distributed inside the lagoon, close to shores as well as in the north of the island, in the shallow waters of the Iris bank (Figure 6.1). Group size ranged from 1 to 30 individuals (mean = 6: median = 5; SD = 4). Group composition was variable with mostly groups of all age classes (including adults, calves and immatures, 35%) and groups of females with calves (>70% of mother-calf pairs in the group; 29%). Photo-identification effort is presented in Table 6.1.

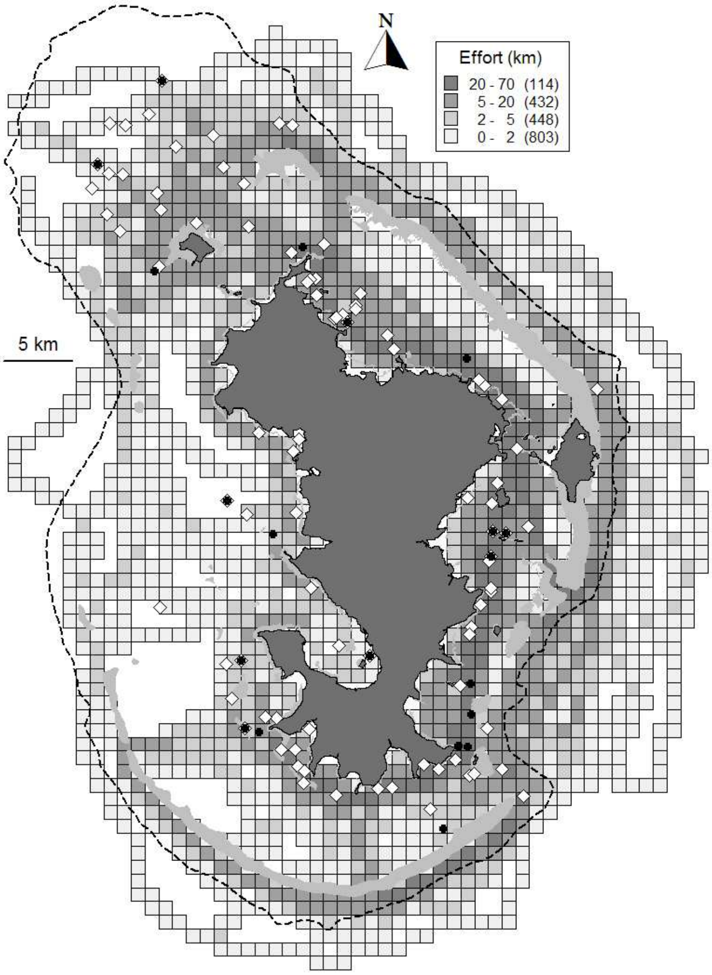


**Figure 6.1:** Distribution of observation effort (expressed in km). Indo-Pacific bottlenose dolphin sightings (white squares) and biopsies (black dots) around Mayotte from 2004 to 2008.

**Table 6.1:** Number of bottlenose dolphin photographs (n = 5,372) used for photo-identification purposes collected around Mayotte from 2004 to 2008. Grey cells correspond to periods were surveys were not conducted.

| **Year/month** | **Jan.** | **Feb.** | **March** | **Apr.** | **May** | **Jun.** | **July** | **Aug.** | **Sept.** | **Oct.** | **Nov.** | **Dec.** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **2004** | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | 100 | 886 | 229 | 1 | 127 | 698 |
| **2005** | 237 | 1279 | 391 | 1082 | 1710 | 1624 | 12 | 522 | 95 | 454 | 32 | 212 |
| **2006** | 1628 | 560 | 509 | 442 | 350 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
| **2007** | ▨ | ▨ | ▨ | ▨ | 126 |  |  | 3 | 726 | 690 | 126 | 459 |
| **2008** | 29 | 850 | 852 | 1156 | 193 |  |  | 259 | 258 |  |  |  |

### Residency

In bottlenose dolphins of Mayotte, most individuals have been sighted on one (18.6%), two (11.6%), three (15.5%) or four occasions (11.3%). Number of recaptures reaches 20 times for one individual (Figure 6.2). The two most frequently seen individuals were recorded in 13 and 12 of the 39 months surveyed. RI reached a maximum of 2.6 for the most frequently seen dolphin, but for most of the individuals, this index is below 0.5 (Figure 6.2). Overall, a fairly high number of individuals were seen on multiple occasions during the study period (at least on 5 occasions; n=25 individuals).

### Genetic diversity and population structure

Mitochondrial data consisted of a 254 base pairs fragment of the cytochrome b gene. A total number of 29 individuals were sequenced. The analyses revealed no mitochondrial polymorphism which suggests a single matriarchal lineage in the Mayotte population. Nuclear markers gave similar results. The genetic diversity was low with allele counts ranging from 2 to 6 depending on the locus considered and a multilocus overall gene diversity of less than 0.6. Bayesian simulations revealed no significant structure with a unique panmictic population at Hardy-Weinberg equilibrium around Mayotte being the most likely scenario.

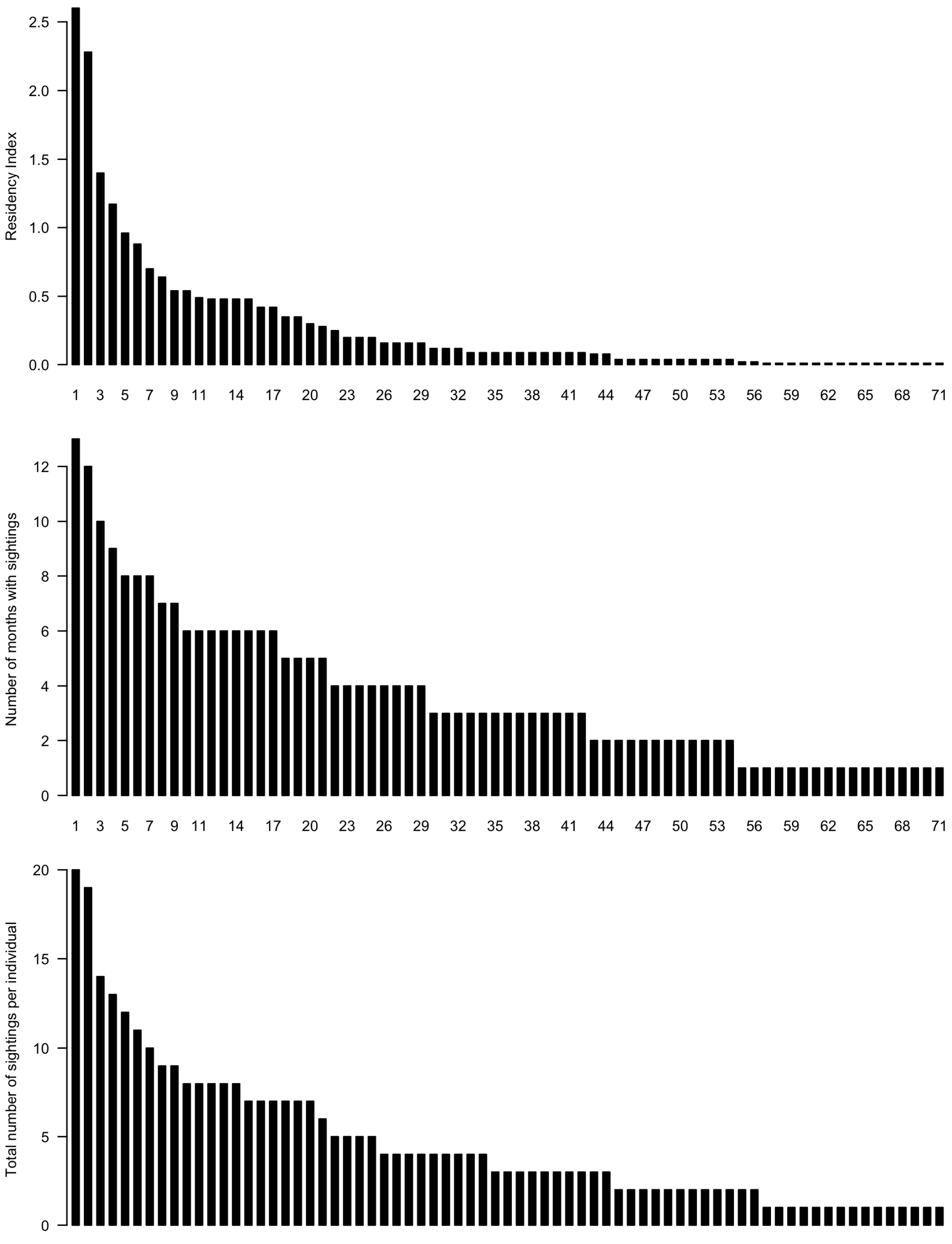


**Figure 6.2:** Sightings of 71 Indo-Pacific bottlenose dolphins around Mayotte from 2004 to 2008: (a) total number of sightings for each indentified individual; (b) number of months in which each individual was seen; (c) values of the residency index (RI) calculated for all identified dolphins.

Ranging patterns and individual habitat preferences

Home range estimate has been performed for 43 dolphins. Sample size has a significant effect in home range estimate ($r^2 = 0.4966$; $P < 0.001$, n = 43). Home range size varied from 2.93 km² (MY71, 3 sightings) to 558.81 km² (MY16, 8 sightings) (mean home range = 218.92 km²: SD = 187.16). Home range size using MCP estimator shows that approximately 5-6 sightings are required to accurately estimate home range of bottlenose dolphins around Mayotte (Figure 6.3).

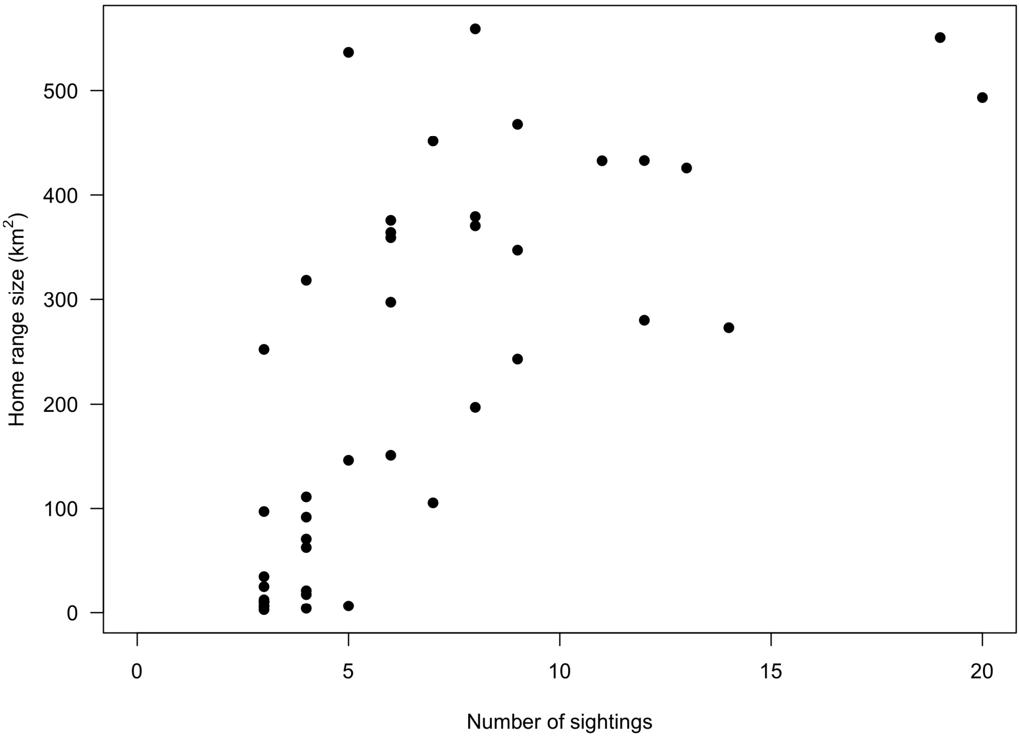


**Figure 6.3:** Evolution of home range size according to number of recaptures (at least 3) in Indo-Pacific bottlenose dolphins around Mayotte from 2004 to 2008.

Overall, we encountered four types of ranging patterns (Figure 6.4). Nine individuals essentially ranged in the north of the island, (at latitude –under 12.6°S). Twenty-one individuals essentially ranged around the coastal waters of the island. Some occurred all around the island. Five individuals were primarily distributed in the southern region of the lagoon, and finally, eight individuals used both the coastal waters of the lagoon and regularly visited the northern area (below the latitude of -12.6°S). These four types have been named as follow: type A (north), type B (coastal waters of the island), type C (south) and type H (hybrid distribution, both coastal waters of the island and north, Figure 6.4).

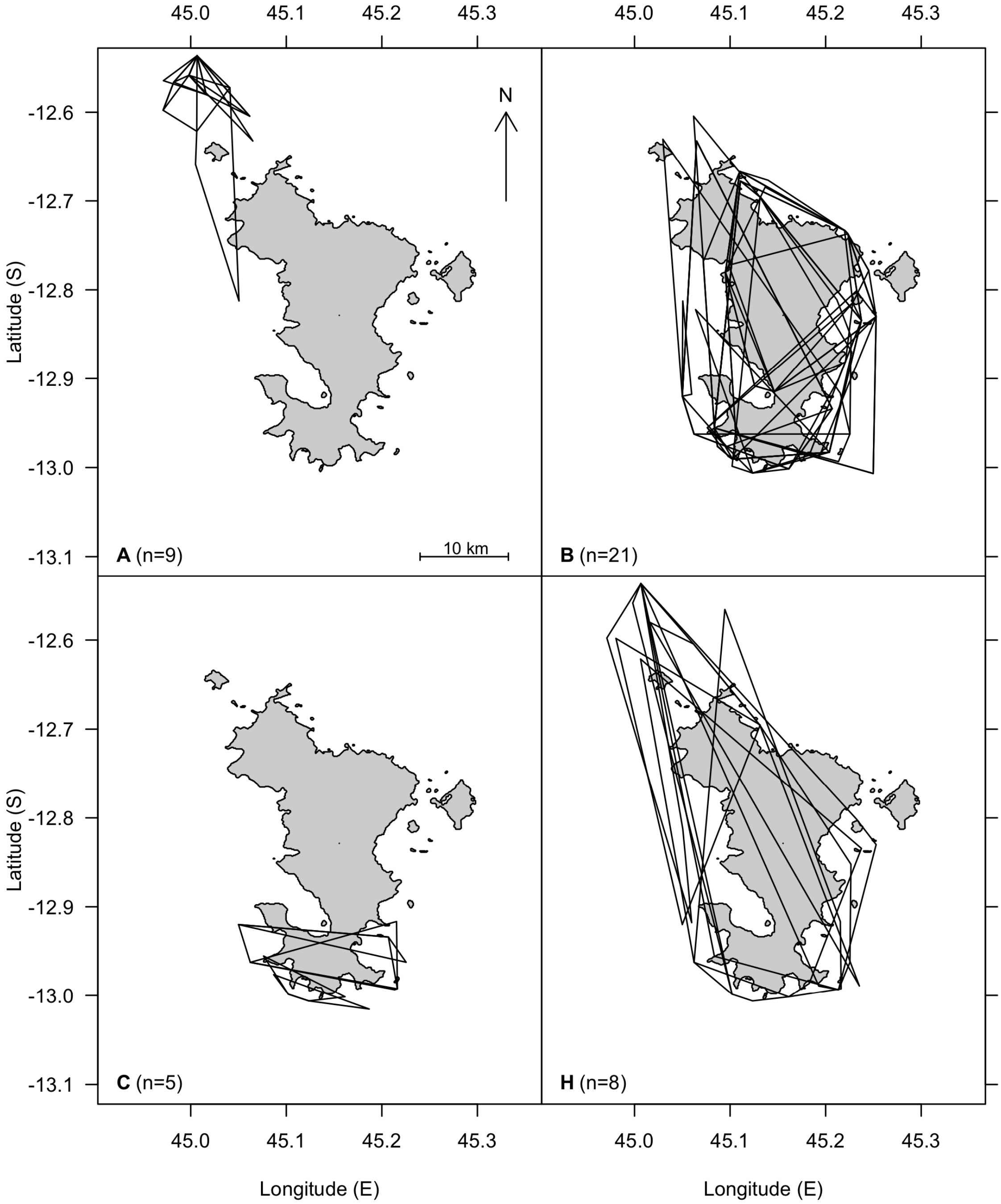


**Figure 6.4:** The four main ranging patterns of Indo-Pacific bottlenose dolphins around Mayotte from 2004 to 2008.

We used the PCA to objectively discriminate communities on the basis of individual habitat characteristics and home range (size and location). Each individual has been assigned to a ranging category based on MCP maps (A, B, C, H; Figure 6.5). For each category, the ellipse pictures the dispersion of the cloud and covers 95% of individual points, the centre of the ellipse being located at the centre of gravity. Here, two main communities can be discriminated. Type “A” typically has a distribution far from shore (Table 6.2), in deeper waters (mean = 44.9 m; SD = 6.8) and has a smaller home range (mean = 15.8; SD = 18.4). Type “B, C and H” considerably overlapped, especially in home range size.

**Table 6.2:** Mean home range size and habitat characteristics of type “A, B, C and H” bottlenose dolphin communities found around Mayotte from 2004 to 2008.

| | Recapture range | Home range size | | Distance from coast (m) | | Distance barrier reef (m) | | Depth (m) | |
|---|---|---|---|---|---|---|---|---|---|
| ***Community type*** | n | Mean | SD | Mean | SD | Mean | SD | Mean | SD |
| Type A | 3 - 5 | 15.8 | 18.4 | 7999.6 | 1529.9 | 6676.4 | 1200.4 | 44.9 | 6.8 |
| Type B | 3 - 20 | 313.4 | 140.5 | 1095.2 | 749 | 6953.3 | 1114.9 | 20.6 | 6.9 |
| Type C | 3 - 5 | 42.4 | 36.8 | 1330.9 | 361.4 | 5514.6 | 1892.2 | 23.2 | 8 |
| Type H | 3 - 9 | 309.7 | 202.6 | 3506.7 | 2181.5 | 6144.1 | 1881.8 | 31.1 | 8.6 |

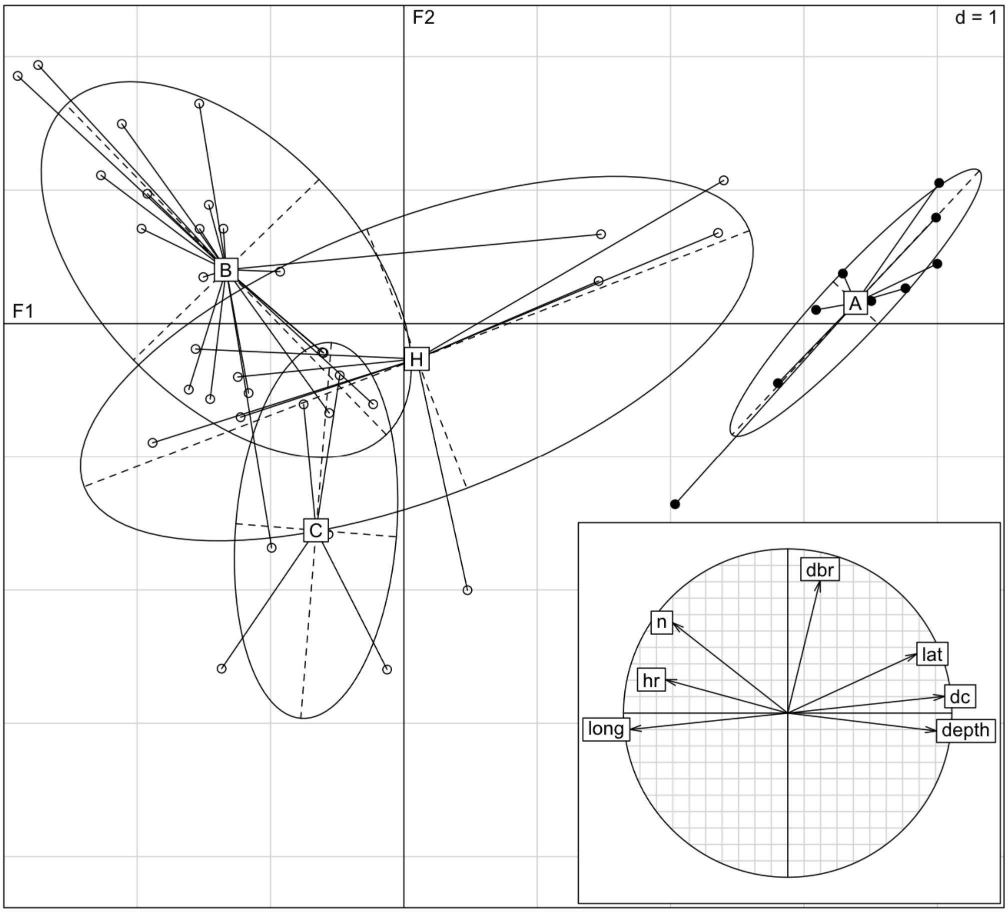


**Figure 6.5:** Principal Component Analysis showing segregation of individual dolphins of Mayotte from 2004 to 2008 based on their home range size, mean location (lat, long) and habitat preferences (depth, distance from coast and barrier reef). The ellipses represent 95% of the information and the central point is the centre of gravity.

However, a few differences were observed, especially related to the spatial extent of their home range (Table 6.2). Overall, home range size differed significantly between the four ranging patterns defined (H = 18.891; *df* = 3; $P < 0.0001$). Habitat, in relation to the three variables considered (depth, distance from shore and from the barrier reef) was also significantly different between the four communities (distance from shore, H = 23.506; *df* = 3; $P < 0.0001$; depth, H = 20.820; *df* = 3; $P < 0.0001$), except for the variable "distance from the barrier reef" (H = 2.569; *df* = 3; $P = 0.463$).

Dietary segregation

We used skin and blubber samples from 31 distinct bottlenose dolphins for stable isotope analyses during the study period. Stable isotope signatures for skin and blubber varied significantly, both for $\delta^{13}C$ ($U = 55$; $P < 0.001$) and $\delta^{15}N$ ($U = 91$; $P < 0.001$; Figure 6.6). $\delta^{13}C$ values were significantly higher in the blubber (mean=-13.05; SD=0.88; range=-16.16 to -11.77) than in the skin (mean=-15.12; SD=0.98; range=-17.05 to -12.98). For $\delta^{15}N$, values were also significantly higher in blubber (mean=15.07; SD=0.66; range=13.32 to 16.21) than in skin (mean=13.07; SD=1.28; range=11.44 to 16.15).

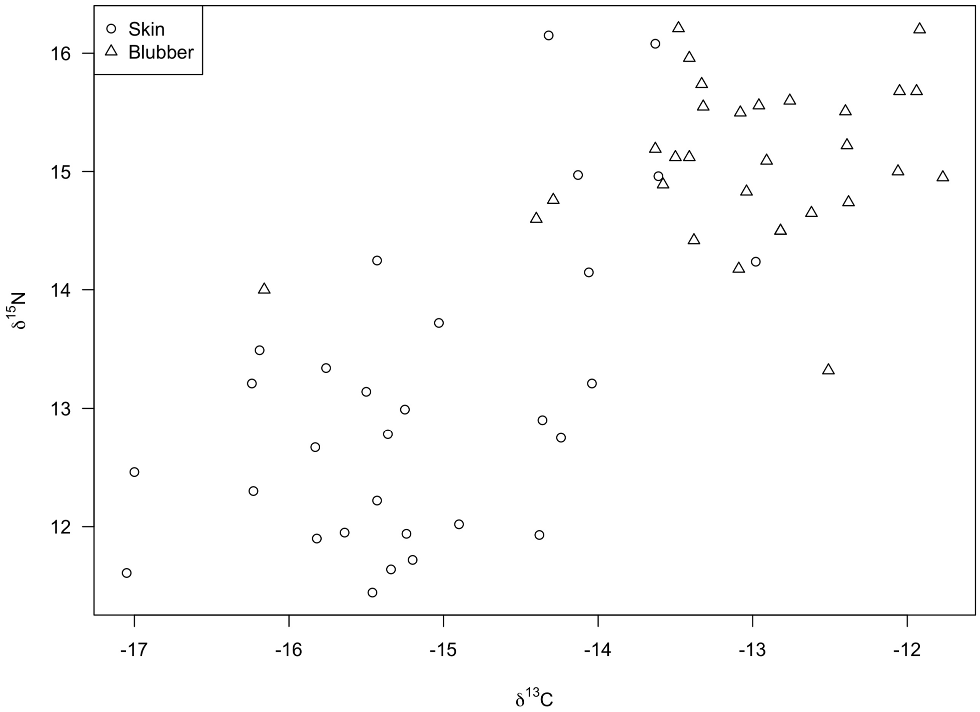


**Figure 6.6:** Stable isotope signatures of $\delta^{13}C$ and $\delta^{15}N$ in skin and blubber from biopsy samples (n=31).

Overall, no particular structure among individuals was found, especially on a long term basis (blubber; Figure 6.6). Due to limited number of sexed individuals and high proportion of females in the sampling, no gender differences of stable isotope signatures were tested.

### Social structure

We investigated association patterns of 31 individuals sighted at least 3 times. Sex has been identified for 17 of them, *i.e.* 6 males and 11 females. Among them, 12 were known individuals (8 females and 4 males). 28 associations between pairs of individuals were found to be statistically significant using an exact test. The HWI index allowed us to construct a similarity tree (Figure 6.7, left). Individuals with strong HWI appear close together and at the right of the tree. The HWI confirmed that preferred associations between type "A" community and all other community types were distinct, confirming the existence of at least two bottlenose dolphin (clearly differentiated) communities around Mayotte.

Beside the association tree, a nuclear genetic similarity tree has been constructed (Figure 6.7, right). Most individuals differ between the two trees because (i) only individuals sighted more than 3 times were used for the half weight index computation and (ii) biopsies were realized opportunistically so that some skin samples have been collected on unknown individuals (i.e. no photo-identification information). The strongest genetic link was observed between a mother and her calf (1c and 1B, Figure 6.7, right). This confirms the validity of the method to identify kinship. Genetic relatives were almost never seen in association. In addition, despite the low number of sexed individuals, we observed that most pairs or small groups of individuals that are strongly associated are of the same sex. Overall, it appears that association patterns and kinship are mostly unrelated.

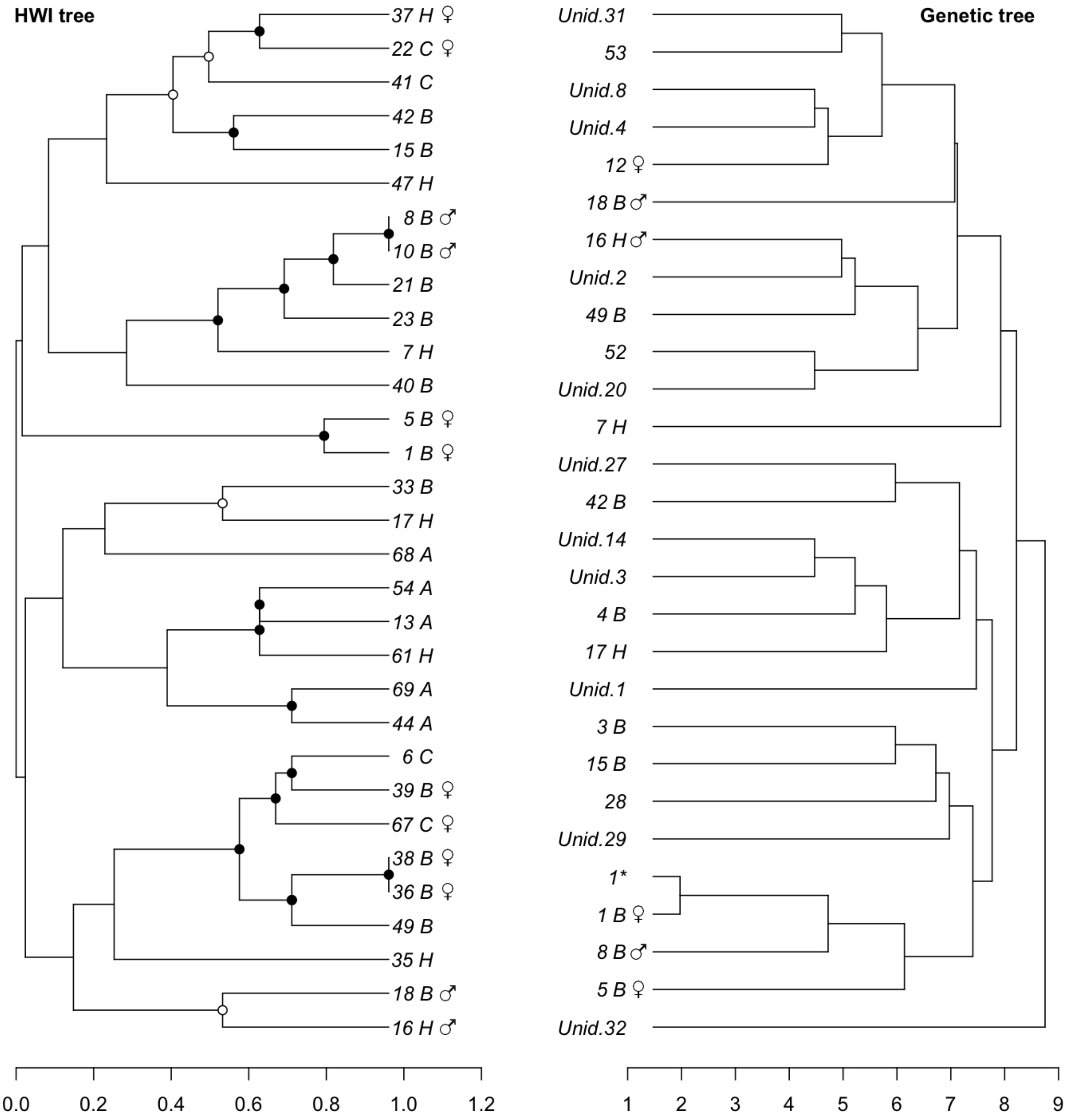


**Figure 6.7:** Association tree (HWI values), left; and genetic relatedness tree, right.

## Discussion

This study documents fine scale population structure of an isolated group of Indo-Pacific bottlenose dolphins around the island of Mayotte, in the Mozambique Channel. It combines analyses of genetic population structure, residency, ranging patterns and social structure to assess the existence of communities around the island. It also explores the social structure of Indo-Pacific bottlenose dolphins in this particular and geographically isolated territory. This work is based on the sampling of 29 (genetic analyses) and 31 (stable isotope analyses) individuals, *i.e.* around one third of the population size and photo-identification data over four years (71 individuals identified). This study provides insights about population structure of a population of bottlenose dolphins over different temporal scales (long term with genetic structure to short term with ranging and association patterns).

### Evaluation of the study

The lack of polymorphism could be due to an inappropriate choice of marker. The DNA sequence we used could have been too short to detect polymorphism or the whole sequence could be conserved (i.e. less likely to accumulate mutations at the infra species level). However, a blast in online sequences databases proved that the marker was polymorphic at the species level: up to 4% of divergence was measured on that same DNA fragment between *Tursiops aduncus* from Mayotte and from the western coast of India (i.e. 8 mutations along the 250 base pair fragment; Jayasankar *et al.*, 2008).

The main limitation of this study is the low rate of recaptures of dolphins and, consequently, the probable underestimation of the size of individual home range. In addition, the MCP method is known for underestimating home range with small samples (White & Garrott, 1990). In addition, our definition of communities and ranging patterns is empirical and it is necessary to be cautious with the interpretation of the results. Nevertheless, the differential rate of encounter of identified individuals, according to the spatial coverage of effort, underlines differential individual patterns of distribution. This suggests that, even limited, the data presented in this work over the four years of the study (i.e. a fairly short period of time), allow documenting some insights of fine scale population structure of Indo-Pacific bottlenose dolphins in this region.

### Population structure

In term of genetic population structure, Indo-Pacific bottlenose dolphins form a single panmictic group around Mayotte, with low genetic diversity. This low genetic diversity may be attributed to the formation of the population by a limited number of individuals (e.g. Barson *et al.*, 2009). Three main situations could explain the genetic profile we observe in this population: (i) bottlenose dolphins around Mayotte population are totally isolated from surrounding populations; (ii) surrounding populations send migrants frequently or not towards Mayotte, and share the same genetic pattern as the one observed in the Mayotte population ; (iii) surrounding populations send individuals towards Mayotte that do not participate to local reproduction, and thus do not contribute to the gene pool of the Mayotte population. This would explain why no signature of admixture has been found. Furthermore, we have the confirmation that the lack of mitochondrial polymorphism at the population level reflects the fact that a single matriarchal lineage is present in Mayotte, and is not due to a poor choice of marker. Indeed, up to 4% divergence has been found between the mitochondrial sequence of Mayotte individuals and the same gene fragment sequenced in Indo-Pacific Bottlenose Dolphins from west India (Jayasankar *et al.*, 2008).

### Residency

Around Mayotte, Indo-Pacific bottlenose dolphins have a shallow-water and inshore distribution. Numerous within-year and between-year resightings suggest that individuals are resident around the island. However, a number of individuals have never been resighted, but overall, this pattern of residency is relatively similar to other areas of their range (Stensland *et al.,* 2006; Wiszniewskia *et al.*, 2009). The relatively high level of residency was expected due to the geographic isolation of the island of Mayotte. The closest island is Anjouan (Union of the Comoros), 60 km away to the west of Mayotte and, the northwest coast of Madagascar, 280 km to the east, suggesting some degree of isolation of Mayotte Indo-Pacific bottlenose dolphins in the northern Mozambique Channel. This island-associated pattern of residency has been previously documented in similar oligotrophic areas for the common bottlenose dolphin, around the main Hawaiian Islands (Baird *et al.*, 2009). A similar pattern could be observed around the Comorian islands. However, information on residency and home range patterns of Indo-Pacific bottlenose dolphins around the other islands of the archipelago, where this species has been previously reported, are lacking (Kiszka *et al.*, 2010).

### Existence of bottlenose dolphin communities around Mayotte

Based on the ranging patterns of individual dolphins, our results suggest the existence of at least two distinguishable bottlenose dolphin communities around Mayotte despite the absence of geographical barriers to movements. The “type A” (n = 9) community is made of individuals with restricted home range, living over higher depths and at greater distances from shore. The second community probably includes three ranging patterns, “type B, C and H”. Individuals have an extended home range and an inshore distribution. However, some variations within this community have been observed. A large number of individuals (type B, n = 21) exclusively range in the coastal waters around the island. An intermediate type of ranging pattern (type H, n = 8), very similar to “type B”, is characterised by a large home range and intermediate bathymetric range. Type “H” dolphins were also observed outside the lagoon waters, within the type “A” individuals range. Finally, a limited number of individuals (type C, n = 5) also differ, as they only range in the south of the island, in the coastal waters. Communities “B, H and C” may be different, but our dataset did not show significant differences among them. The use of association data also supported the information on ranging patterns and individual habitat preferences. We observed that type “A” individuals were preferentially associated while the three other community types were mostly associated together. These two communities use different environments. One uses open and deeper waters of a reef bank with higher fish biomass and higher predator presence in the north-west of Mayotte reef complex (Type A; Wickel *et al.*, 2010) and the other(s) use more coastal waters located inside the lagoon. No evidence of difference in group composition and size among communities was detected.

The existence of communities has been documented for bottlenose dolphin (especially in *T. truncatus*) and in chimpanzee societies (Goodall, 1986). These communities are not genetically isolated and individuals may change community membership over time (Wells, 1986; Wells *et al.*, 1996). Among geographical areas, patterns of community home range may be variable. Indeed, communities may overlap in their ranging patterns and live in direct sympatry but differ in their foraging behaviour and social associations (Chilvers & Corckeron, 2001; Lusseau *et al.*, 2005). In other areas such as Tampa bay, in Florida, most communities show little overlap in their ranges (Urian *et al.*, 2009). Our study confirms that the two main communities that were identified (A and B-C, i.e. the “northern community” and the “lagoon community”, respectively) show little overlap. However, some substructure among communities B, C and H could occur but more data are clearly needed in order to resolve this issue. The situation observed in individuals belonging to the H community is intermediate between communities B and C, and individuals make large movements across the study area.

### Origin of community formation

Certain ecological factors may be more likely than others to promote the formation of communities (Urian *et al.*, 2009). These factors can be directly linked to social behaviour, as foraging strategies may be culturally transmitted along matrilines (Nowacek, 1999; Krützen *et al.*, 2004). Our stable isotope analyses did not revealed differences of feeding strategies between individuals, especially on the long-term (analyses conducted in the blubber). We also expected that some individuals, such as those from the north (occurring farther from shore), would have lower δ13C signatures and that structure may occur within the population. The high variability of stable isotope signatures between marine habitats around Mayotte (revealed by stable isotope signatures in fishes) has been recently revealed (Kiszka *et al.*, submitted). The important isotopic gradients within the lagoon underlined the probable existence of high stable isotope variability among individuals. In the present study, we rather showed a high variance of the stable isotope signatures in skin tissues, revealing a wide width of the feeding niche of Indo-Pacific bottlenose dolphins around Mayotte (Bearhop *et al.*, 2004), but not any significant dietary segregation within the population. Consequently, we do not have evidence that bottlenose dolphins use distinct resources at the species level around Mayotte. However, only differences in isotopic signatures are informative whereas similarities do not necessarily imply that individuals share a similar trophic niche, as different foraging strategies may result in similar isotopic signatures. Nevertheless, we showed that some individuals do have different ranging patterns. This could be linked to competition at the species level. Competition is an interaction between individuals, brought about by a shared requirement for resources, and leading to a reduction in survivorship, growth and/or reproduction success (Begon *et al.*, 1986). Here we hypothesize Indo-Pacific bottlenose dolphins around Mayotte use similar resources (but they can considerably vary over time, cf. stable isotope signature information from skin). However, they form communities in order to optimize space (and obviously resources) sharing.

### Social structure

Based on association and kinship analyses, it is evident that Indo-Pacific bottlenose dolphins around Mayotte form a fission-fusion society, as observed elsewhere in the world and in the sibling species *T. truncatus* (e.g. Connor *et al.*, 2000). This pattern of fission-fusion society is also confirmed through sex information (even limited) of preferred duos, as pairs of known sex were only made of same-sex individuals. However, since only a single matriarchal lineage has been identified, we cannot totally exclude a matrilineal society. To do so, we would need to know the history of Indo-Pacific bottlenose dolphins at the scale of the region.

In some extreme environments, community structure may be more stable with the presence of mixed groups with strong associations, such as in Doubtful sound, New Zealand (Lusseau *et al.*, 2003). Such situation may be enhanced by geographic isolation and ecological constraints, as in environments with low productivity where bottlenose dolphins would need to greater cooperate and increase group stability (Lusseau *et al.*, 2003). Mayotte is an isolated oceanic island and similar conditions, such as insularity and geographic isolation, than in Doubtful sound could have been encountered. However, no such situation has been observed. This could be related to the relatively high predictability of resources in time and space in low-latitude environments, such as in the lagoon of Mayotte (Rossbach & Herzing, 1999). Analyses of kinship did also show that community members are not genetically related. This confirms that bottlenose dolphin communities are not closed demographic units.

### Conservation implications

The island of Mayotte is fast developing, with an increasing human population (annual growth of 3.47%). Multiple threats have been clearly identified in the coastal waters of Mayotte and adjacent reef complexes, including decrease of fishing resources and habitat degradation. Bottlenose dolphins are also affected by disturbances induced by dolphin watching tours. It has also been recently shown that bottlenose dolphins around Mayotte were affected by skin diseases that may be due to coastal environment degradation (Kiszka *et al.*, 2009b). According to the first management plan of marine mammals around Mayotte, the Indo-Pacific bottlenose dolphin is one of the priority species for rapid management and conservation measures due to high levels of interactions between the species and anthropogenic threats (Pusineri & Kiszka, 2007). This study significantly contributes to better understand the fine scale population structure of bottlenose dolphin in this area. For management purposes, marine mammals are generally divided into management units and, ideally, the boundaries of these units should correspond to those of a biological population (Urian *et al.*, 2009). Within our study area, we underlined the existence of at least two bottlenose dolphin communities. We suggest that these units need to be managed independently. Indeed, fishing pressure (and related fish depletion) and disturbances seem prevalent in the coastal waters of the lagoon, while in the northern area, less disturbances and fishing pressure probably provide better habitat conditions for “type A” bottlenose dolphins. In other words, “type B” bottlenose dolphins, living around the island and closer to shore, may be overexposed to human induced (direct and indirect) disturbances.

## Synthèse

Dans le lagon de Mayotte, le grand dauphin de l'Indo-Pacifique forme une unique population panmictique. Toutefois, au moins deux communautés d'individus ont été identifiées. Ces communautés sont constituées par des individus se partageant un domaine vital commun et étant préférentiellement associés. Une communauté semble vivre dans les eaux plus profondes du nord de l'île, notamment dans la zone du banc récifal de l'Iris. L'autre se distribue dans les eaux côtières du lagon. D'autres communautés semblent exister, mais davantage de données de photo-identification sont nécessaires pour le confirmer ou non, notamment à travers l'analyse du domaine vital individuel. Les communautés sont formées d'individus qui ne sont pas forcément apparentés, ce qui confirme le statut de société de type « fission-fusion » du grand dauphin. La formation des communautés pourrait avoir comme origine le partage de l'espace et le comportement territorial chez cette espèce. Les traceurs isotopiques n'ont pas permis de détecter de la ségrégation des habitats d'alimentation et des ressources. Ceci exclut la possibilité de différences culturelles d'utilisation des ressources. Toutefois, cette tendance pourrait être liée au faible échantillonnage par biopsies effectué.

Enfin, l'étude multi-échelle de la structure de population s'avère utile pour la gestion et la conservation, notamment du grand dauphin de l'Indo-Pacifique du lagon de Mayotte.

# Partie 7 :

# Discussion générale et conclusion

## 7.1 Synthèse des résultats

### *7.1.1 Structure de la communauté de delphinidés de Mayotte*

Les eaux entourant l'île de Mayotte se caractérisent par une forte diversité des cétacés odontocètes, tout particulièrement de delphinidés (13 espèces au total). Les delphinidés occupent tous les habitats présents autour de l'île, de la côte et du lagon à pente insulaire et à la province océanique. Le lagon est dominé par une espèce, le grand dauphin de l'Indo-Pacifique (*T. aduncus*). La pente externe de la barrière récifale est dominée par la présence de deux espèces : le dauphin à long bec (*S. longirostris*) et le dauphin tacheté pantropical (*S. attenuata*). Enfin, les eaux océaniques et de la pente insulaire sont fréquentées par un cortège diversifié d'espèces plus rares, qui font également de régulières incursions à proximité de la barrière récifale comme le péponocéphale (*P. electra*) et le dauphin de Fraser (*L. hosei*). La forte diversité de ces espèces semble étroitement liée à la grande diversité d'habitats marins se succédant autour de l'île à des échelles spatiales faibles. En effet, dans certains secteurs de l'île, la côte et l'isobathe des 1000 m sont espacés de 5 km. Entre ces deux « extrêmes » peuvent se succéder le lagon (herbiers, récifs frangeants, pinacles coralliens, lagon profond), la barrière récifale et la pente insulaire (incluant des canyons et des monts sous-marins). Cette situation suggère l'existence de processus à fine échelle de ségrégation écologique des delphinidés, définis par les trois dimensions de la niche écologique : l'habitat, les ressources et leurs variations temporelles.

### *7.1.2 Ségrégation écologique des delphinidés de Mayotte*

L'étude de la ségrégation écologique des delphinidés de Mayotte montre que les différentes espèces se partagent les habitats et les ressources à travers les trois dimensions de la niche écologique. Toutefois, aucun indicateur (habitats préférentiels, signatures isotopiques, variations temporelles) pris indépendamment ne permet de détecter une nette ségrégation entre toutes les espèces étudiées. Cependant, l'ensemble des indicateurs combinés permet aisément de détecter cette ségrégation. L'étude met donc en évidence la nécessité d'explorer les différents axes de la niche écologique d'une communauté, notamment si celle-ci est constituée par des espèces aux caractéristiques morphologiques proches, qui se partagent un habitat spatialement restreint. De manière générale, toute la communauté vit en sympatrie large, c'est-à-dire dans les eaux côtières et péri-insulaires de Mayotte. Toutefois, certaines espèces vivent en sympatrie directe. C'est tout particulièrement le cas des espèces qui utilisent les eaux de la pente externe de la barrière récifale, comme le dauphin à long bec, le dauphin tacheté pantropical et dans une moindre mesure le péponocéphale et d'autres espèces océaniques comme le dauphin de Fraser.

### 7.1.2.1 Partage des habitats

Le grand dauphin de l'Indo-Pacifique vit dans le lagon et interagit très peu sur le plan spatial avec d'autres delphinidés. D'autres espèces sont présentes dans le lagon, mais en très faibles effectifs (dauphin à bosse) ou de manière très irrégulière (dauphins à long bec et tacheté). L'habitat et les ressources alimentaires de cette espèce se chevauchent très probablement avec le dauphin à bosse, mais ce chevauchement doit être mineur étant donné la très faible taille de la population de cette dernière (trois individus, J. Kiszka & C. Pusineri, données non publiées). Le dauphin à bosse de l'Indo-Pacifique n'a pu être étudié du fait de sa rareté et donc de sa faible accessibilité (peu de possibilités pour réaliser des biopsies, de suivis focaux, etc.). De manière générale, le grand dauphin de l'Indo-Pacifique est exclusivement associé aux zones côtières peu profondes (< 30 m). Les signatures isotopiques élevées de $\delta^{13}C$ indiquent une source benthique de carbone, qui est essentiellement disponible en zone côtière (Figure 7.1). Le grand dauphin de l'Indo-Pacifique se distribue également sur les hauts fonds récifaux, notamment au nord de Mayotte où il interagit spatialement avec d'autres espèces de delphinidés, notamment le dauphin à long bec et le dauphin tacheté pantropical.

Les habitats des delphinidés présents à l'extérieur du lagon de Mayotte se chevauchent en grande partie, ce qui induit l'existence de mécanismes fin de ségrégation écologique. Le dauphin à long bec fréquente les abords externes du récif barrière, notamment pour accomplir les phases de repos et de socialisation durant la journée. Cette espèce occupe la zone de la pente insulaire durant la nuit pour l'alimentation (Norris & Dohl, 1979 ; Norris *et al.*, 1994 ; Gannier & Petiau, 2006). L'habitat du dauphin tacheté pantropical est très proche de celui du dauphin à long bec. Toutefois, le premier tend à se distribuer à une plus grande distance de la barrière récifale. Les signatures de $\delta^{13}C$ sont faibles chez les deux espèces et très proches, ce qui confirme la nature relativement similaire de leurs habitats d'alimentation (Figure 7.1).

Le péponocéphale est un delphinidé océanique qui fait des incursions irrégulières le long des abords de la barrière récifale de Mayotte. Cette espèce n'occupe donc les abords péri-insulaires que partiellement. Toutefois, autour des îles océaniques, il semblerait que cette espèce ait un comportement proche de celui du dauphin à long bec. La journée, il est essentiellement observé au repos ou en déplacement peu actif, à proximité des côtes ou des complexes récifaux (Brownell *et al.*, 2009). Enfin, pour le dauphin de Fraser, peu de données ont pu être collectées sur cette espèce présente très irrégulièrement autour de Mayotte (une observation durant toute la période d'étude). Elle est toutefois très régulièrement signalée tout au long de l'année par les usagers de la mer, notamment en association avec le péponocéphale (N. Bertrand, communication personnelle). Ces deux espèces sont de loin plus rarement observées près du récif barrière, ce qui serait probablement dû à leur mode de vie plus océanique (les campagnes d'observation autour de Mayotte se sont essentiellement concentrées le long du récif barrière). Les signatures isotopiques de $\delta^{13}C$ sont plus élevées chez ces deux espèces, notamment si on les compare avec celles des deux espèces du genre *Stenella* (Figure 7.1). Ceci pourrait être lié à l'influence plus importante des sources de carbone d'origine détritique, dont le gradient croissant de concentration va de la surface vers le fond. Le péponocéphale serait une espèce qui s'alimente à des profondeurs plus importantes que le dauphin de Fraser et davantage encore que les deux espèces du genre *Stenella.*

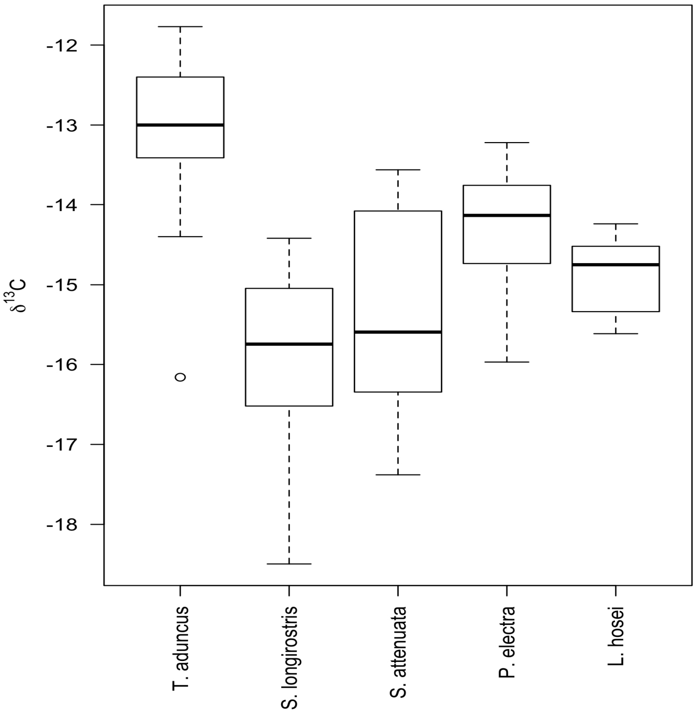


**Figure 7.1 :** Boîtes à moustaches des signatures isotopiques du carbone dans le lard des delphinidés de Mayotte.

7.1.2.2 Partage des ressources

La variance importante de la niche isotopique du grand dauphin met en évidence que la variabilité interindividuelle de sa niche alimentaire est large (Figure 7.2 ; Bearhop *et al.*, 2004). Le large spectre de proies de cette espèce a déjà été mis en évidence dans d'autres secteurs proches de Mayotte comme Zanzibar (Amir *et al.*, 2005). Le grand dauphin de l'Indo-Pacifique se nourrit de proies diversifiées des récifs et des petits fonds. Les observations des activités de chasse du grand dauphin ont permis de déterminer quelques proies de son alimentation. Il s'agit à la fois de proies proches des côtes comme le mulet (associés aux sédiments vaseux proche des mangroves) ou de proies épipélagiques de haut niveau trophique comme les Carangidés (notamment *C. melampygus*).

Chez les espèces océaniques, la variance des signatures isotopiques est plus faible, suggérant que ces espèces présentent une plus faible variabilité interindividuelle de l'alimentation (Bearhop *et al.*, 2004). Il est possible que leurs proies aient une prédictibilité plus importante, ce qui est généralement admis en zone océanique. De manière générale, le dauphin à long bec a le niveau trophique le plus faible. Le péponocéphale et le dauphin tacheté pantropical exploitent des proies d'un niveau trophique proche, alors que le dauphin de Fraser a un niveau trophique très supérieur à toutes les autres espèces de delphinidés océaniques (Figure 7.2).

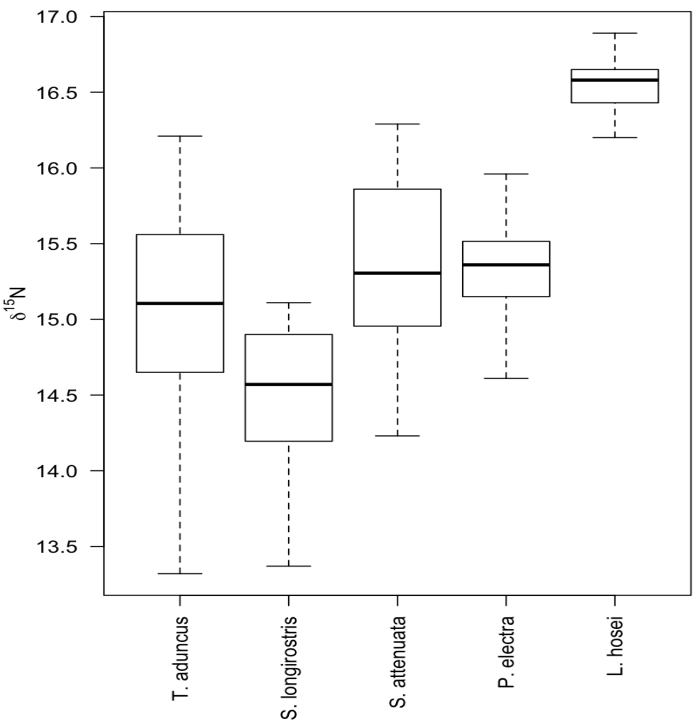


**Figure 7.2 :** Boîtes à moustaches des signatures isotopiques de l'azote dans le lard des delphinidés de Mayotte.

Ces caractéristiques reflètent assez bien les données de la littérature sur le régime alimentaire de ces différentes espèces. Ainsi, le dauphin à long bec s'alimenterait de céphalopodes et poissons mésopélagiques (< 20 cm) de la surface (lors des migrations nycthémérales) à environ 400 m de profondeur (Dolar *et al.*, 2003). Le dauphin à long bec exploiterait des proies épi- à mésopélagiques de petite taille (Perrin *et al.*, 1973 ; Norris & Dohl, 1979 ; Norris *et al.*, 1994). Le dauphin tacheté pantropical s'alimente essentiellement durant la journée de proies essentiellement épipélagiques (Perrin *et al.*, 1973). La nuit, cette espèce s'alimente également de proies épipélagiques de la famille des Exocoetidae (Richard & Barbeau, 1994).

La différence plus significative entre les deux espèces jumelles du genre *Stenella* est que le dauphin tacheté s'alimente durant le jour (peut-être également la nuit, ce qui n'a pu être mis en évidence) sur des espèces épipélagiques à proximité de la barrière récifale. Les comportements de chasse observés autour de Mayotte ont montré que les poissons de la famille des Exocoetidae étaient tout particulièrement ciblés. Toutefois, la niche isotopique du dauphin tacheté pantropical est étendue, ce qui suggère que cette espèce exploite une grande diversité de proies (Bearhop *et al.*, 2004).

Le péponocéphale et le dauphin tacheté pantropical ont des niveaux trophiques relativement proches (Figure 7.2). Toutefois, leurs habitats d'alimentation (cf. signatures de $\delta^{13}$C) diffèrent et le péponocéphale semble s'alimenter dans des secteurs plus profonds, ce qui serait en accord avec un régime alimentaire basé sur des proies (poissons et céphalopodes) mésopélagiques (Young, 1978 ; Brownell *et al.*, 2009). Enfin, le dauphin de Fraser se distingue très nettement des autres par son niveau trophique très supérieur (sur le lard en particulier), notamment en comparaison avec le péponocéphale avec qui il s'associe très souvent (Jefferson & Barros, 1997). Ceci confirme également les données de la littérature, indiquant que le dauphin de Fraser se nourrit de la surface à environ 600 m de profondeur sur des proies de grande taille (notamment en comparaison d'autres espèces comme le dauphin à long bec ; Dolar *et al.*, 2003).

#### 7.1.2.3 Variations temporelles

En termes de préférences de l'habitat, aucune variation saisonnière n'a été observée chez les différentes espèces de la communauté. Par contre, les signatures isotopiques étaient variables chez l'ensemble des espèces. Toutefois, celles-ci seraient liées à des modifications hydrodynamiques durant la saison des pluies davantage qu'un changement saisonnier de l'alimentation. L'absence de variations saisonnières de l'écologie des delphinidés de Mayotte confirme la tendance générale de faible variabilité saisonnière des milieux tropicaux (e.g. Cherel *et al.*, 2008).

A l'inverse, les différentes espèces de la communauté dont les budgets d'activités ont été étudiés (*T. aduncus* et les deux espèces de *Stenella*) montrent que ces espèces se caractérisent par des schémas différents. C'est tout particulièrement le cas chez les deux espèces jumelles, *S. longirostris* et *S. attenuata*. Le premier est un prédateur nocturne observé essentiellement au repos et en phase de socialisation durant la journée. Le second est aussi observé dans des phases d’activité similaires, mais également en phase de prospection alimentaire et de chasse. Cette variabilité de l’utilisation des ressources permet également de discriminer ces deux espèces.

### 7.1.2.4 Comparaison avec d’autres études similaires

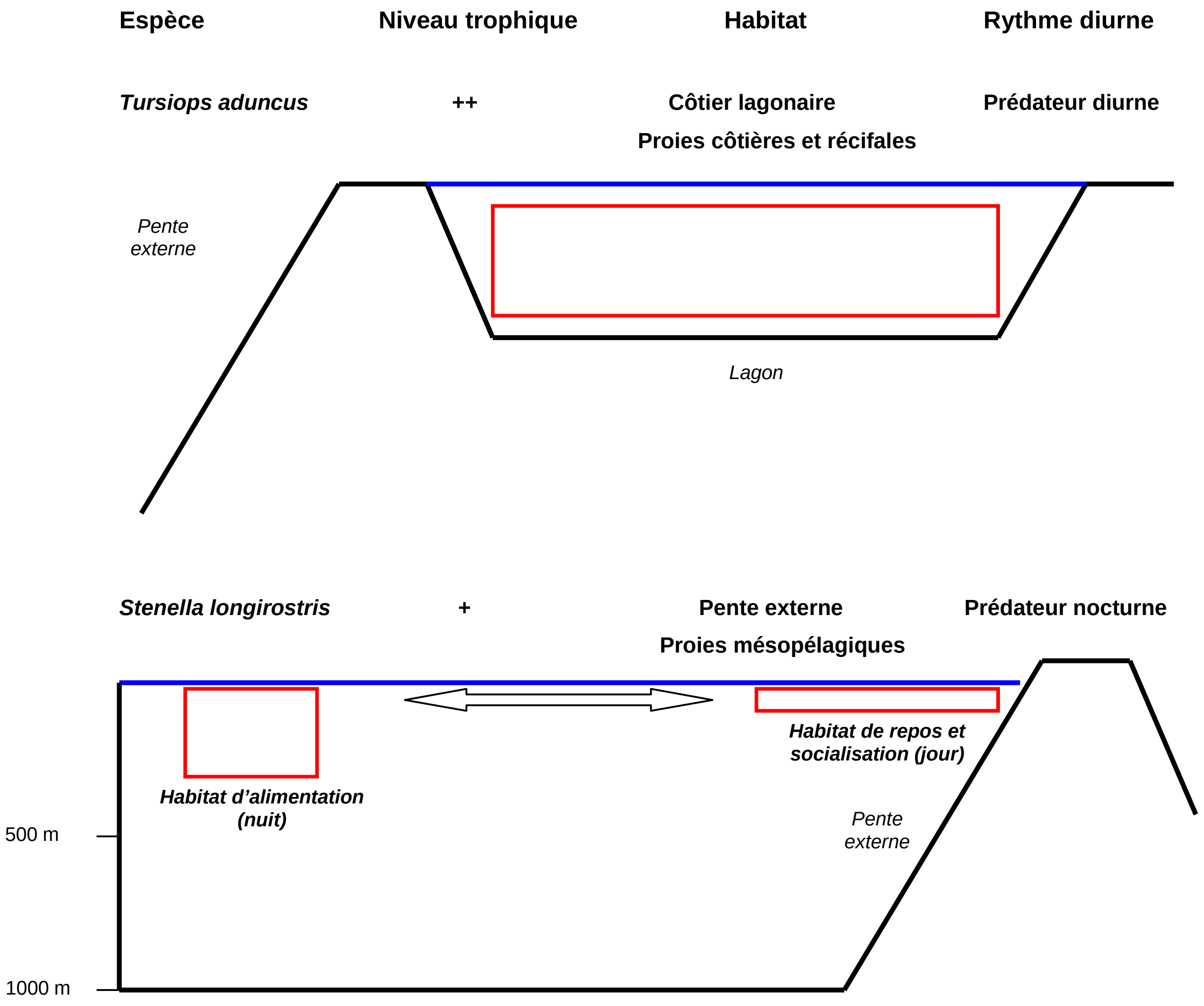
Plusieurs études ont été réalisées sur la ségrégation écologique des prédateurs marins supérieurs. La majorité des travaux s’axe surtout sur la ségrégation alimentaire d’espèces vivant en sympatrie (Ridoux, 1994 ; Das *et al.*, 2003 ; Pusineri *et al.*, 2008), mais intègrent également parfois l’habitat (Papastamatiou *et al.*, 2006). La seule approche intégrant les trois dimensions de la niche écologique est très récente et concerne une étude sur les cétacés (Praca, 2008). Des comparaisons avec des travaux antérieurs peuvent être envisagées selon les différentes dimensions de la niche pris indépendamment ou combinés.

L’étude indirecte des niches alimentaires par analyse des signatures isotopiques du carbone et de l’azote, que nous avons entreprise à Mayotte, s’est fortement développée chez les prédateurs marins supérieurs depuis une décennie, que ce soit chez les poissons osseux (Ménard *et al.*, 2007), les oiseaux de mer (Cherel *et al.*, 2008), les requins (Domi *et al.*, 2005) ou encore les phoques polaires (Zhao *et al.*, 2004). Des approches concernant plusieurs grands groupes d’espèces (poissons, mammifères, oiseaux) ont également été envisagées, permettant d’intégrer une plus large diversité de prédateurs (Das *et al.*, 2003). Selon les modèles biologiques et les zones géographiques, il apparaît que la ségrégation isotopique varie considérablement. Ainsi, la communauté des phoques polaires en Antarctique se ségrége de manière significative (Zhao *et al.*, 2004). A l’inverse, chez les oiseaux marins épipélagiques du sud du Canal de Mozambique, un chevauchement important des niches isotopiques a été observé à l’échelle de la communauté (Cherel *et al.*, 2008). Toutefois, les delphinidés de Mayotte montrent des différences relativement significatives entre les espèces, que ce soit sur le carbone que pour l’azote. Ceci serait lié à la nature très structurée des écosystèmes marins péri-insulaires (également révélée par les différences importantes entre les différents compartiments du lagon et de sa périphérie, cf. partie 4), de la côte au domaine océanique. De plus, les prédateurs plongeurs comme les delphinidés (à l’inverse des oiseaux marins du sud du Canal de Mozambique cités précédemment) s’alimentent à des profondeurs variables où les gradients verticaux de sources de carbone (notamment d’origine détritique) sont importants.

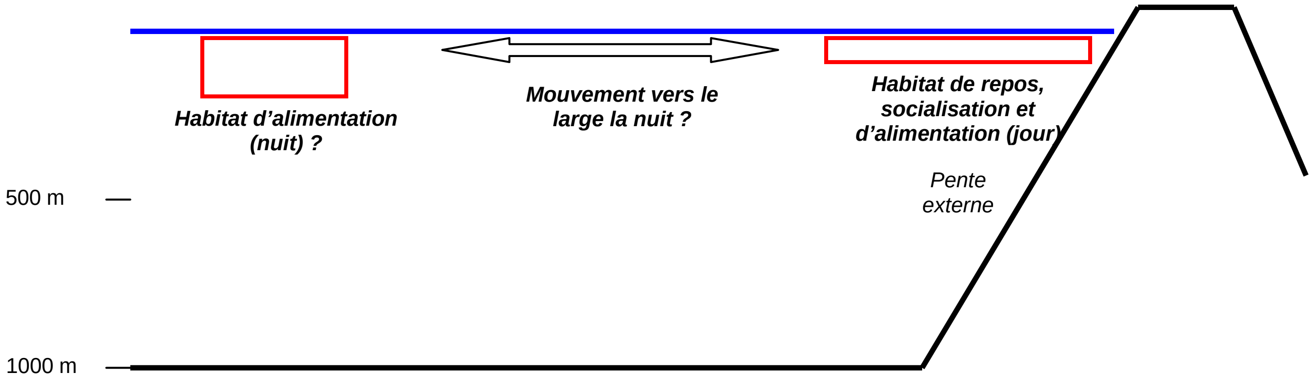
Au sein de la communauté de cétacés plongeurs de la Méditerranée nord-occidentale, les trois dimensions de la niche écologique ont été explorées pour étudier les mécanismes de partage des habitats et des ressources. Pour chaque dimension, les différentes espèces de la communauté se ségrégent (Praca, 2008). A Mayotte, cette ségrégation ne pouvait s'observer que par la combinaison des trois dimensions de la niche. Ceci nous permet de montrer que le climat et les gradients horizontaux et verticaux (côte-large et surface-fond) semblent être des facteurs importants permettant ou non d'observer des différences significatives dans le partage des habitats et des ressources au sein d'une communauté.

La ségrégation écologique des delphinidés de Mayotte peut être schématisée (Figure 7.3).

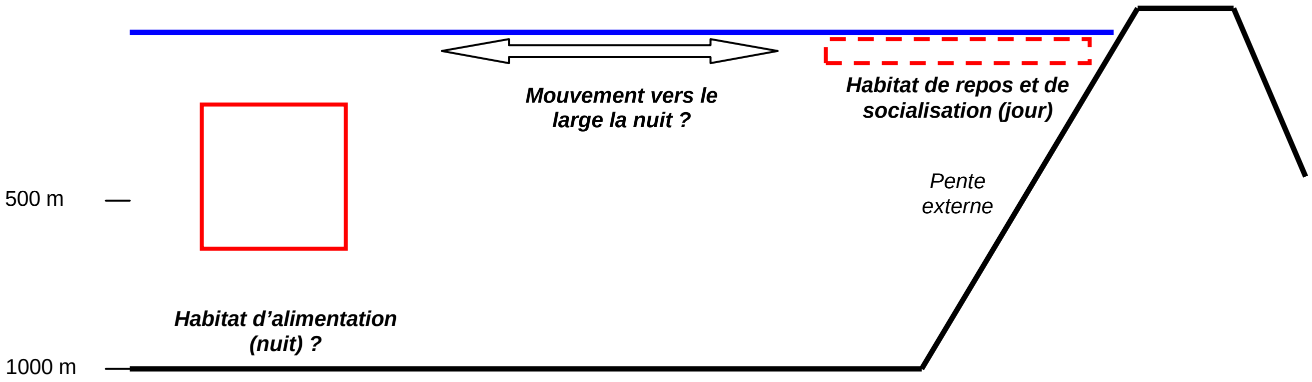
**Figure 7.3 :** Mode schématique d'utilisation des habitats et des ressources par les delphinidés de Mayotte (sources : cette étude ; Perrin *et al.*, 1973 ; Norris *et al.*, 1994 ; Dolar *et al.*, 2003 ; Amir *et al.*, 2005 ; Brownell *et al.*, 2009).



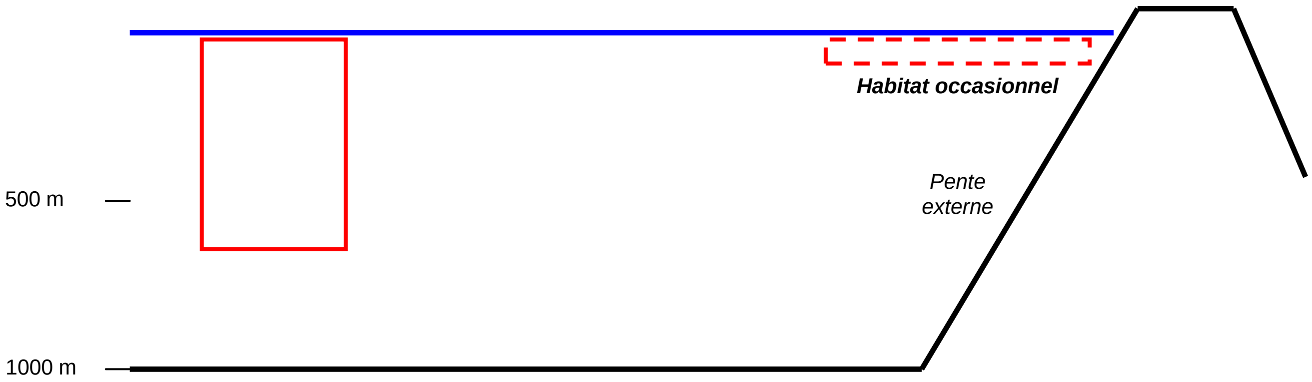
| Espèce | Niveau trophique | Habitat | Rythme diurne |
|---|---|---|---|
| *Stenella attenuata* | ++ | Pente externe<br>Proies épipélagiques | Prédateur diurne (nocturne ?) |



| | | | |
|---|---|---|---|
| *Peponocephala electra* | ++ | Pente externe<br>Proies mésopélagiques | Prédateur nocturne |



| | | | |
|---|---|---|---|
| *Lagenodelphis hosei* | +++ | Domaine océanique<br>Proies mésopélagiques | Prédateur nocturne ? |



### *7.1.3 Associations poly-spécifiques des espèces jumelles*

L’étude a montré que les delphinidés pouvaient former des associations poly-spécifiques et donc évoluer ensemble, au moins temporairement, au cours de la journée. Ces espèces occupent des habitats relativement similaires lorsqu’elles ne sont pas associées. C’est tout particulièrement le cas chez les espèces jumelles de la communauté de delphinidés de Mayotte, en l’occurrence le dauphin à long bec et le dauphin tacheté pantropical. Ceci pourrait être en contradiction avec la théorie des niches écologiques, car ces associations temporaires induisent un chevauchement de l’habitat mais potentiellement aussi des ressources. En effet, les trois avantages à la formation des associations poly-spécifiques sont : une utilisation plus efficace (donc moins énergivore) des ressources, une vigilance plus accrue face aux prédateurs et les avantages sociaux, permettant d’exploiter une plus grande gamme d’habitats et d’expérimenter les interactions sociales (une espèce ayant une plus grande taille peut ainsi expérimenter le comportement de reproduction sur une espèce de plus petite taille, par exemple ; Herzing & Johnson, 1997).

La présente étude montre que le dauphin à long bec et le dauphin tacheté pantropical utilisent des niches écologiques distinctes, notamment révélées par les signatures isotopiques et les budgets d’activités significativement différents. Par ailleurs, aucun comportement d’alimentation lors des associations poly-spécifique n’a été observé durant toute la période d’étude. Ceci signifie donc que les associations entre les deux espèces jumelles sont liées à la lutte (ou vigilance) contre les prédateurs. Le dauphin à long bec semble être le principal bénéficiaire de ces associations. Celui-ci change d’habitat durant la journée lorsqu’il est associé au dauphin tacheté pantropical pour bénéficier de la présence de cette espèce, notamment lorsqu’il se déplace d’un site de repos à un autre. Les avantages sociaux sont également possibles, puisque le dauphin à long bec peut exploiter une plus grande diversité d’habitats lorsqu’il est associé au dauphin tacheté pantropical. Toutefois, le comportement d’association de ces deux espèces met plus clairement en évidence un avantage lié à la lutte contre les prédateurs, abondants à l’extérieur du lagon. Aucune interaction directe entre les deux espèces, caractérisant des contacts sociaux, n’a pu être observée à Mayotte. Ceci ne permet donc pas de valider l’hypothèse selon laquelle les dauphins tachetés pantropicaux bénéficieraient également de ces associations pour la pratique de comportements sexuels, par exemple.

Les associations poly-spécifiques ont été documentées dans plusieurs zones géographiques dans le monde entier chez les delphinidés (e.g. Norris & Dohl, 1979 ; Scott & Chivers, 1990 ; Ballance & Pitman, 1998 ; Psarakos *et al.*, 2003 ; Dulau-Drouot *et al.*, 2008). Toutefois, l'interprétation de l'origine de la formation de ces associations n'est pas systématiquement réalisée (e.g. Quérouil *et al.*, 2008). En théorie, les associations poly-spécifiques, lorsqu'elles ont un rôle fonctionnel (et qu'elles ne se forment pas par chance), fournissent un bénéfice évolutifs aux espèces qui s'associent, ce qui ne serait pas le cas pour les espèces ne formant pas de telles associations (Whitesides, 1989 ; Heymann & Buchanan-Smith, 2000). Aux Açores, il a pu être démontré que les delphinidés, notamment le dauphin tacheté de l'Atlantique (*Stenella frontalis*), le dauphin commun (*Delphinus delphis*) et le dauphin bleu et blanc (*Stenella coeruleoalba*) s'associaient pour permettre le regroupement et la capture plus efficaces de leurs proies (Quérouil *et al.*, 2008). Au Bahamas, le grand dauphin (*T. truncauts*) interagit très fréquemment avec le dauphin tacheté de l'Atlantique pour pratiquer des interactions sociales (Herzing & Johnson, 1997). La lutte contre les prédateurs a été surtout été documentée en zone tropicale pour plusieurs paires d'espèces, là où les grandes espèces de requins exercent une forte pression de prédation sur les delphinidés. C'est le cas pour le globicéphale tropical et le grand dauphin commun dans le Pacifique est tropical ainsi que pour le dauphin à bosse et le grand dauphin de l'Indo-Pacifique en Australie (Stensland *et al.*, 2003). Dans certains endroits du monde, les associations entre dauphin à long bec et dauphin tacheté pantropical ont été documentées comme autour de l'île d'Oahu (Hawaii ; Psarakos *et al.*, 2003) ou en zone océanique comme dans le Pacifique est tropical (Norris & Dohl, 1979) et dans l'océan Indien occidental (Ballance & Pitman, 1998). Alors que les associations en zone océanique sont plutôt attribuées à la lutte contre les prédateurs, l'origine des associations en zone péri-insulaire n'est pas claire. Ainsi, la pression de prédation serait plus forte en zone océanique qu'à proximité des îles (Norris & Dohl, 1979). Cependant, les pentes externes des barrières récifales sont l'habitat d'un grand nombre d'espèces de grands requins, responsables d'attaque sur les delphinidés comme le requin tigre (*Galeocerdo cuvier*), le requin océanique (*Carcharhinus longimanus*) ou le requin bouledogue (*Carcharhinus leucas*). Notre étude sur les associations entre dauphin à long bec et dauphin tacheté pantropical montre que le partage des ressources ne constitue par l'origine de ces associations. Cette étude est donc complémentaire à celle sur les niches écologiques de la communauté de delphinidés. Elle montre que d'autres processus, en l'occurrence liés à la survie, sont à l'origine de ces associations, en l'occurrence la lutte contre les prédateurs lors des déplacements. Notre étude confirme donc l'importance des associations entre deux espèces pour la vigilance contre les prédateurs.

### *7.1.4 Formation des communautés chez le grand dauphin de l'Indo-Pacifique*

Le grand dauphin de l'Indo-Pacifique est une espèce vivant dans les eaux côtières de l'île de Mayotte. C'est également l'espèce pour laquelle nous avons le plus d'information, et ce du fait de sa grande accessibilité, de la grande proportion d'individus identifiables et du fait de la faible taille de sa population qui rend l'analyse des données de photo-identification relativement aisée. De ce fait, l'analyse de la structure de population à fine échelle et de la ségrégation intra-spécifique a pu être étudiée, et ce à plusieurs échelles temporelle emboitées : de l'échelle évolutive (structure génétique) à l'échelle de la vie de l'individu (ségrégation écologique et fonctionnement social). Autour de Mayotte, un unique groupe panmictique de grands dauphins a été détecté génétiquement. Compte tenu des caractéristiques bioécologiques de cette espèce (préférence pour les zones côtières peu profondes et forte sédentarité), il semble que la population de grands dauphins de Mayotte soit relativement isolée des autres populations de la région. Toutefois, l'utilisation d'autres indicateurs de ségrégation intra-spécifique a permis de détecter la formation de communautés. Les indicateurs écologiques utilisés, comme les signatures isotopiques du carbone et de l'azote, n'ont pas permis de détecter des phénomènes de ségrégation écologique entre les communauté de grands dauphins. Ceci reflète probablement qu'il n'existe pas de différences d'utilisation des ressources entre les communautés ou, tout aussi probablement, que les éventuelles différences ne sont pas discernables par les analyses isotopiques. De plus, l'étendue de la niche alimentaire du grand dauphin, reflétée par l'importante variance des signatures isotopiques, semble importante. Ceci est conforme à la littérature scientifique, le grand dauphin de l'Indo-Pacifique exploitant une grande diversité de proies associées aux récifs coralliens, aux herbiers marins de phanérogames et aux zones côtières au sens large (Mann *et al.*, 2000 ; Amir *et al.*, 2005). L'étude individuelle des habitats préférentiels et du domaine vital des grands dauphins du lagon de Mayotte a permis d'identifier au moins deux communautés : une communauté vivant loin de la côte et à l'extérieur du lagon en eaux plus profondes et une (ou plus) vivant préférentiellement à l'intérieur du lagon, proche des côtes et dans des eaux moins profondes. Les communautés ne sont pas formées d'individus apparentés, ce qui suggère qu'elles doivent bénéficier de l'apport de nouveaux individus ou du départ de membres, assurant un brassage génétique. L'étude de la structure sociale des grands dauphins, plus particulièrement des associations entre individus, a permis de confirmer l'existence de ces deux communautés. Cependant, l'origine de la formation des communautés n'a pu être déterminée et pourrait être due à des facteurs écologiques, notamment au partage des habitats et des ressources qui s'y trouvent mais aussi comportementaux (territorialité).

L’étude de la ségrégation écologique à l’échelle intra-spécifique a très peu été documentée, notamment chez les delphinidés. Les études existantes montrent par exemple que certaines espèces ont des stratégies alimentaires qui diffèrent et qui seraient liées à la culture de groupe, comme chez le globicéphale noir dans le détroit de Gibraltar (de Stephanis *et al.*, 2008). Ceci pourrait constituer un mécanisme de ségrégation écologique. Ainsi, le fonctionnement social et la culture de groupe peuvent avoir une influence sur l’exploitation des ressources, comme c’est le cas chez les mammifères évolués comme les delphinidés. Certaines espèces de delphinidés se caractérisent par d’importantes variations intra-spécifiques de l’alimentation de l’occupation de l’espace, héritées des parents (e.g. Krützen *et al.*, 2005). Dans notre cas, aucune évidence ne permet de montrer une culture de groupe dans l’alimentation, qui a pourtant été montrée chez la même espèce dans la baie des requins, en Australie (Connor *et al.*, 2000). Les communautés de grands dauphins de Mayotte ont un domaine vital distinct et sont composées d’individus qui s’associent préférentiellement mais qui n’ont aucun lien de parenté. Les situations diffèrent à travers le monde. Les grands dauphins de la baie de Moreton (Queensland, Australie) vivent en sympatrie mais se caractérisent par des stratégies alimentaires différentes (Chilvers & Corkeron, 2001). Dans la baie de Tampa, en Floride, les grands dauphins ont des traits communs à ceux de Mayotte puisque leur domaine vital ne se chevauche pas (Urian *et al.*, 2009). L’hypothèse de l’origine de la formation des communautés semble donc étroitement liée avec l’écologie mais également le fonctionnement social. Ainsi, les grands dauphins pourraient se partager l’espace (Mayotte, baie de Tampa) ou les ressources (baie de Moreton) pour éviter d’entrer en compétition. Une situation où les grands dauphins se partageraient à la fois l’espace et les ressources est également envisageable. Notre étude, réalisée sur une espèce facilement étudiable, permet donc de démontrer que les mécanismes de ségrégation écologique existent à l’échelle spécifique et qu’ils s’articulent probablement à travers les trois dimensions de la niche écologique. La dimension sociale doit également être considérée (dans notre cas les associations), puisqu’elle constitue une conséquence de la fragmentation de populations en communautés.

### *7.1.5 Synthèse générale*

A la lumière des différents éléments de la ségrégation écologique, une synthèse peut être établie aux deux niveaux abordés : les ségrégations inter- et intra-spécifique (Figure 4.3).

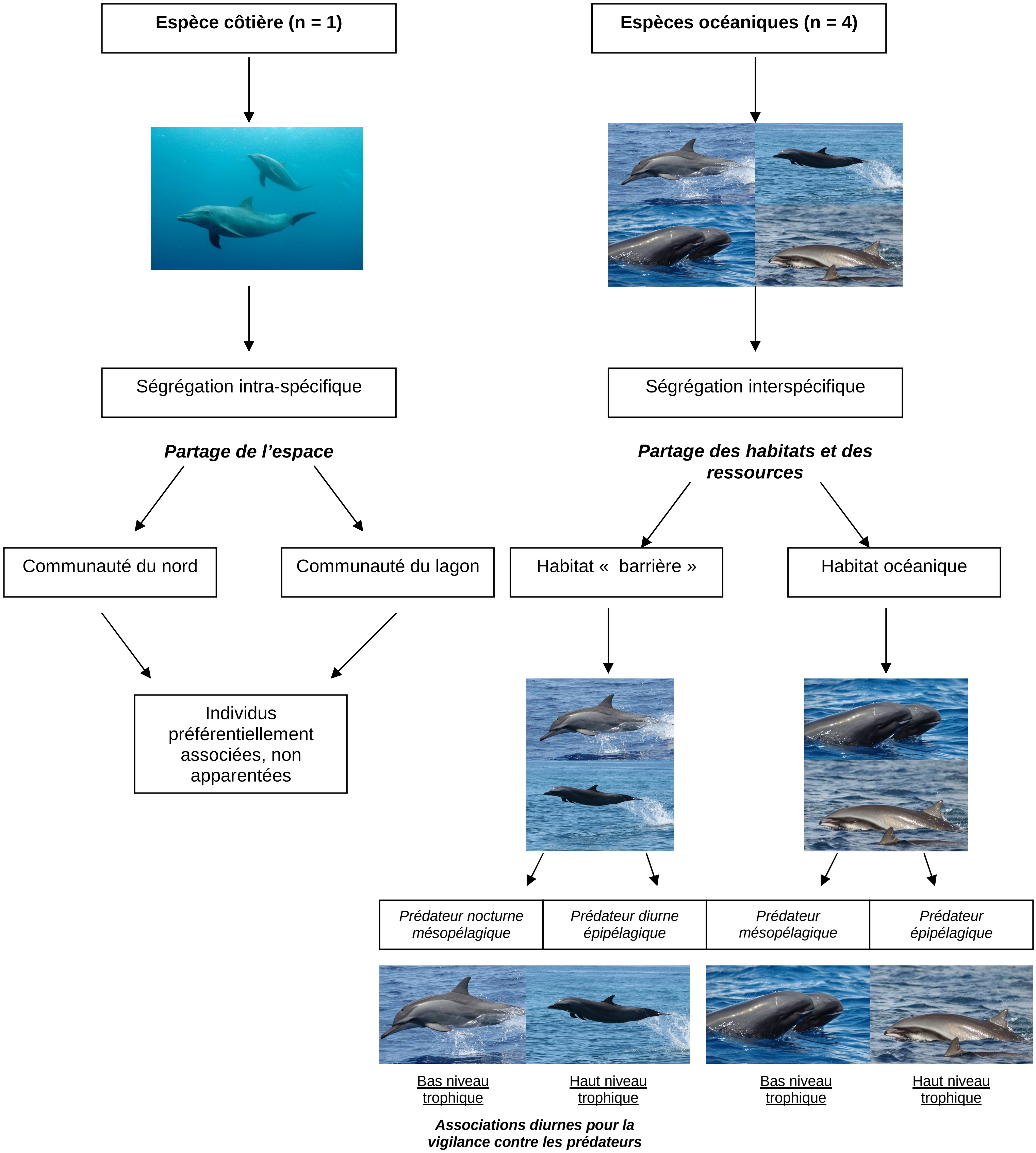


**Figure 4.3 :** Ségrégation écologique inter- et intra-spécifique chez les delphinidés de Mayotte.

## 7.3 Intégration de l'étude pour la gestion et la conservation

Cette étude fournit les bases écologiques de la gestion et de la conservation des delphinidés autour de Mayotte. Elle décrit la composition du peuplement (diversité), ses caractéristiques générales telles que l'abondance relative, la taille des groupes et la distribution spatiale. Des éléments fondamentaux d'écologie sont également présentés, notamment l'utilisation des habitats et des ressources (habitats préférentiels, budgets d'activités, utilisation des ressources). Cette étude permet donc de fournir des bases écologiques de la conservation des delphinidés de Mayotte, qui constituent également des indicateurs pertinents de la mesure de la biodiversité (Sergio *et al.*, 2006). Cette étude fourni des éléments pour la gestion du delphinidé qui semble le plus exposé aux activités humaines, en l'occurrence le grand dauphin de l'Indo-Pacifique. Il est notamment affectés par les dérangements dus à l'activité de *dolphin watching*, le trafic maritime de manière générale, la diminution potentielle de ses ressources alimentaires mais également la dégradation de la qualité de son habitat (Pusineri & Kiszka, 2007 ; Kiszka *et al.*, 2009b). Deux principales communautés de grands dauphins ont été identifiées autour de Mayotte : l'une qui occupe les zones côtières du lagon et l'autre qui a un habitat plus profond et plus éloigné à la côte dans le nord de l'île. Les deux zones géographiques correspondant au domaine vital de ces deux communautés sont différentes : les eaux côtières du lagon sont plus dégradées par les polluants, l'érosion littorale et sont plus appauvries sur le plan des ressources halieutiques. Enfin, les dérangements issus du trafic maritime et de l'observation commerciale des mammifères marins sont plus importants, ce qui implique que la communauté présente dans le lagon est plus vulnérable que celle présente dans le nord. Cet élément doit donc être intégré pour la gestion de cette espèce à valeur patrimoniale et économique forte.

## 7.4 Perspectives

Cette thèse a permis d'étudier la ségrégation écologique des delphinidés de l'île de Mayotte à plusieurs échelles : inter- et intra-spécifique. Elle met en évidence les processus de ségrégation à travers les dimensions de la niche écologique : habitats, ressources et variations temporelles. La dimension comportementale est également importante pour ces espèces évoluées, que ce soit à l'échelle de la communauté d'espèces (formation des associations poly-spécifiques pour le renforcement de la survie) mais également à l'échelle intra-spécifique (influence de l'écologie sur la structure sociale).

Toutefois, certaines approches complémentaires permettraient de mieux caractériser les processus de ségrégation, notamment par une analyse individuelle des comportements diurnes et nocturnes, qui pourrait être envisagée par la télémétrie. Le développement actuel des balises pour leur adaptation à la nage rapide des delphinidés, en évitant des impacts physiques sur les animaux, permettront à l'avenir d'envisager cette approche. A l'échelle intra-spécifique, notamment pour le cas du grand dauphin, la poursuite de son étude devrait constituer une priorité, notamment pour la gestion et la conservation de cette espèce. La continuité du suivi par photo-identification et la réalisation de biopsies cutanées sur d'autres individus permettraient d'affiner les informations sur le domaine vital individuelles, l'existence d'autres communautés ou encore les variations inter-communautés de l'alimentation à travers les traceurs de l'alimentation (isotopes stables notamment). Enfin, une meilleure connaissance des proies (abondance, diversité) par observations directes dans les différentes zones du lagon (*Underwater Visual Censuses*, pour le grand dauphin) ou par échantillonnage grâce à d'autres prédateurs « échantillonneurs » dont les contenus stomacaux sont disponibles (thons, espadons de la pêche palangrière locale) permettrait de mieux appréhender la contrainte des delphinidés face à la disponibilité de leurs ressources.

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# Annexes

# A preliminary study of habitat and resource partitioning among co-occurring tropical dolphins around Mayotte, south-west Indian Ocean

Alexandra Gross [1], Jeremy Kiszka [1,2], Olivier Van Canneyt [3], Pierre Richard [1] & Vincent Ridoux [1,3]

[1] LIttoral ENvironnement et Sociétés (LIENSs), UMR6250, Université de la Rochelle, 2 rue Olympe de Gouges, 17000 La Rochelle, France.
[2] Direction de l'Environnement et du Développement Durable, Collectivité Départementale de Mayotte, BP 101, 97600 Mamoudzou, Mayotte, France.
[3] Centre de Recherche sur les Mammifères Marins, Université de la Rochelle, 23 avenue Albert Einstein, F-17071 La Rochelle cedex, France.

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## Résumé

La diversité des delphinidés à Mayotte est très importante. Les espèces vivant en sympatrie autour de l'île pourrait vivre dans une zone limitée car elles n'exploiteraient ni les mêmes habitats, ni les mêmes ressources alimentaires. Cette étude préliminaire a pour objectif d'étudier la ségrégation écologique des delphinidés présents autour de Mayotte, notamment le grand dauphin de l'Indo-Pacifique, *Tursiops aduncus*, le dauphin tacheté pantropical, *Stenella attenuata*, le dauphin à long bec, *Stenella longirostris* et le péponocéphale, *Peponocephala electra.* Deux approches seront utilisées. Les habitats préférentiels seront étudiés par l'analyse de données d'observations collectées en mer et associées aux caractéristiques abiotiques de l'habitat. Le partage des ressources sera étudié par l'analyse les signatures isotopiques du carbone et de l'azote dans les biopsies de peau et de lard des dauphins. Les résultats montrent que seul *T. aduncus*, clairement associé avec les zones côtières peu profondes, se distingue des autres espèces en terme d'habitat. Les trois autres espèces partagent des habitats similaires à l'extérieur du lagon, dans des zones à la profondeur, inclinaison de la pente et distance à la côte plus importantes. Ces espèces n'ont pas pu être distinguées par l'analyse discriminante. L'analyse des isotopes stables confirment l'isolation écologique du grand dauphin de l'Indo-Pacifique avec les trois autres espèces océaniques. De plus, *P. electra* est clairement distingué par rapport aux deux espèces du genre *Stenella*, ce qui ne fut apparent dans les analyses d'habitat préférentiel. Ceci reflète des différences d'écologie qui ne peuvent être constatées grâce à des données d'observations en mer collectées durant la journée.

## Abstract

Mayotte in the southwest Indian Ocean is characterized by high dolphin diversity. They may coexist within a fairly small area around the island because they exploit neither the same preferential habitats nor the same resources. This preliminary study aimed to investigate ecological niche segregation among these delphinid communities: the Indo-Pacific bottlenose dolphin, *Tursiops aduncus*, the pantropical spotted dolphin, *Stenella attenuata*, the spinner dolphin, *Stenella longirostris*, and the melon-headed whale, *Peponocephala electra*. Two approaches were used. Habitat preferences were investigated by analysing dolphin sighting data and associated physiographical characteristics. Resource partitioning was explored by analysing C and N stable isotopes in skin and blubber biopsies. Only *T. aduncus*, which showed clear association with coastal habitats in the lagoon, differed from the others in terms of habitat preferences, characterised by shallow depth and slope, and proximity to the coast. All other species shared similar oceanic habitats immediately outside the lagoon, these being of higher depth and slope, greater distance from the coast and were not discernable by discriminant analysis. The two *Stenella* species and the melon-headed whale displayed very high overlap in habitat physiographic variables. The analysis of stable isotopes confirmed the ecological isolation of *T. aduncus* and revealed a clear segregation of *P. electra* compared to the two *Stenella* that was not apparent in the habitat analysis. This may reflect ecological differences that were not observable from diurnal surface observations.

**Keywords:** dolphins, ecological niche, habitats, stable isotopes, south-west Indian Ocean, Mayotte.

## Introduction

In biological communities, each species has its own unique niche, which provides the conditions and resources needed for its survival. A shared resource in limited supply will bring about competition between members of the same species (intra-specific competition) or between individuals of different species (inter-specific competition). Competition can take two different forms: interference, which is a direct, often aggressive, interaction between individuals, or exploitation-competition, in which individuals interact with each other indirectly, by responding to a resource level which has been depressed by the activity of competitors (Begon *et al.*, 1986).

A niche occupied by a species in the absence of competitors is termed its fundamental niche, whereas in the presence of competitors, species may be confined to a realized niche, which is shaped by the presence of competing sympatric species (Begon *et al.*, 1986). Hence, the coexistence of potentially competing species is often made possible by the differentiation of their realized ecological niches. The first mechanism that allows for niche differentiation is resource partitioning. In this case, different species living in the same habitat exploit the resources differently. For example, predators of different size may feed on prey of different size, hence minimising the overlap between the various predators' prey size ranges. Prey specialization presumably allows for niche partitioning in areas of sympatry (Ballance, 2002). The second mechanism involves spatial (microhabitat differentiation) or temporal separation in the availability of the different resources (these become available at different times of the day or different seasons of the year; Huisman & Weissing, 2001).

Small delphinids belong to numerous species which have similar morphological characteristics. This situation suggests that fine-scale mechanisms allow for the partitioning of habitats and resources when and where the different species live in sympatry. A study of the cetacean community of Great Abaco, Bahamas, has shown that the ecological niches of the four species that permanently live there do not overlap (MacLeod *et al.*, 2004). These species capture prey at different depths of the water column. Other cetacean species are observed in the study area only during the season when prey abundance is sufficiently high to support their presence, while they are competitively excluded for the rest of the year (MacLeod *et al.*, 2004). Indeed, the spatial distribution of marine predators is mainly determined by the distribution and availability of their prey, these in turn varying according to physical, chemical and biological characteristics of the water masses (Forcada, 2002).

The dietary ecology of marine mammals and their trophic level can be determined using different methods: traditional methods analyse faeces and regurgitated food of living animals, as well as the stomach contents of dead animals (from strandings or by-catch; e.g. Pusineri *et al*., 2007). A more recent method for studies of dietary ecology is stable isotope analysis of blubber, skin or muscle samples (Bearhop *et al*., 1993). The carbon and nitrogen isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$, expressed hereafter as $\delta^{13}C$ and $\delta^{15}N$) of a consumer reflect those of its diet, with a slight retention of the heavier isotope and excretion of the lighter one (Das *et al*., 2003). As a consequence, tissues will be enriched with heavy isotopes at every trophic level. The minor stepwise trophic enrichment of the carbon-isotope ratio limits its use in assessing trophic levels, but enhances its use in tracking carbon sources through a food chain. The carbon isotope ratio of secondary and tertiary consumers should thus reflect the source of carbon at the base of their food chain (Kelly, 2000). The higher enrichment of the nitrogen isotope ratio of consumers compared to their prey makes it very useful for the determination of their trophic level (Kelly, 2000). Thus, both ratios help elucidate trophic relations and habitat use.

Mayotte, a volcanic island in the northern Mozambique Channel (southwest Indian Ocean), is characterized by the permanent presence of more than 20 species of cetaceans (Kiszka *et al*., 2007). Of these, the most important in coastal waters are the Indo-Pacific bottlenose dolphin, *Tursiops aduncus* (Ehremberg, 1833), the pan-tropical spotted dolphin, *Stenella attenuata* (Gray, 1846), the spinner dolphin, *S. longirostris* (Gray, 1828), and the melon-headed whale, *Peponocephala electra* (Gray, 1846). The island has a great variety of marine ecosystems offering a large diversity of habitats: coasts, mangroves, an extended lagoon (1100 km$^2$), different kinds of reefs (fringing, pinnacles, and barrier), a steep insular slope with many submarine canyons and seamounts, and the open ocean (Quod *et al*., 2000). At least twelve species of delphinids may coexist in a fairly small area around the island because they exploit neither the same habitats nor the same resources (Kiszka *et al*., 2007). The present study aimed to investigate ecological niche segregation among the resident dolphin community of Mayotte, especially the Indo-Pacific bottlenose dolphin, the pantropical spotted dolphin, the spinner dolphin and the melon-headed whale. We concentrated on these four species as they are of fairly similar size and can be found within the same proximity around Mayotte, in closely-related habitats within a small area and at all seasons (Kiszka *et al*., 2007). This is particularly so for the two *Stenella* species and the melon-headed whale which are all encountered immediately outside the barrier-reef and in the channels, whereas existing literature suggests that they would be more differentiated habitat-wise, with the spinner dolphin feeding offshore but resting inshore, the melon headed whale being an oceanic squid-eater and the Indo-Pacific bottlenose dolphin dwelling in nearshore coastal habitats (Norris *et* *al*., 1994; Silva *et al*., 2005; Perryman, 2002; Wells & Scott, 2002). Two approaches were used for the study: a comparison of habitat by the analysis of dolphin sighting data and associated behavioural and physiographic characteristics (group size, depth, slope, distance to the coast and proximity to the different kinds of reefs), and the study of habitat and resource partitioning by the analysis of C and N stable isotopes from skin and blubber biopsies.

## Material and methods

### Study area

The volcanic island of Mayotte (45°10'E, 12°50'S), which is part of the Comoros archipelago, is located in the northern Mozambique Channel (Indian Ocean) between Madagascar and Southeast Africa. Its surface area is 376 km$^2$ and it is composed of two main islands and about 30 islets scattered within and around a lagoon. Mayotte is surrounded by a large lagoon-reef complex, whose width varies from 3 to 15 km. Fringing reefs surround the archipelago, an inner double-reef is present off the south-west end of Mayotte, and the barrier reef, which is interrupted by numerous channels, separates the lagoon itself (maximum depth 80 m) from the external slope and more oceanic habitats. The four species of interest, the Indo-Pacific bottlenose dolphin, the pantropical spotted dolphin, the spinner dolphin, and the melon-headed whale, range in size from about 200 cm and 90 kg for the spinner dolphin to 250 cm and 250 kg for the melon-headed whale (Perrin, 2002a,b; Perryman, 2002; Wells & Scott, 2002).

### Data and sample collection

Data were collected from 1997 to 2005, during small boat-based surveys dedicated to studying marine mammals (Figure 1). Several types of boats were used: a 7 m catamaran equipped with two, four-stroke, 60-hp outboard engines; a 7 m boat equipped with two, two-stroke, 40-hp outboard engines; a 6.4 m cabin boat equipped with an inboard four-stroke and 150-hp outboard engine. Surveys were conducted during daylight hours, i.e. between 0700 h and 1800 h, in sea conditions not exceeding Beaufort 3. The survey vessels did not follow pre-defined transects but sampling covered all habitats within the lagoon and over the external insular slope (Figure 1). Effort varied according to month (Figure 2), with more effort being applied in the austral summer (November to January). When dolphins were encountered, preliminary information records included group size (maximum, minimum, best estimate), geographic position, activity (travelling, resting, foraging/feeding, socialising, milling, play), group classification on the basis of the relative size of individuals (adults, sub-adults, calves), research boat disturbance (bowride, approach, avoidance, no response) as well as group formation (tight, loose, dispersed, variable, convergent; Shane, 1990; Würsig *et al.*, 1998). This study is still on-going and, therefore, only the sighting locations and associated physiographic variables are analysed here.

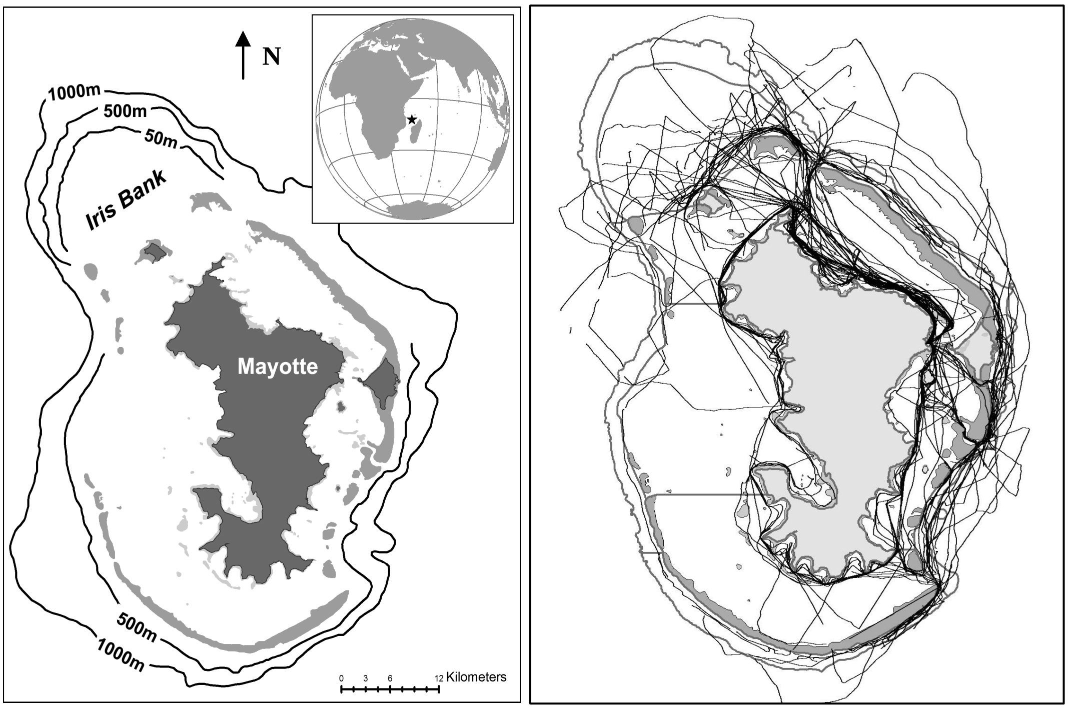


**Figure 1**: Location of the study area and observation routes from July 2004 to August 2005. Isobath (left) and GPS tracks of sighting surveys (right) are shown around Mayotte Island with barrier reef.

When conditions were optimal (good weather and sea state, dolphins closely approaching the boat), biopsies were collected using a cross-bow (*BARNETT Veloci-Speed® Class*) with Finn Larsen bolts and tips (20-mm). The dolphins were hit below the dorsal fin, when close (3-10 meters) to the research boat. Sampling periods spanned all seasons but sample sizes did not allow seasonal comparisons (January, August and December for *T. aduncus*, N=4; January, February, March and October for *S. attenuata*, N=4; February, March, May and October for *S. longirostris*, N=5; March, July and December for *P. electra*, N=4). It was not possible to determine sex, size or age of the individuals biopsied. Blubber and skin biopsy samples were preserved separately in 90° ethanol before shipping and subsequent analysis. Biopsy sampling was conducted under scientific permit #78/DAF/2004.

Database

We constituted a database in which every dolphin observation was associated with the physiographic characteristics (distance to the coast, to the different reefs and to the closest channel, as well as depth and slope of seafloor and the variance of these two parameters) corresponding to the GPS (Global Positioning System) fixes of the observation. The distance data were obtained using GIS (Geographic Information System) software ArcView (ArcGIS 8.2) by ESRI (Environmental Systems Research Institute). Bathymetric data were obtained from Service Hydrographique et Océanographique de la Marine (SHOM). Interpolation of bathymetry data, needed to generate depth and slope data for each sighting, was undertaken with the extension Spatial Analyst by kriging transformation of the raster file into an interpolated data file. This was obtained by calculating the mean value of the twelve points closest to every bathymetric point in a 1 $km^2$ grid. This interpolated data file thus allowed us to generate depth and slope data over the whole study area and therefore to associate bathymetry data to any dolphin observation in the area.

Data analysis

The environmental data were first compared between species using basic methods (non-parametric analyses and ANOVA). Then we used multivariate statistical methods including discriminant linear and quadratic analyses to examine how well sightings were assigned to the correct species from the combination of associated physiographic variables. All methods were implemented with the software R (R-2.2.1, R Development Core Team, 2005).

Stable isotope analyses

Blubber and skin were separated for each biopsy. The ethanol they contained was evaporated at 45°C over 48 h and the samples were ground and freeze-dried (Hobson *et al*., 1997). Lipids were extracted using cyclohexane ($C_6H_{12}$) prior to analysis because they are depleted in $^{13}C$; if they were not extracted, this would cause a bias in the isotopic signature of $^{13}C$ (De Niro & Epstein, 1978; Tieszen *et al*., 1983). Small sub-samples (0.35 to 0.45 mg ± 0.001 mg) were prepared for analysis. Stable isotope measurements were performed with a continuous-flow isotope-ratio mass spectrometer (Isoprime, Micromass) coupled to an elemental analyser (Eurovector EA 3024). Results are expressed in $\delta$ notation relative to PeeDee Belemnite and atmospheric $N_2$ for $\delta^{13}C$ and $\delta^{15}N$, respectively, according to the equation

$$\delta X = \left[ \frac{R_{sample}}{R_{s\tan dard}} - 1 \right] \times 1000$$

Where X is $^{13}C$ or $^{15}N$ and R is the isotope ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicated that measurement errors were <0.15‰ and <0.20‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Percent C and N elemental composition of tissues were obtained using the elemental analyzer and used to calculate the sample C:N ratio, indicating a good lipid removal efficiency when <4.

## Results

### General

Our cetacean sightings comprised 394 positional data for *S. longirostris* (*n* = 208), *S. attenuata* (*n* = 88), *T. aduncus* (*n* = 83) and *P. electra* (*n* = 15) in all sectors around Mayotte (Figure 2) and all seasons (Figure 3). Indo-Pacific bottlenose were mostly found within the lagoon, very often in the immediate proximity of the fringing reef, and to a lesser extent over the North West bank located outside the main barrier reef. The two *Stenella* species were observed all along the barrier reef on its outer side and made only a few incursions into the lagoon. Finally, the melon-headed whale was only seen outside the barrier reef.

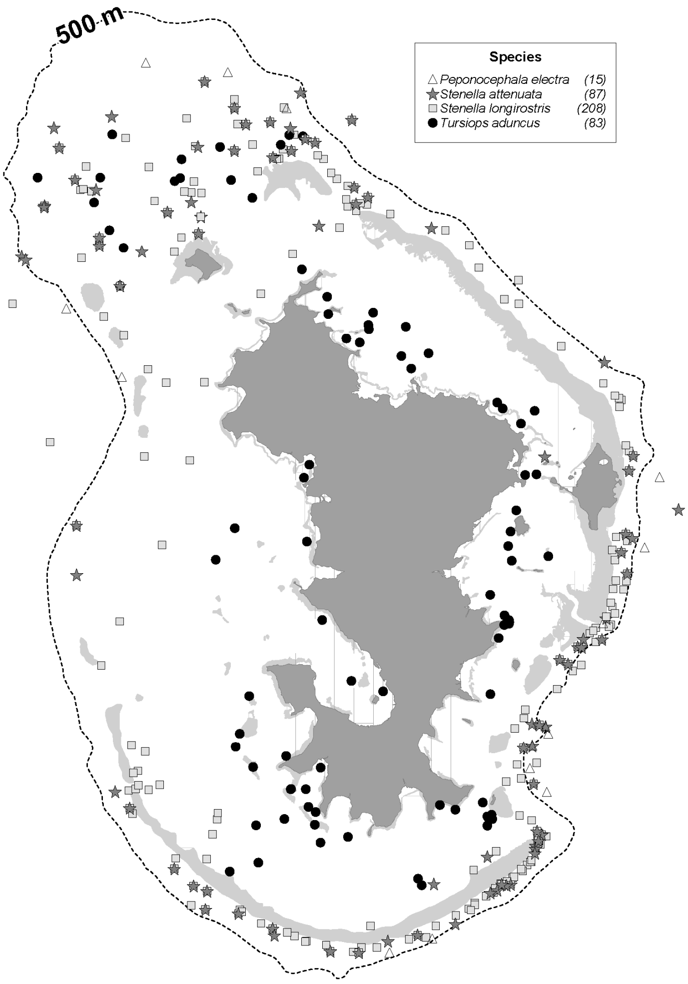


**Figure 2**: General locations of delphinid sightings around Mayotte and its reefs.

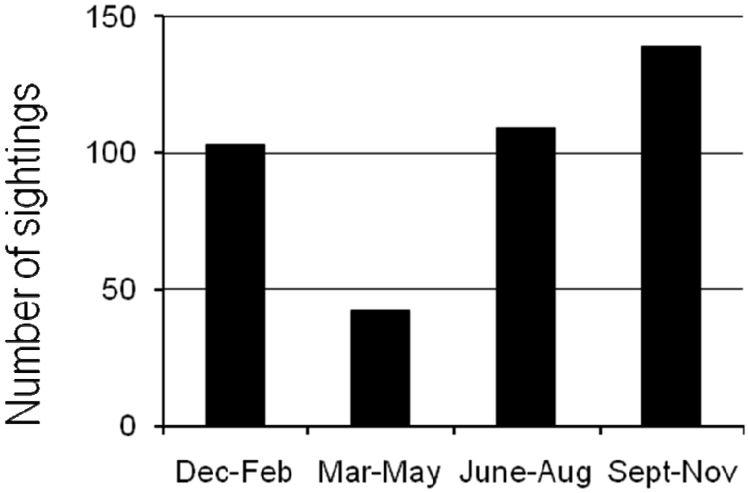


**Figure 3**: Temporal distribution of effort expressed as number of sightings per three-month period.

### Habitat use and niche partitioning

A preliminary Principal Component Analysis (PCA plot not shown) allowed us to select group size, distance to coast, depth and slope as the set of physiographic variables with least redundancy. Distances to the various reefs and to the nearest channel were heavily redundant relative to distance from coast and therefore not retained. A simple comparison of the distribution of these variables for the four focal species was performed using Kruskall-Wallis tests (Figure 4). *T. aduncus* is observed at short distances from the coast with shallow bathymetry and moderate slopes, whereas the other three species cannot be significantly differentiated in terms of habitat characteristics. In particular, the two *Stenella* species manifested similar characteristics in group size and environmental preferences. On the other hand, group size differed strongly between *T. aduncus* that lives in small groups (median = 6) and *P. electra* that is mostly found in groups of several hundred individuals (median = 300). Linear discriminant analysis separated the species according to their environmental characteristics (Figure 5). The predictive power of the linear discriminant analysis was good only for *T. aduncus* which can be explained by its habitat preferences (Table 1, upper part). The other species' habitat characteristics were too similar to permit acceptable predictions. The good prediction for *S. longirostris* might be attributable only to the considerable number of sighting data for this species. Finally, the quadratic discriminant analysis provided slightly better predictive results, especially for *P. electra* (Table 1, lower part).

The different methods used to compare the preferred habitats of the four delphinid species under study all clearly showed that *T. aduncus* differs from the other species in its preferred environmental parameters. *S. attenuata* and S. *longirostris* share similar environmental characteristics. *P. electra* is characterised by a larger group size and deeper depth preference, but resembles *Stenella* in terms of the majority of its other environmental preferences (distance and slope).

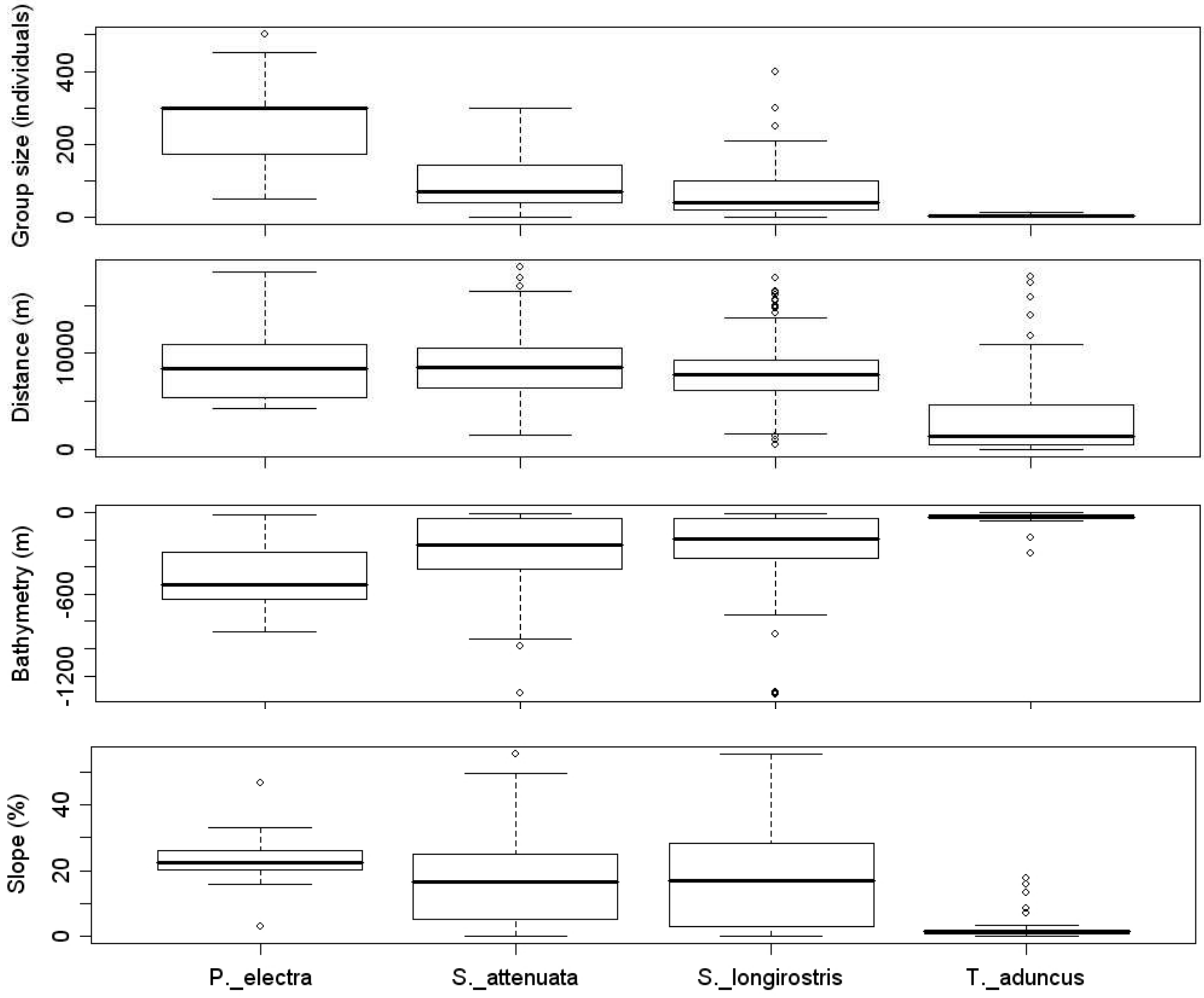


**Figure 4**: Delphinid sighting median values, 50, 75 percentiles and outliers of (a) group size, (b) distance to the coast, (c) depth and (d) seafloor slope. Kruskal Wallis tests showed that *T. aduncus* differed significantly in all cases with *p*-values $<10^{-6}$.

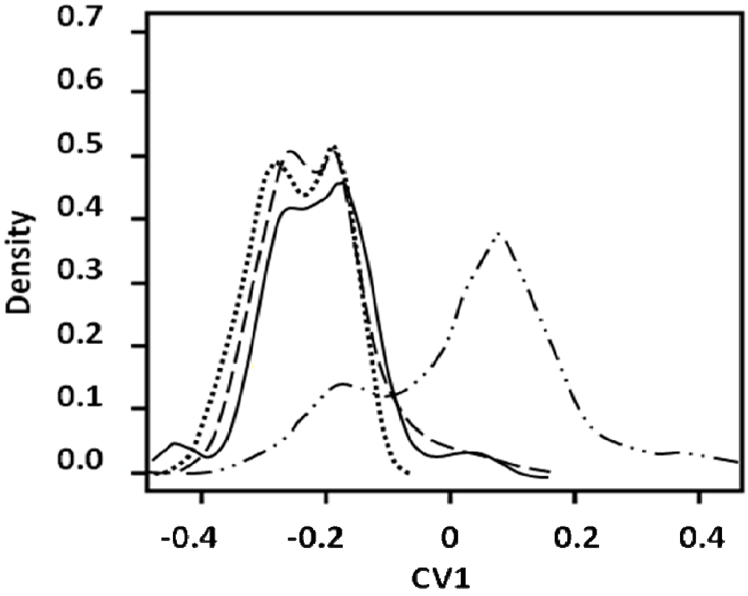


**Figure 5**: Sighting density for melon-headed whale (dotted line), pantropical spotted (black line), spinner (dashed line) and Indo-Pacific bottlenose dolphin (dashed and dotted line) along the first discriminant axis.

**Table 1**: Discriminant analysis: linear and quadratic predictions for the four species. Each sighting was assigned to one of the four study species on the basis of its associated physiographic characteristics. Only *T. aduncus* data were correctly assigned to the right species whereas all others were mostly assigned to *S. longirostris* as they all share similar habitat characteristics.

**Linear discriminant analysis**

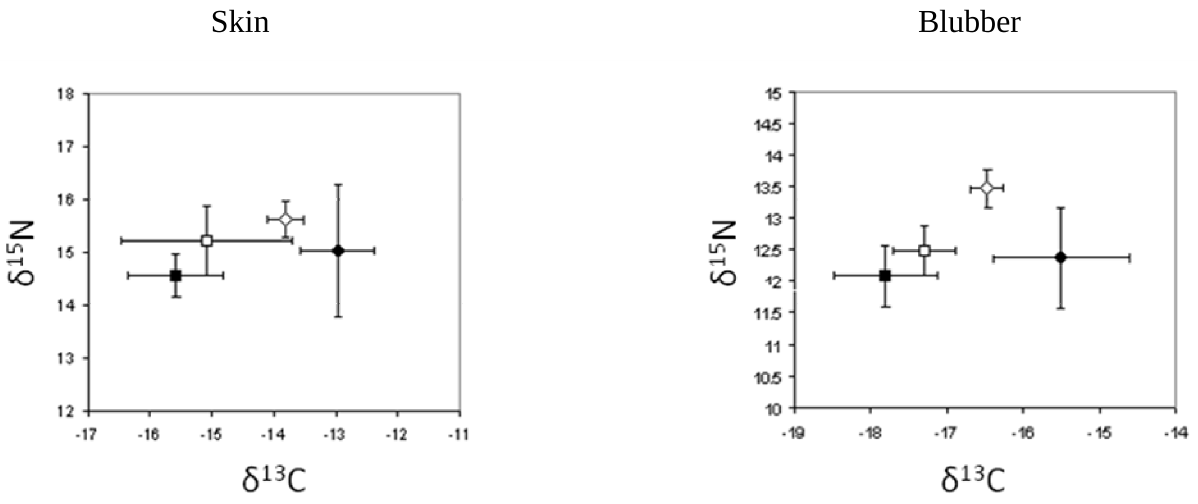
| | *Peponocephala electra* | *Stenella attenuata* | *Stenella longirostris* | *Tursiops aduncus* |
|---|---|---|---|---|
| *P. electra* | **2** | 3 | 5 | 0 |
| *S. attenuata* | 1 | **3** | 1 | 2 |
| *S. longirostris* | 12 | 79 | **194** | 19 |
| *T. aduncus* | 0 | 2 | 8 | **62** |
| **Good prediction** | **14%** | **3%** | **93%** | **77%** |

**Quadratic discriminant analysis**

| | *Peponocephala electra* | *Stenella attenuata* | *Stenella longirostris* | *Tursiops aduncus* |
|---|---|---|---|---|
| *P. electra* | **11** | 4 | 4 | 0 |
| *S. attenuata* | 1 | **18** | 18 | 1 |
| *S. longirostris* | 3 | 46 | **131** | 4 |
| *T. aduncus* | 0 | 19 | 55 | **78** |
| **Good prediction** | **79%** | **20%** | **63%** | **96%** |

### Resource partitioning

Stable isotope ratios were lower in blubber than in skin but the pattern of differences observed between species was similar in both tissues (Figure 6). Skin and blubber of *T. aduncus* have the highest values of $\delta^{13}$C. The two *Stenella* species are not discernable from each other as shown by the extensive overlap in standard deviation for both $\delta^{15}$N and $\delta^{13}$C, and have the lowest values for $\delta^{13}$C. *P. electra* has the highest $\delta^{15}$N and a $\delta^{13}$C values that are intermediate between those for the two *Stenella* species and *T. aduncus*. The intra-specific variance is represented by the standard deviation, which is more important for the $\delta^{13}$C values than for the $\delta^{15}$N, except in the blubber samples of *T. aduncus* where intra-specific variance in the $\delta^{15}$N is prevalent.


Skin

Blubber

**Figure 6**: Stable isotope ($\delta^{13}C$ and $\delta^{15}N$ in ‰) values in delphinid blubber (right-hand graph) and skin (left-hand graph). Graphs show average values and standard deviations. Black squares represent *S. longirostris* (N=5), whites squares *S. attenuata* (N=4), black diamonds *T. aduncus* (N=4) and white diamonds *P. electra* (N=4).

## Discussion

The present study comprises a preliminary analysis of habitat and resource use among an assemblage of co-existing tropical delphinids living around Mayotte in the southwest Indian Ocean. The principal finding is that, among the four species of interest, the Indo-Pacific bottlenose dolphin is clearly differentiated from the other species in terms of both habitat preference and stable isotope analyses. From the variables tested here, the other three species can hardly be separated in terms of their preferred habitats but stable isotope analysis revealed a dietary segregation between the melon-headed whale and the two species of the genus *Stenella*. This was not initially evident in the sighting data analyses that described the dolphins' diurnal use of habitats. However, some limitations render these findings preliminary. The sightings constituted presence-only data as the observation effort could not be readily quantified and, hence, the data cannot provide significant information concerning dolphin absence. In this work, we tried to characterise the habitats where dolphins were found, not assess the overall distribution of each species around the island. Nevertheless, the field surveys comprehensively covered the study area such that all habitats were visited and the sighting data of the four focal species were considered representative of their habitat preference.

The Indo-Pacific bottlenose dolphin, *Tursiops aduncus*, occupies an ecological niche that clearly differs from those occupied by the other study species. *T. aduncus* was observed only inside the lagoon except in the northern part of the island where the reef system is in the form of an open bank outside the lagoon. This species is generally found close to the fringing reef which constitutes the ecosystem where prey of this coastal dolphin may be concentrated. The high $\delta^{13}C$ value in its tissues indicates a benthic carbon source that dolphins more easily access in coastal habitats (Hobson, 1999). This species has indeed been observed feeding near mangroves, along the fringing reefs or over seagrass beds. Its isotopic signature of $\delta^{15}N$ is similar to that of the two *Stenella*, but this cannot be interpreted as an indication of similar trophic levels as the $\delta^{15}N$ values of the local primary producers *versus* those outside the lagoon have not been investigated at this stage.

*T. aduncus* lives and forages individually or in small groups inside the lagoon, where the water is shallow and large predators are absent, and probably feeds on prey that would not aggregate in large schools (Mann *et al*., 2000). Indo-Pacific bottlenose dolphins forage over reefs or soft bottom substrata and near the shore relatively close to the island of Mayotte and around Zanzibar (Tanzania) (Amir *et al*., 2005).

The pantropical spotted dolphin and the spinner dolphin share a barrier reef-associated habitat outside the lagoon. They are also found where the water depth rapidly attains a depth of 100 m. In comparison to the Indo-Pacific bottlenose dolphin, their tissues had a lower $\delta^{13}C$, suggesting it was derived from an oceanic carbon source; oceanic phytoplankton is reported to be $^{13}C$-depleted relative to marine phanerogams (Hobson, 1999). Their isotopic ratios suggested their diet comprised oceanic prey.

*S. attenuata* and *S. longirostris* can occasionally be observed inside the lagoon where they might take advantage of the safety it provides for resting. This kind of behaviour has been observed in Hawaiian spinner dolphin populations (Norris *et al*., 1994). *S. longirostris* generally lives in single-species groups from several dozens to several hundreds of individuals, e.g. around the main Hawai'i island (Norris *et al*., 1994). Their aggregation in large groups might offer some protection against predators but it might also facilitate feeding through communal hunting on large pelagic fish schools. In the present work, *S. attenuata* was rarely observed in single-species groups but was generally found in association with *S. longirostris*, forming important mixed-species groups. Both species might take advantage of a larger group size for safety and foraging. Nevertheless, a large group size increases the potential for intra-specific competition as well as inter-specific competition if the two species feed together. A study in the southwest Atlantic has shown that distributions of spotted dolphins and spinner dolphins may partially overlap (Moreno *et al*., 2005). Associations of spotted dolphins and spinner dolphins are frequently found in Hawai'i, where the two species travel together while showing many aggressive interactions, but they do not seem to feed together (Psarakos *et al*., 2003). Conversely, in the Azores, common dolphins, *Delphinus delphis*, and Atlantic spotted dolphins, *Stenella frontalis*, associate and forage together (Clua & Grosvalet, 2001). As *S. attenuata* and *S. longirostris* have similar habitat preferences and similar isotopic signatures, both for carbon and nitrogen, there is no evidence of ecological niche differentiation in these two species. Two options could be investigated in the future: either the two dolphins share the same resources in the same habitats, presumably because food is not limiting there, or they segregate when feeding on different resources but their prey have similar isotopic signatures because they rely on the same carbon source at the same trophic level.

The melon-headed whale, *Peponocephala electra*, prefers steep slopes and slightly deeper water than the two *Stenella* species. *Peponocephala electra* forms large groups of several hundred individuals. As it was always observed in a habitat that overlaps with that of the spinner and spotted dolphins, analysis of its habitat characteristics failed to distinguish between it and the two *Stenella* species. This might be due to the fact that melon-headed whale sightings were only made on groups that occasionally approached the island, as the surveys were conducted in a limited area around Mayotte and groups living farther offshore in the open ocean would not have been observed. In this case, our understanding of the preferred habitat of this species remains marginal, being limited to its nearshore fringe. Stable isotope analysis, on the other hand, clearly showed that there is an ecological differentiation between *P. electra* and the two *Stenella* species. Values of $\delta^{13}C$ for *P. electra*'s were intermediate between those of the *Stenella* species and *T. aduncus*. This would suggest that carbon isotopic composition of *P. electra* is influenced more by benthic primary production than that of the two *Stenella* species. *Peponocephala electra* is known for its oceanic habitat (Perryman, 2002), and possible interpretations for its $\delta^{13}C$ include the possibility that it is a deep-diving species that feeds on prey derived from a detritus-based food web unlike the *Stenella* that feed on a phytoplankton-based food web. In addition, *P. electra* clearly differs in its $\delta^{15}N$, this being indicative of a higher trophic level, suggesting its diet includes more carnivorous fish and squid than the spotted and spinner dolphins. Again, as in *T. aduncus*, all sources of primary production should be investigated concerning their $\delta^{15}N$ to adequately interpret the trophic levels.

If there is high inter-individual variance in the $\delta^{15}N$ (*versus* $\delta^{13}C$) values within a species, the interpretation is that the species is composed of individuals that have varied feeding habits and prey on organisms at different trophic levels ($\delta^{15}N$) or are found in different habitats

($\delta^{13}C$). A low variance indicates that all the individuals are specialist feeders on similar prey or within the same habitat. Thus, stable isotope variance is sometimes considered a measure of niche width (Bearhop *et al*., 2004) or at least the inter-individual measure of niche width. Results of our stable isotope analysis indicate that *P. electra* is a fairly specialized feeder, whereas *S. attenuata*, *S. longirostris* and especially *T. aduncus* would be more eclectic feeders, which, in the latter case, is in line with previous studies (Mann *et al*., 2000).

Detectable differences between the standard deviations in the stable isotope composition in the skin and blubber samples might be attributable to their differential rates in tissue renewal: this takes a few days for epidermis but several months for the collagen matrix of the blubber (Abend & Smith, 1995). The residence time of elements in tissues depends on metabolic turnover rates (Rubenstein & Hobson, 2004). This enables tracking of an animal's foraging history as demonstrated by a study on pilot whales (*Globicephala melas*) in the North Atlantic (Abend & Smith, 1995). *T. aduncus* and the two *Stenella* species clearly differ in the respective isotopic carbon signatures in their skin and blubber, indicating that they feed on trophic webs with different carbon sources over the long term.

Each species' habitat preference is presumably based on their prey distributions (Baumgartner *et al*., 2000) which, in turn, are related to water depth (Hastie *et al*., 2005) and, indirectly, bathymetric features that influence currents and productivity (Fiedler, 2002). Foraging behaviour seems to be closely related to submarine habitat characteristics (Hastie *et al*., 2004). It has been demonstrated that a variable bathymetry contributes to global delphinid abundance, promoting the regional abundance of different species (Gannier, 2005). The rich marine biodiversity of Mayotte is possibly related to its variety of habitats and these provide numerous ecological niches for delphinid prey.

## Conclusions

The present study provides preliminary ecological indications of niche differentiation and resource partitioning within the Mayotte delphinid communities. The only species that differs from the others in terms of habitat characteristics is the coastal-dwelling Indo-Pacific bottlenose dolphin, whereas pantropical spotted and spinner dolphins and the melon-headed whale share similar oceanic habitats immediately outside the lagoon. Stable isotope analysis confirmed the ecological specialisation of *T. aduncus* and, in addition to this, revealed a clear segregation of *P. electra*, from to the two *Stenella* species in terms of their feeding that was not apparent in the habitat analysis. This may reflect behavioural differences that were not detectable from diurnal surface observations. Further work should strengthen these conclusions through dedicated sampling of habitat preference and an expansion of the stable isotope studies. These should focus on seasonal changes in food partitioning and the isotopic composition of a series of putative prey species and primary producers characteristic of the inshore-offshore gradient of habitats found around Mayotte.

## Acknowledgements

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# Individual and group behavioural reactions of small delphinids to remote biopsy sampling

Jeremy Kiszka [1, 2], Benoit Simon-Bouhet [1], Claire Pusineri [3] & Vincent Ridoux [1, 4]

[1] LIENSs (LIttoral, ENvironnement et Sociétés), UMR 6250, CNRS-Université de La Rochelle, 2, rue Olympe de Gouges, F-17000, La Rochelle, France.

[2] Direction de l'Environnement et du Développement Durable, Collectivité Départementale de Mayotte. BP 101 F-97600 Mamoudzou, Mayotte.

[3] Office National de la Chasse et de la Faune Sauvage, Délégation Régionale Outre-Mer, Coconi, Mayotte.

[4] Centre de Recherche sur les Mammifères Marins, Université de la Rochelle, 23 avenue Albert Einstein, F-17071 La Rochelle cedex, France.

***Animal Welfare*, sous presse**

## Résumé

L’échantillonnage par biopsie est une technique de collecte de tissus efficace pour bon nombre d’analyses biologiques. Cependant, déterminer l’impact comportemental de cette pratique de recherche est important du fait que celui-ci peut potentiellement varier en fonction des localités, des espèces ciblées et du matériel utilisé. Dans cette étude, nous avons examiné les réactions comportementales de quatre espèces de petits delphinidés (d’une longueur totale variant de 160 à 278 cm), à savoir *Stenella longirostris*, *Stenella attenuata*, *Tursiops aduncus* et *Peponocephala electra*, face à l’échantillonnage par biopsie autour de l’île de Mayotte (12$^{o}$50’S, 45$^{o}$10’E, sud-ouest de l’océan Indien). Deux échelles ont été considérées : 1- la réaction comportementale de l’individu ciblé par l’échantillonnage ; 2- la réaction du groupe focal dont l’individu ciblé dépend. Trois grandes catégories de réactions ont été définies sur la base des caractéristiques et de la durée des réactions : faible, modérée et forte. Cette étude met en évidence que l’échantillonnage par biopsie induit des réactions essentiellement modérées de la part des individus ciblés. Aucune différence significative des réactions ont été observées entre les espèces, que ce soit à l’échelle des individus ou des groupes focaux. En d’autres termes, les petites espèces de delphinidés (*Stenella* sp.) ne montrent pas de réactions plus importantes et plus fréquentes que les plus grandes (*T. aduncus*, *P. electra*). Aucun effet de la taille des groupes sur l’intensité des réactions. Cependant, il est clair que le succès de collecte d’échantillon est plus important lorsque les groupes sont plus importants (plus grande disponibilité d’individus autour du bateau). Enfin, chez le dauphin à long bec, espèce pour laquelle nous disposons d’un grand nombre de données, nous avons étudié si l’activité comportementale des animaux avait un effet sur les niveaux de réaction. Les groups au repos et en phase de socialisation montraient des réactions plus fortes que les groupes en déplacement ou engagés dans des déplacements non directionnels. Cette étude met donc en évidence que l’impact des biopsies sur le comportement des dauphins demeure limité. Cependant, pour le principe de précaution et pour limiter l’impact des biopsies, il est recommandé de pratiquer l’échantillonnage quand les dauphins sont en déplacement.

## Abstract

Biopsy sampling is an effective technique to collect cetacean skin and blubber samples for various biological studies. However, determining the impact of this research practice is important, as impact may vary among sites, species and gear used. We examined the short-term behavioural reactions of four small (160-278 cm in length) delphinid species (*Stenella longirostris*, *Stenella attenuata*, *Tursiops aduncus* and *Peponocephala electra*) to remote biopsy sampling around the island of Mayotte ($12^o$50’S, $45^o$10’E, SW Indian Ocean). Two scales of behavioural reactions were considered: 1- the behavioural reaction of the individual, and 2- the reaction of the focal group to which the targeted individual belonged. Three main categories of behavioural responses were defined on the basis of the character and duration of behavioural response: low, moderate and strong. This study underlines that biopsy sampling induces moderate reactions of individuals. No inter-specific variations of responses, at the scale of individuals or focal groups, were observed. In other words, smaller delphinids were not more reactive than larger ones. No effect of group size was observed on the strength of behavioural reactions. However, it was clear that biopsy success during sampling sessions was higher in species with large group size. Finally, in the spinner dolphin (*S. longirostris*), we investigated whether initial behavioural state affected the level of reaction. Resting and socialising groups showed a stronger response than milling and travelling groups. This study confirms the limited impact of remote biopsy sampling in small delphinids, especially in the spinner dolphin. However, as a precautionary approach, in situations where it is possible, biopsy sampling of milling and travelling dolphins may be preferred.

**Keywords:** animal welfare, delphinids, group reactions, individual reactions, Indo-Pacific bottlenose dolphin, melon-headed whale, pantropical spotted dolphin, spinner dolphin, remote biopsy sampling.

## Introduction

In wildlife studies, some invasive techniques may be used to collect biological samples to answer a variety of questions which may be of particular relevance for management and conservation purposes. It is critical that the impact of such research practices is quantitatively assessed and managed, as the process of sample collection may negatively impact individuals and/or populations over a range of scales (e.g. injuries, individual stress, individual/group displacement, change of behaviour, etc.).

The use of skin and blubber biopsy samples from free-ranging cetaceans is a widespread and powerful technique to answer many questions, including population genetics (stock identity, social organization, population size, phylopatry, genetic connectivity, Amos & Hoelzel, 1990; Bérubé *et al*., 1998), feeding ecology and trophic relationships using stable isotope and fatty acid analyses (Herman *et al.*, 2005; de Stephanis *et al.*, 2008; Gross *et al.*, 2009), and pollutant analysis (Godard *et al.*, 2004). In order to collect samples, modified crossbows, rifles and hand held biopsy poles have been used, both for large and small cetaceans, including delphinids (Weinrich *et al.*, 1991; Barrett-Lennard *et al.*, 1996; Krützen *et al.*, 2002; Bilgmann *et al.*, 2007). The behavioural effect of biopsy sampling has been investigated in large whales, such as right whales (*Eubalaena glacialis* and *E. australis*, Brown *et al.*, 1991; Best *et al.*, 2005), humpback whales (*Megaptera novaeangliae*, Weinrich *et al.*, 1991; Clapham & Mattila, 1993), other large balaenopterid whales (Gauthier & Sears, 1999), and delphinids such as short-beaked common (*Delphinus delphis*, Bearzi, 2000), bottlenose dolphin (*Tursiops* spp., Krützen *et al.*, 2002; Bilgmann *et al.*, 2007; Gorgone *et al.*, 2008) and Indo-Pacific humpback dolphin (*Sousa chinensis,* Jefferson & Hung, 2008).

The International Whaling Commission considers biopsy sampling to be acceptable, since no long-term effects (change of behaviour) have been shown on individuals and populations (International Whaling Commission, 1991). Levels of short-term reactions to biopsy sampling could potentially vary among species, populations and individuals. However, for both small and large cetaceans, the behavioural impact of biopsy sampling is generally considered to be low. Responses from the animals can be typified as reactions to a noxious stimulus of brief duration and low-to-moderate amplitude (Weinrich *et al.*, 1992; Best *et al.*, 2005; Bilgmann *et al.*, 2007; Jefferson & Hung, 2008). In small cetaceans, a case of death has been reported in a short-beaked common dolphin, underlining that remote biopsy sampling is not without risk (Bearzi, 2000). Consequently, the use of less invasive sampling techniques may be preferred. Other methods include skin swabbing and faecal sampling (Harlin *et al.*, 1999; Parsons *et al.*, 1999). However, these techniques provide a limited amount of material, and DNA may not be of sufficient quality to undertake multiple markers analyses and other analyses (such as pollutant analyses, for example). Biopsy sampling is generally preferred for molecular genetic studies (Parsons *et al.*, 2003) and other analyses such as those of stable isotopes (Gross *et al.*, 2009). In addition, the use of remote techniques, using a gun or a crossbow, is more effective than a pole system for studies of population structure and parentage because animals can be sampled even if they do not bowride. Remote sampling also allows the individual identification of targeted dolphins (Bilgmann *et al.*, 2007). Proper identification of bowriding animals is generally not possible (good photograph angle).

The objective of this study is to characterize short-term reactions of four small delphinid species to remote biopsy sampling: the spinner dolphin (*Stenella longirostris*, 160-208 cm), the pantropical spotted dolphin (*Stenella attenuata*, 160-260 cm), one of the smallest delphinids, the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*, 230-270 cm) and the melon-headed whale (*Peponocephala electra*, 240-278 cm), one of the least known delphinids. This study provides, to the best of our knowledge, the first information on the effect of biopsy sampling on these species.

In order to collect skin and blubber samples for stable isotope, genetic and histopathological investigations, remote biopsy sampling was conducted from December 2004 to October 2008. Levels of behavioural reactions were recorded at two different scales: 1- the individual reaction of the sampled dolphin and 2- the behavioural reaction of the focal group to which the targeted animal belonged. The latter component of the study has not been investigated in previous studies for any other cetacean, as far as we are aware, and allows understanding the impact of remote biopsy sampling at a broader scale, i.e. groups and not only targeted individuals.

## Materials and methods

### Study area

The island of Mayotte (45°10’E, 12°50’S), which is part of the Comoros archipelago, is located in the northern Mozambique Channel (western Indian Ocean) between Madagascar and Southeast Africa. Its surface area is 376 km$^2$. This territory is composed of two main islands: the main inhabited island, on the east and on the barrier reef, a smaller inhabited island. The other islands are small islets dispatched all over the lagoon. The island of Mayotte is characterized by the presence of high marine mammal diversity (22 species including 12 delphinids; Kiszka *et al.*, 2007). The most common species are the spinner dolphin, the pantropical spotted dolphin, the Indo-Pacific bottlenose dolphin and the melon-headed whale; these are resident year-round (Kiszka *et al.*, 2007).

### Biopsy collection

From December 2004 to September 2008, small-boat-based cetacean surveys were conducted throughout the year in Mayotte waters in sea conditions not exceeding Beaufort 3. Observation effort concentrated mostly on the lagoon and over the insular slope in adjacent waters of the barrier reef. Biopsy attempts were made opportunistically, when groups and individuals were easily approachable and when conditions were optimal (Beaufort < 2, dolphins closely approaching the boat). Optimal weather conditions allowed stability of the research boat and better chances to sample the animals successfully and safely. Several types of boats were used: a 7-m catamaran equipped with two, four-stroke, 60-hp outboard engines; a 7-m mono hull boat equipped with two, two-stroke, 40-hp outboard engines; a 6.4-m cabin cruiser equipped with one, four-stroke, and 150-hp outboard engine; and a 10.8-m cabin cruiser equipped with two, four-stroke, 115-hp outboard engines. Biopsies were collected by using a crossbow (BARNETT Veloci-Speed® Class, 68-kg draw weight) with Finn Larsen (Ceta-Dart, Copenhagen, Denmark) bolts and tips (dart 25-mm long, 5-mm-diameter). A conical plastic stopper caused the bolt to rebound after the impact with the dolphin. The dolphins were hit below the dorsal fin when sufficiently close (3-10 m) to the research boat. Focal groups/individuals were approached under power at speeds of 1-4 knots. Blubber and skin biopsy samples were preserved individually in 90% ethanol before shipping and subsequent analysis. Biopsy sampling was conducted under French scientific permit #78/DAF/2004 (September 10, 2004) and permit #032/DAF/SEF/2008 (May 16, 2008) after examination of the project by Conseil National de Protection de la Nature.

### Behavioural observations

During biopsy sampling sessions, an observer recorded behavioural reactions of dolphins at two different scales: the targeted individual and the focal group with which the targeted individual was associated. The focal group was defined as a group of dolphins engaged in the same activity and travelling in the same direction (Shane, 1990). Three levels of behavioural reaction were defined for individuals and focal groups. These reactions followed Hooker *et al.* (2000) and were adapted for the species investigated in this study:

- No reaction: the individual and focal group continued to show the same behaviour as before the biopsy attempt;

- Moderate reaction: the individual or the focal group modified its behaviour but gave no prolonged (>5 min) evidence of behavioural disturbance; reactions included e.g. acceleration, twitch and immediate dive and simple immediate dive. A dive was considered as a behavioural response to biopsy sampling when it lasted more than 5 minutes;
- Strong reaction: the individual or the focal group modified its behaviour in a succession of percussive behaviours (strong and short-lived reactions), including escape from the research boat of the individual or/and focal group (leaping, breaches, tail slaps).

Data analysis

We investigated the occurrence (events and their proportions) of reactions described above and factors responsible for the variability of reactions (group size, species, activity), at the scale of hit/targeted individuals as well as focal groups. Group size was defined prior to biopsy sampling as the number of animals at the surface within five body lengths of each other (Smolker *et al.,* 1992). The estimates of group size were more stochastic for spinner dolphins, pantropical spotted dolphins and melon-headed whales, as group size for these species was important (mostly > 50 individuals). Determining absolute group size was not possible for large groups of delphinids. The predominant behaviour was recorded as the activity displayed by the majority of the animals of the group during the first 10 minutes. These data were collected during scan sampling of the group (Mann, 1999) using six different behavioural categories: travelling, milling, resting, feeding/foraging, playing and socializing (Shane, 1990).

Analysis of individual behavioural reactions were differentiated when the animal was missed (the bolt did not reach the animal) or hit. An individual is considered as hit when the bolt reached the body. There was no differentiation between biopsy hit providing or not providing a sample. We tested how group size may affect individual behavioural reactions, especially for the most frequently sampled species, the spinner dolphin. For this species, we also investigated the effect of initial behavioural state on the levels of reaction and the long term effect of biopsy sampling. In this later case, we hypothesised that avoidance behaviour would increase across the study period. Significance of this increase has been tested using a Pearson’s correlation. For comparisons, Fisher exact tests, Kruskal Wallis tests and contingency table analyses were performed using Rv2.10.0 (R Development Core Team, 2010).

## Results

Biopsy sampling was undertaken from December 2004 to September 2008 (n = 271 attempts, n = 193 samples). Four species (spinner dolphin, pantropical spotted dolphin, melon-headed whale and Indo-Pacific bottlenose dolphin) constituted 96% of the biopsies sampled (n = 259 attempts, n = 181 samples). Other species included the Fraser's dolphin (*Lagenodelphis hosei*, n = 7), the common bottlenose dolphin (*Tursiops truncatus*, n = 2), the Indo-Pacific humpback dolphin (n = 2) and the short-finned pilot whale (*Globicephala macrorhynchus*, n = 1), but this data was not been included in this study. We used three types of vessels to undertake biopsy sampling, but no significant differences of individual behavioural reactions were found between boat types (all species combined, $\chi^2 = 3.7$, $df = 6$; $P = 0.391$).

**Table 1:** Number of attempts, biopsy samples collected and sampling success in delphinids sampled around the island of Mayotte from December 2004 to September 2008.

| Species | n attempts | n samples | % success | Number of biopsy sessions | Mean group size | Average n biopsies/ session |
|---|---|---|---|---|---|---|
| *Stenella longirostris* | 137 | 96 | 70 | 30 | 70.5 | 3.2 |
| *Stenella attenuata* | 77 | 50 | 65 | 20 | 78.5 | 2.5 |
| *Peponocephala electra* | 23 | 18 | 78 | 5 | 310 | 3.6 |
| *Tursiops aduncus* | 22 | 17 | 77 | 15 | 6.3 | 1.1 |

Among the four species, no significant inter-specific differences in reactions were recorded, both at the scales of individuals (Fisher exact test; $P = 0.9$) and groups ($P = 0.643$). Sampling success (a hit) varied between species from 65 to 78% (Table 1). On 34 occasions overall, the hit was successful but no sample was retained in the biopsy tip. Individual behavioural reactions to remote biopsy sampling were recorded on 252 occasions (180 hits, 72 misses), while focal group behavioural reactions were recorded on 271 occasions (193 hits, 78 misses). There were no statistical differences between individual behavioural reactions between biopsy hits and misses (all species combined, Fisher exact test, $P = 0.068$). Similarly, at the scale of focal groups, no significant differences between biopsy hits and misses were found (all species combined, KW test; $H = 0.702$; $df = 1$; $P = 0.402$).

At the individual scale, 94% of individual reactions were moderate, i.e. twitch and immediate dive, and simple immediate dive (Figure 1, Table 2). Strong reactions (tail slap, leaping, successive breaches and escape) only represented 2% of behavioural responses of individual dolphins. Escape and leaping was only observed in spinner and spotted dolphins. Increase of speed was observed once in a bottlenose dolphin group (Table 2).

Group behavioural reactions were frequent (54% of sampling sessions), with dive being the commonest moderate reaction (45%, Figure 2, Table 2). Strong reactions of focal groups were rare, representing only 4% of responses. These strong reactions consisted of increased swimming speed or escape (Table 2, Figures 1 and 2).

We did not find any correlation between group size and behavioural reactions (Fisher exact test; $P = 0.431$). However, there is a clear relationship between the mean specific group size and the mean number of biopsies collected per biopsy session (Table 1). The average number of biopsies collected during each session was the lowest for the Indo-Pacific bottlenose dolphin, which had the lowest mean group size (Table 1).

On six occasions, hit dolphins were observed bow-riding just after being sampled (fresh wound of the biopsy hit observed below the dorsal fin or in adjacent areas). These cases were observed in the pantropical spotted dolphin (n = 2 events), spinner dolphin (n = 2) and Indo-Pacific bottlenose dolphin (n = 2). During sampling sessions, significant signs of avoidance of the research vessel by groups were observed on few occasions: in spinner dolphins (n = 2, after one and four biopsy attempts) and in melon-headed whales (n = 2, after one and six biopsy attempts).

We hypothesized that group reactions to biopsy sampling would differ according to activity (milling/travelling, resting, socializing, and playing). We tested this for spinner dolphins, as the dataset for that species was the largest. A statistical difference was found between group reactions and initial behavioural states in which spinner dolphin groups were engaged (Fisher exact test; $P = 0.041$). Spinner dolphins predominantly showed a stronger response to biopsy sampling when resting and socialising. When milling and travelling, reactions were moderate.

We did not observe changes of dolphin reactions (increase of avoidance behaviour) to the research vessel prior to biopsy sampling over the study period (nearly four years; Pearson's correlation, $r = 0.324$, $P > 0.05$).

**Table 2:** Individual and focal group behavioural reactions of *Stenella longirostris*, *Stenella attenuata*, *Peponocephala electra* and *Tursiops aduncus* to remote biopsy sampling (numbers represents events).

| | *Stenella longirostris* | *Stenella attenuata* | *Peponocephala electra* | *Tursiops aduncus* |
|---|---|---|---|---|
| **Individual reactions** | | | | |
| Twitch and dive | 83 | 21 | 8 | 10 |
| Successive breaches | 1 | 1 | 0 | 0 |
| Tail slap | 2 | 0 | 0 | 0 |
| Escape (leaping) | 1 | 0 | 0 | 0 |
| No reaction | 1 | 0 | 0 | 0 |
| **Group behavioural reactions** | | | | |
| Dive | 41 | 19 | 7 | 9 |
| Increase swimming speed | 2 | 0 | 0 | 0 |
| Escape | 1 | 1 | 0 | 1 |
| No reaction | 40 | 28 | 10 | 6 |

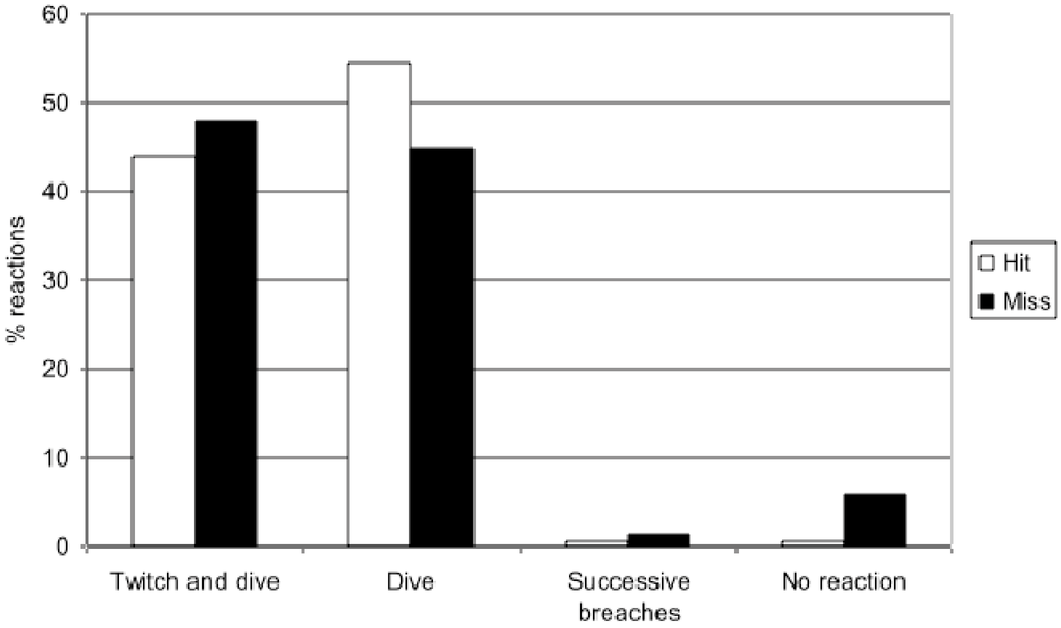

**Figure 1:** Individual behavioural reactions of delphinids (*Stenella longirostris*, *Stenella attenuata*, *Tursiops aduncus* and *Peponocephala electra*) to a biopsy hit or miss.

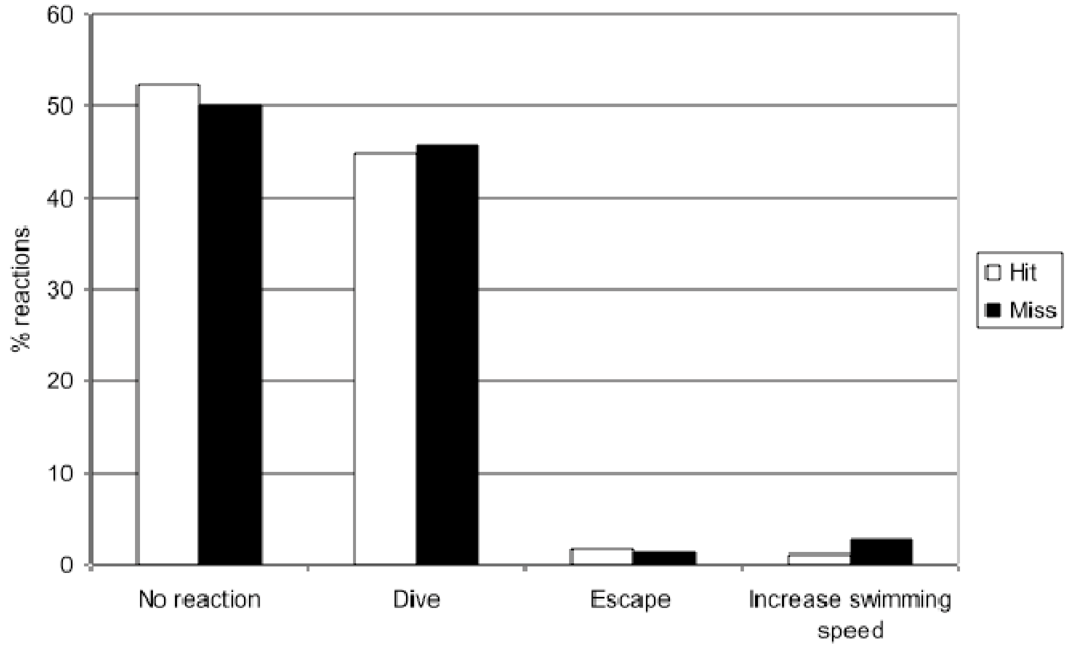

**Figure 2:** Focal group behavioural reactions of delphinids (*Stenella longirostris*, *Stenella attenuata*, *Tursiops aduncus* and *Peponocephala electra*) to a biopsy hit or miss.

## Discussion

In this study, we observed behavioural reactions of four delphinid species to remote biopsy sampling. The biopsy success reached 65-78%, which is consistent with previous studies. This was mostly due to the high accessibility of the targeted species. They generally came close to the research vessel, especially dolphins of the genus *Stenella*, often coming to ride waves created by the bow of the boat. No significant inter-species differences were found in reactions to remote biopsy sampling. Indeed, the smallest species (spinner and pantropical spotted dolphins) did not have a higher occurrence of moderate reactions than larger ones (Indo-Pacific bottlenose dolphin and melon-headed whale), as might have been expected. However, the strongest reactions, such as breaches and escape, occurred (but were very rare). Such extreme reactions were only observed in the smaller species, especially spinner and pantropical spotted dolphins. However, due to the small sample size for Indo-Pacific bottlenose dolphins and melon-headed whales, we can not exclude that these species could also react strongly, like spinner and spotted dolphins do.

The mean number of biopsies per session was greater for species with a larger mean group size, i.e. melon-headed whales, spinner and pantropical spotted dolphins. In larger groups, animals are more accessible for biopsying, as there are more individuals to choose from. This is likely to be not just a function of the behaviour or the group reaction, but also because of the higher number of individuals.

Despite the fact that we used three different types of boats, no differences in reactions were found among boats. These differences have been documented in other studies, with generally stronger reactions when smaller boats were used (Bilgmann *et al.*, 2007). However, in this later study, sampling was done on bowriding dolphins, and the boat types and length differed to a much larger extent than in the study presented here.

Delphinids around Mayotte exhibited short-term behavioural reactions to biopsy attempts, characterized by acceleration, twitch and immediate dive and simple immediate dive. Strong reactions to biopsy sampling were previously recorded in common bottlenose dolphins (Parsons *et al.*, 2003). Conversely, reactions of common bottlenose dolphins appear to be minimal in other areas such as in eastern US (Gorgone *et al.*, 2008). Dolphins of all species sampled react in a similar fashion to biopsy hits and misses. This has been previously documented for other species such as the Indo-Pacific humpback dolphin (Jefferson & Kung, 2008), meaning that the hit of the bolt on the water has a significant effect on the reactions of dolphins at the proximity of the impact. In the study presented here, focal groups were frequently impacted by biopsy sampling, meaning that remote biopsy sampling does have a broader effect on small cetaceans, i.e. on adjacent individuals belonging to the group. This effect was also greater on species constituting small groups, i.e. Indo-Pacific bottlenose dolphins, as the biopsy success decreased during sampling sessions for such species. The group behavioural reactions of spinner and pantropical spotted dolphins were relatively low, apparently because they formed larger aggregations. However, results underlined that there is a variability of reactions according to initial behavioural state. Indeed, for the spinner dolphin, we observed that the animals had stronger reactions to remote biopsy sampling when resting and socialising. When milling and travelling, reactions were more moderate. This suggests that remote biopsy sampling should be preferably conducted during travelling and milling activities.

### Animal welfare implications

Overall, conducting remote biopsy sampling is effective on small delphinids and induces a limited short-term (less than 5 minutes) behavioural impact on hit and missed individuals, including in the smallest delphinid species (especially dolphins of the genus *Stenella*). However, we observed that biopsy sampling does not only impact hit individuals, but groups to which the targeted individual belongs. No long-term effect of biopsy sampling was observed, such as an increase of avoidance of the research vessel of the animals. This confirms that the method has no long term impact on the animals. However, as a precautionary approach, our findings suggest that biopsy sampling may preferably be conducted when the animals are milling or travelling. However, it is critical to reconsider practicing biopsy sampling to answer scientific questions.

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# The use of stable isotope analyses from skin biopsy samples to assess trophic relationships of sympatric delphinids off Moorea Island (French Polynesia)

Jeremy Kiszka [1,*], Marc Oremus [2, 3], Pierre Richard [1], Michael Poole [4] & Vincent Ridoux [1, 5]

[1] LIttoral ENvironnement et Sociétés (LIENSs), UMR 6250 (CNRS-Université de la Rochelle). Institut du Littoral et de l'Environnement. 2, rue Olympe de Gouges, 17000 La Rochelle, France.

[2] University of Auckland, School of Biological Sciences, 3A Symonds Street, Private Bag 92019, Auckland, New Zealand.

[3] Centre de Recherches Insulaires et Observatoire de l'Environnement, BP 1013 Papetoai, Moorea, French Polynesia.

[4] Marine Mammal Research Program, BP698, 98728 Maharepa, Moorea, French Polynesia.

[5] Centre de Recherche sur les Mammifères Marins, Université de la Rochelle, 23 avenue Albert Einstein, F-17071 La Rochelle cedex, France.

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## Résumé

Déterminer les relations entre les organismes d’une communauté est fondamental en écologie. Cependant, accéder à des données (des échantillons, par exemple) peut être difficile dans des environnements isolés. L’île de Moorea (Polynésie Française) est caractérisée par une diversité importante d’espèces de dauphins. Les différentes espèces ne peuvent coexister que si elles n’exploitent ni les mêmes habitats, ni les mêmes ressources alimentaires. Cette étude a pour objectif d’étudier la ségrégation écologique au sein de la communauté de delphinidés vivant de manière permanente autour de Moorea : le dauphin à long bec, *Stenella longirostris*, le dauphin à bec étroit, *Steno bredanensis*, le globicéphale tropical, *Globicephala macrorhynchus*, et le péponocéphale, *Peponocephala electra*. Nous avons également étudié les variations intra-spécifiques de l’écologie, tout particulièrement entre les genres. Le partage des ressources et des habitats a été étudié via l’analyse des signatures isotopiques du carbone ($\delta^{13}C$, reflétant les habitats d’alimentation) et de l’azote ($\delta^{15}N$, reflétant le niveau trophique). Des échantillons de peau issus de biopsies cutanées (collectés de juillet à octobre 2002 à 2004) ont été utilisés pour réaliser les analyses. Les résultats révèlent que le dauphin à long bec a le niveau trophique le plus bas. Les trois autres espèces ont des signatures isotopiques de l’azote relativement similaires. Le dauphin à long bec se distingue bien du dauphin à bec étroit et du globicéphale tropical mais pas du péponocéphale. Pour ces trois dernières espèces, le chevauchement des signatures isotopiques est important. Pour *S. longirostris, S. bredanensis* and *G. macrorhynchus*, pas de variations des signatures de $\delta^{13}C$ et de $\delta^{15}N$ étaient significatives entre les sexes. Ceci suggère qu’il n’existe pas de processus de ségrégation entres espèces ou que ceux-ci ne sont pas détectables. Ceci suggère que les isotopes stables peuvent masquer des processus fins de ségrégation écologique et que les méthodes traditionnelles d’analyse de l’alimentation (contenus stomacaux), de l’habitat et des budgets d’activité sont fondamentaux pour l’étude de la ségrégation écologique d’une communauté d’organismes.

## Abstract

Defining trophic relationships among organisms of a community is critical in ecology. However, the access to data is sometimes difficult, particularly in remote environments. The island of Moorea (French Polynesia) is characterized by high dolphin diversity. The different delphinid species may coexist around the island because they exploit neither the same preferential habitats nor the same resources. This study aimed to investigate ecological niche segregation among the most common delphinid species: the spinner dolphin (*Stenella longirostris*), the roughed-toothed dolphin (*Steno bredanensis*), the short-finned pilot whale (*Globicephala macrorhynchus*), and the melon-headed whale (*Peponocephala electra*). We also investigated intra-specific variation in feeding ecology, particularly between sexes. Resource partitioning was explored by analysing $\delta^{13}C$ (reflecting foraging habitats) and $\delta^{15}N$ stable isotopes (reflecting trophic level) from skin biopsies collected around Moorea from July to October 2002 to 2004. Results revealed that spinner dolphins had the lowest trophic level. The three other species had similar $\delta^{15}N$ signatures, i.e. trophic level. The most significant result is the differentiation of the spinner dolphin from the rough-toothed dolphin and the short-finned pilot whale but not from the melon-headed whale. For the latter three species, some degrees of overlap were apparent. For *S. longirostris*, *S. bredanensis* and *G. macrorhynchus*, variation of $\delta^{13}C$ and $\delta^{15}N$ stable isotope was not significant between sexes, suggesting no or undetectable intra-specific segregation processes. This study suggests that stable isotopes reveal some degree of segregation and overlap within the delphinid community of Moorea. However, some fine-scale segregation processes may be concealed by stable isotope analyses, meaning that traditional dietary analyses and diving behaviour investigations are complementary in answering questions related to niche segregation.

**Keywords:** delphinids, ecological niche, stable isotopes, carbon, nitrogen, biopsy samples, Moorea, French Polynesia, South Pacific.

## Introduction

Sympatric species with similar ecological requirements can compete for resources and thus their coexistence requires some degree of habitat and resource segregation (Pianka, 1974). Indeed, similar species that co-occur are thought to compete for resources unless they occupy different physical locations and/or feed on different prey. A shared resource in limited supply will bring about competition between members of the same species (intra-specific competition) or between individuals of different species (inter-specific competition) (Roughgarden, 1976).

Oceanic delphinids belong to 35 species worldwide (Jefferson *et al.*, 2008). Many of them have similar morphological characteristics, feeding habits and habitat preferences. This phenomenon has been documented around tropical oceanic islands, where delphinid diversity and biomass is generally high and where closely-related species co-occur (Gross *et al.*, 2009). Around these islands, high cetacean diversity may be explained by the presence of a wide range of marine habitats in close proximity to one another (Kiszka *et al.*, 2007). In addition, oceanic islands appear to constitute areas of particular density of top predators due to an “island mass” effect. Similar to continental margins, insular slopes of islands potentially provide more abundant resources in the oligotrophic tropical marine environment (Guilmartin & Revelante, 1974). This situation of sympatry suggests that fine-scale mechanisms allow for the partitioning of habitats and/or resources. A study of the tropical delphinid community around the island of Mayotte, in the Comoros Archipelago (south-western Indian Ocean), has shown that the ecological niches of the delphinids occurring there do not overlap (Gross *et al.*, 2009). Indeed, these species capture prey at different depths of the water column. In other areas, such as the Bahamas, the cetacean community shares habitat and resources but only during the season when prey abundance is sufficient to support its needs, while competitive exclusion exists for the rest of the year (MacLeod *et al*., 2004). On the other hand, top predators may overlap in their feeding habits due to low productivity of tropical waters (Cherel *et al.*, 2008). If these shared resources are limited quantitatively, inter-species competition can occur.

The dietary ecology of cetaceans and their trophic level can be determined using different methods. The most extensively used consist in analysing the stomach contents of dead animals. However, the specimens required for performing such analyses are often unavailable, particularly in tropical islands where carcasses rapidly disappear and coastline configuration is often unfavourable to cetacean stranding. The use of naturally occurring nitrogen and carbon stable isotopes analysed in skin biopsies has provided alternative information from which to better understand top predator feeding ecology, including marine mammals (Hobson & Welch, 1992; Abend & Smith, 1995; Das *et al.*, 2003; Zhao *et al.*, 2004; Gross *et al.*, 2009). This approach is generally considered as complementary to stomach content studies as it integrates feeding habits on a longer-term basis. Various tissues, having varying temporal resolution (turnover rates), may be used in stable isotope analyses, including skin (Gross *et al.*, 2009). Turnover rate for this tissue has been estimated for the beluga whale (*Delphinapterus leucas*; St Aubin *et al.*, 1990) and the common bottlenose dolphin (*Tursiops truncatus*; Hicks *et al.*, 1985). The estimated time required for cell migration, from the basal lamina to the outermost surface, is at least two months. The carbon and nitrogen isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$, expressed hereafter as $\delta^{13}C$ and $\delta^{15}N$) of a consumer reflect those of its diet, with a slight retention of the heavier isotope and excretion of the lighter one (Das *et al.*, 2003). As a consequence, tissues will be enriched with heavy isotopes at every trophic level (1‰ for $\delta^{13}C$ and 3‰ for $\delta^{15}N$). The minor stepwise trophic enrichment of the carbon-isotope ratio limits its use in assessing trophic levels but enhances its use in tracking carbon sources through a food chain. The carbon isotope ratio of secondary and tertiary consumers should thus reflect the source of carbon at the base of their food chain (Kelly, 2000).

Moorea, a volcanic tropical island in French Polynesia (South Pacific), is characterized by the presence of many species of cetaceans, including several resident odontocetes, mostly delphinids (Poole, 1993, 1995; Oremus *et al.*, 2007). At least thirteen species of dolphins may coexist around the island. Of these, the most common are the spinner dolphin (*Stenella longirostris*), the rough-toothed dolphin (*Steno bredanensis*), the short-finned pilot whale (*Globicephala macrorhynchus*) and the melon-headed whale (*Peponocephala electra*) (Gannier, 2000). The present study aimed to investigate ecological niche partitioning in the dolphin community of Moorea, especially for the spinner dolphin, the rough-toothed dolphin, the short-finned pilot whale and the melon-headed whale. We concentrated on these four species as they can be found within the same proximity around the island, in closely-related habitats within a small area and at all seasons (Poole, 1993). We hypothesised that these four species have different feeding niches that could be reflected in diverging stable isotope signatures. We also investigated some potential segregation processes that may occur intra-specifically, especially between sexes. Resource partitioning between sexes has been documented for a number of species, including mammals such as the giraffe (*Giraffa camelopardalis*) and several primate species (Beier, 1987; Young & Isbell, 1991). Sexual segregation in foraging habitats has also been documented for some marine mammals, such as the grey seal (*Halichoerus grypus*) (Breed *et al.*, 2006). Females may use higher quality food, especially during gestation and lactation; therefore, it is often assumed that the energetic costs are greater for females than they are for males (Key & Ross, 1999). This could result in diverging stable isotope signatures if females develop sex-specific foraging strategies to fulfil their elevated energy requirements. On the other hand, in dimorphic species, such as long-finned pilot whales (*Globicephala melas*), males seem to have higher energetic needs (due to their larger size and weight) and potentially higher diving capabilities, and consequently use larger and deeper-living prey than females (Desportes & Mouritsen, 1993). As a consequence, males may have a higher trophic level than females.

In order to answer the question of niche segregation among the four most common dolphin species around Moorea Island, and intra-specifically between sexes, we analysed $\delta^{13}C$ and $\delta^{15}N$ stable isotopes from skin biopsies collected from 2002 to 2004.

## Material and methods

### Study area

Moorea (17°30'S, 149°50'W) is a high volcanic island of the Society Archipelago (134 km$^2$), French Polynesia, located in the central South Pacific (Figure 1). The island is almost entirely surrounded by a barrier reef which delimits a lagoon system connected to the open ocean by twelve passes varying in width and depth. Depth drops to more than 1000m just 1 to 2 nmi outside the barrier reef. All species are usually observed outside the barrier reef, except the spinner dolphin (*Stenella longirostris*) which commonly enters the lagoon through passes during daytime (Poole, 1995) and feed in the open ocean only at night (Norris *et al*., 1994).

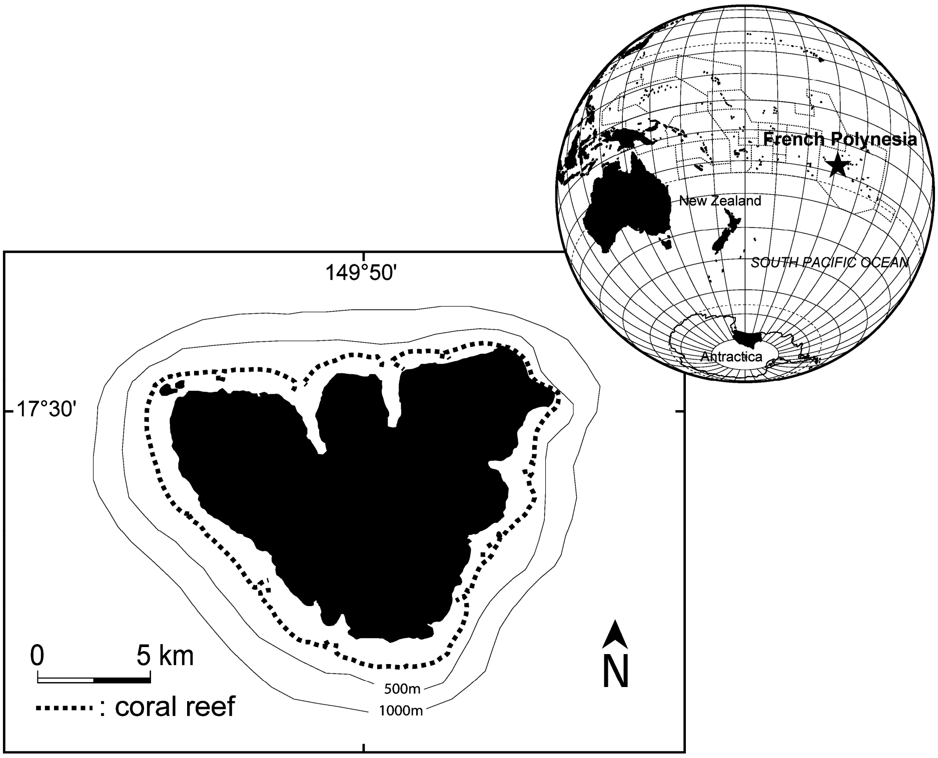

**Figure 1:** Location of the study area.

### Sample collection

Samples were collected from 2002 to 2004, during small-boat-based surveys (2002, n = 107; 2003, n = 32, 2004, n = 63), in sea conditions not exceeding Beaufort 3. Most of the observation effort concentrated in austral winter (July – October). Efforts were made to survey the entire coastline. However, the targeted species during these surveys were the spinner dolphin and the humpback whale (*Megaptera novaeangliae*), and efforts were primarily concentrated in nearshore waters (i.e., within 500 m from the barrier reef or within the lagoon), where these species are preferentially distributed during daytime (Poole, 1995; 2002). Therefore, it must be noted that search efforts were not optimal for encounters of more oceanic species. During each encounter with dolphins, geographical position was recorded, group size was estimated by visual counts, and photographs were taken using a digital camera equipped with a 70-300 mm lens. Skin samples for genetic analyses were collected from adult dolphins using a small stainless-steel biopsy dart fired from a modified veterinary capture rifle equipped with a variable pressure valve (Krützen *et al.*, 2002). Behavioural responses to biopsy attempts were recorded and reported in Oremus (2008). Level of short-term responses was low for all species and similar to that reported elsewhere (e.g. Krützen *et al.*, 2002). All samples were preserved in 70% ethanol and stored at –20°C for subsequent analysis.

### Stable isotope analyses

Blubber and skin were separated for each biopsy. Stable isotope analyses were only performed on the skin. The ethanol was evaporated at 45°C over 48 h and the samples ground and freeze-dried (Hobson *et al.*, 1997). Because lipids are depleted in $\delta^{13}C$, they were extracted to avoid a bias in the isotopic signature of $\delta^{13}C$ (De Niro & Epstein, 1978; Tieszen *et al.*, 1983). This was done by shaking (1 h at room temperature) in cyclohexane ($C_6H_{12}$), and subsequent centrifugation prior to analysis. After drying, small sub-samples (0.35 to 0.45 mg $\pm$ 0.001 mg) were prepared for analysis. Stable isotope measurements were performed with a continuous-flow isotope-ratio mass spectrometer (Delta V Advantage, Thermo Scientific, Germany) coupled to an elemental analyser (Flash EA1112 Thermo Scientific, Italy). Results are expressed in $\delta$ notation relative to PeeDee Belemnite and atmospheric $N_2$ for $\delta^{13}C$ and $\delta^{15}N$, respectively, according to the equation:

$$\delta X = \left[ \frac{R_{sample}}{R_{s\tan dard}} - 1 \right] \times 1000$$

where X is $^{13}C$ or $^{15}N$ and R is the isotope ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicated that measurement errors were <0.1‰ for $\delta^{13}C$ and $\delta^{15}N$. Percent C and N elemental composition of tissues were obtained using the elemental analyzer and used to calculate the sample C:N ratio, indicating good lipid removal efficiency when <4.

### Species identification and molecular sexing

Species sampled for this study were identified visually and confirmed using photographic and genetic evidences. Mitochondrial DNA control region were sequenced for all samples, as reported in Oremus *et al.* (2007), and sequences were submitted to the program DNA-surveillance v. 3.01 (Ross *et al.*, 2003) to determine species identity. Sex was identified by co-amplification of the male-specific *sry* gene and ZFX positive control gene (Gilson *et al.*, 1998).

### Data analysis

Differences of stable isotopes signatures of $\delta^{15}N$ and $\delta^{13}C$ among species were tested using non-parametric Kruskal-Wallis tests. Pairwise tests to compare $\delta^{13}C$ and $\delta^{15}N$ values between species were performed using Mann-Whitney-*U* tests. Variability of $\delta^{13}C$ and $\delta^{15}N$ signatures among sexes was also tested using *U* tests. For all statistical analyses, a significance level of $\alpha$=0.05 was used.

## Results

### Sampling

During the sampling period, we collected skin samples from 91 delphinids: spinner dolphin (*N* = 40; 29 males and 11 females), rough-toothed dolphin (*N* = 35; 23 males and 12 females), short-finned pilot whale (*N* = 12; 6 males and 5 females) and melon-headed whale (*N* = 4; not sexed). All samples were collected during the same season, i.e. austral winter (July to October). All sampled individuals were considered to be adults based on their size.

### Resource partitioning

The distribution of $\delta^{15}$N and $\delta^{13}$C values is given in Figure 2. Overall, overlap among species is present, and intra-specific variability appears high. However, significant statistical differences were found among the four species for $\delta^{15}$N ($H$ = 24; *df* = 3; $P < 0.001$) and $\delta^{13}$C values ($H$ = 37; *df* = 3; $P < 0.001$). Even with the melon-headed whale removed from the analysis, differences remained significant (for $\delta^{15}$N: $H$ = 12.3; *df* = 2; $P = 0.001$ and $\delta^{13}$C: $H$ = 13; *df* = 2; $P = 0.002$). Short-finned pilot whales had the highest $\delta^{15}$N and $\delta^{13}$C signatures, spinner dolphins had the lowest $\delta^{15}$N values (Figure 2), and melon-headed whales had the lowest $\delta^{13}$C signatures. Rough-toothed dolphins had an intermediate position between spinner dolphins and short-finned pilot whales. At a finer scale, when looking at differences in $\delta^{13}$C and $\delta^{15}$N signatures between species, some degrees of overlap and differentiation can be observed (Table 1).

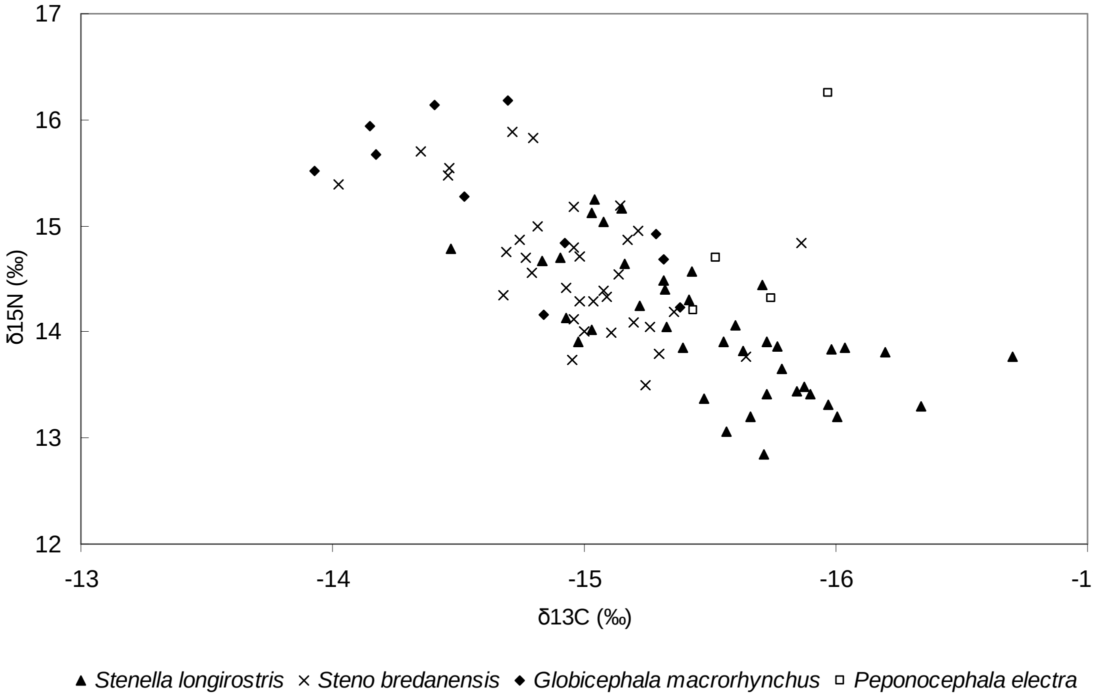

**Figure 2:** Stable isotope distribution ($\delta^{13}C$ and $\delta^{15}N$ in ‰) in delphinid skin tissues from Moorea. *Stenella longirostris* (n = 40), *Steno bredanensis* (n = 35), *Globicephala macrorhynchus* (n = 12) and *Peponocephala electra* (n = 4).

In $\delta^{13}C$, differences were not significant between the spinner dolphin and the melon-headed whale nor between the rough-toothed dolphin and the short-finned pilot whale. For other pairwise comparisons of $\delta^{13}C$ values, statistically significant differences were found. For $\delta^{15}N$, overlap was statistically significant between the melon-headed whale, the rough-toothed dolphin and the short-finned pilot whale. The spinner dolphin could not be differentiated from the melon-headed whale but differed significantly from the rough-toothed dolphin and short-finned pilot whale.

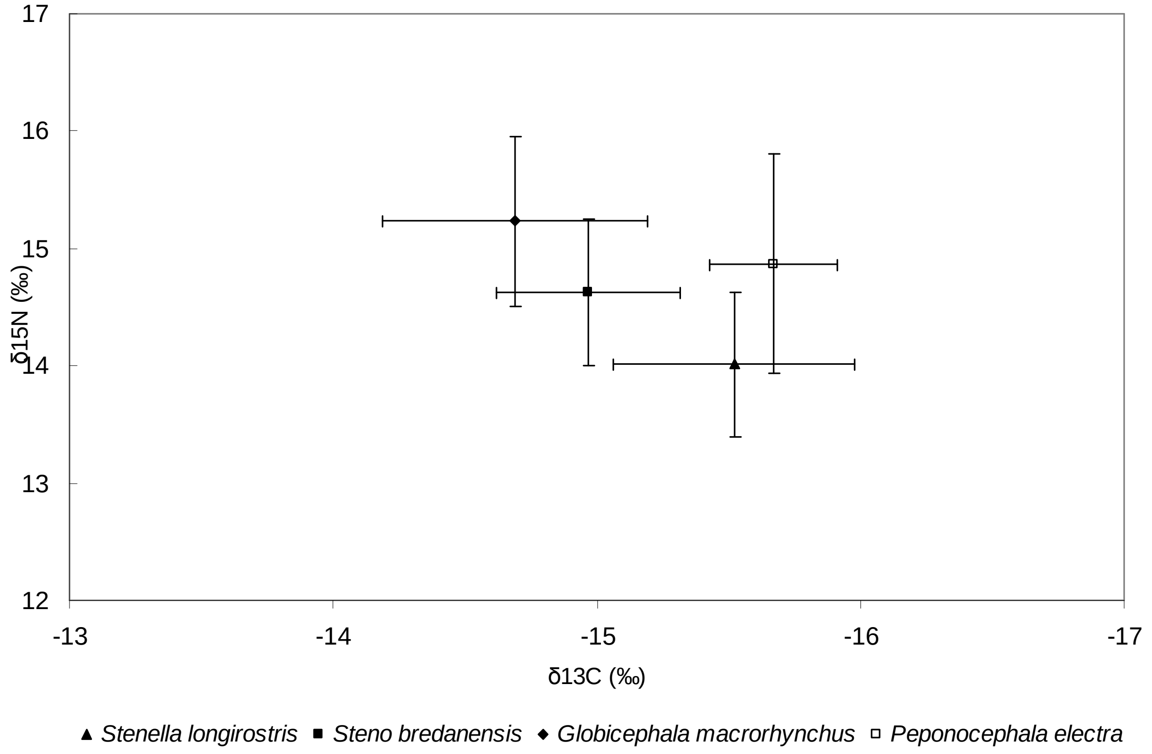

**Figure 3:** Stable isotopes ($\delta^{13}C$ and $\delta^{15}N$ in ‰) in delphinid skin tissues from Moorea. Graphs show average values and standard deviations. *Stenella longirostris* (n = 40), *Steno bredanensis* (n = 35) and *Globicephala macrorhynchus* (n = 12) and *Peponocephala electra* (n = 4).

**Table 1:** Pairwise Mann-Whitney U test p values for each pairs of delphinid species in carbon and nitrogen. Values in bold are statistically significant.

| **$\delta^{13}C$** | *Peponocephala electra* | *Globicephala macrorhynchus* | *Steno bredanensis* |
|---|---|---|---|
| *Stenella longirostris* | 0.394 | **0.0001** | **0.0001** |
| *Steno bredanensis* | **0.005** | 0.131 | |
| *Globicephala macrorhynchus* | **0.006** | | |
| **$\delta^{15}N$** | | | |
| *Stenella longirostris* | 0.09 | **0.00001** | **0.00004** |
| *Steno bredanensis* | 0.235 | 0.06 | |
| *Globicephala macrorhynchus* | 0.07 | | |

### Differences between sexes

We tested differences in stable isotope signatures between males and females, both for $\delta^{15}$N and a $\delta^{13}$C, in all species except the melon-headed whale; in the latter case, sample size was too small and sex data unavailable. Box plots (Figure 4) show stable isotope median values, 50, 75 percentiles and outliers of the three species. Male spinner dolphins and rough-toothed dolphins seem to have a lower trophic position than females. In addition, both species seem to feed on less $^{13}$C-enriched preys (Figure 4). An opposite situation was found for short-finned pilot whales, with males having higher mean $\delta^{15}$N and $\delta^{13}$C signatures. For the short-finned pilot whale, males seem to have a wider range of $\delta^{13}$C signatures (Figure 4). Conversely, females had a wider range of $\delta^{15}$N values. However, none of the differences were statistically significant (spinner dolphins: $\delta^{15}$N: $U = 59$; $P = 0.236$; $\delta^{13}$C: $U = 33$; $P = 0.203$, rough-toothed dolphin: $\delta^{15}$N: $U = 51$; $P = 0.266$; $\delta^{13}$C: $U = 57$; $P = 0.409$ and short-finned pilot whales: $\delta^{15}$N: $U = 50$; $P = 0.193$; $\delta^{13}$C: $U = 13$; $P = 0.074$).

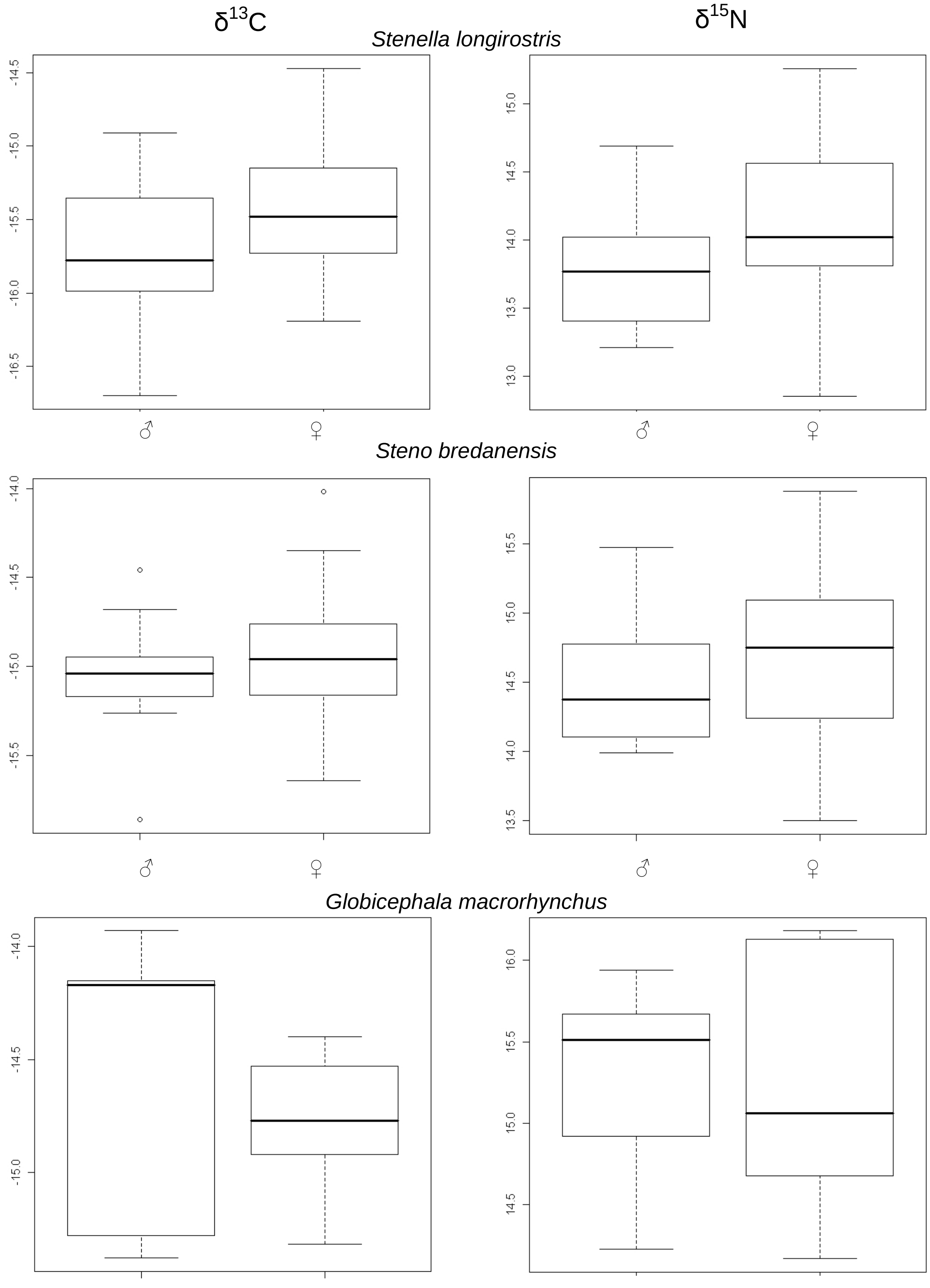

**Figure 4:** Stable isotope ($\delta^{13}C$ and $\delta^{15}N$ in ‰) median values, 50, 75 percentiles and outliers of *Stenella longirostris* (n = 40), *Steno bredanensis* (n = 35) and *Globicephala macrorhynchus* (n = 12) males versus females.

## Discussion

Stable isotope approaches are powerful analytical tools to link the foraging ecology of top predators with habitat, diving behaviour and diet (Das *et al.*, 2003; Zhao *et al.*, 2004). This has been shown for a number of taxa, including seabirds (Cherel *et al.*, 2008), sharks (Comi *et al.*, 2005), pinnipeds (Zhao *et al.*, 2004) and cetaceans such as tropical delphinids (Gross *et al.*, 2009). These results were the first describing the isotopic niches of sympatric delphinids in French Polynesia; they can be used in the future to examine seasonal, year-to-year or long term variation in delphinid trophic ecology in the region. Lack of significance in some comparisons may partly result from insufficient sample size. Analytical resolution was <0.1‰ as shown by replicate measurements of internal laboratory standards, and delipidation was successfully carried out on all samples since C:N ratios were always <4. Carbon sources and reference levels of nitrogen were not investigated in this work; hence isotopic data can only be interpreted in terms of relative values among the four species studied.

### Isotopic niche segregation

Very few other studies have attempted to address issues regarding ecological segregation in delphinid assemblages by analysing isotopic signature in skin biopsies (Gross *et al.*, 2009), but more work has been done on communities of other marine top predators including sharks, large teleost fishes, seabirds and marine mammals (Hobson & Welch, 1992; Abend & Smith, 1995; Das *et al.*, 2003; Zhao *et al.*, 2004; Domi *et al*., 2005; Ménard *et al*., 2007; Cherel *et al.*, 2008; Jaeger, 2009). In top predator communities, significant habitat partitioning has been found in polar communities, such as in pinnipeds from the Antarctic (Zhao *et al.*, 2004). Conversely, in tropical sympatric seabirds, significant overlap of feeding niches has been found at the community level (Cherel *et al.*, 2008). This may be laid to the low productivity of tropical oligotrophic waters, leading top predators to share the same feeding resources. However, significant differences in isotopic niches were found in delphinids from the tropical island of Mayotte, in the south-western Indian Ocean (Gross *et al.*, 2009). In the Southern Hemisphere, clearly structured latitudinal carbon isoscapes have been found from the Antarctic to the subtropical zones (Jaeger *et al.*, submitted). This structured shape of latitudinal isoscapes may not exist in tropical waters. However, around oceanic islands such as Mayotte, clear differences of $\delta^{13}$C and $\delta^{15}$N values were observed between the three delphinid genera investigated, which could be interpreted by the structured nature of marine habitats (high carbon gradients from coastal to oceanic surface waters; Kiszka *et al.*, unpublished data) around the island, from lagonal to oceanic waters. In addition, diving predators such as small cetaceans use resources at varying depth, where carbon gradients are significant (from the surface to bottom, where organic matter accumulates and provides carbon sources). In conclusion, investigating trophic relationships of predators living in a structured system (such as around an oceanic island) and feeding at varying depth may result in diverging isotopic niches, while in surface feeders like seabirds, feeding in the homogenous oceanic system may result in low to no difference in isotopic niches.

In our study, overall analyses show some degrees of niche partitioning among the four species investigated, the most significant result being the differentiation in trophic level revealed by $\delta^{15}N$ values among spinner dolphin, rough-toothed dolphin and short-finned pilot whale, but not between spinner and melon-headed whale. In terms of foraging habitats, $\delta^{13}C$ values were significantly different between all species except two pairs of species that could not be discriminated: spinner dolphin/melon-headed whale and rough-toothed dolphin/short-finned pilot whale. No significant intra-specific difference was found between sexes. Finally, it must be kept in mind that differences in isotopic signatures are informative, whereas similarities do not necessarily imply that species share a similar trophic niche; indeed different foraging strategies may result in similar isotopic signatures. If stable isotope signatures and preys of two predators are effectively similar, other segregation processes may occur, such as differential spatial and temporal use of habitat and resources. Published studies from other areas in the Pacific suggest that the community of delphinids around Moorea is likely to feed on pelagic and oceanic prey. The spinner dolphin had the lowest trophic level and, with the melon-headed whale, the lowest $\delta^{13}C$ values. The spinner dolphin feeds primarily on mesopelagic fishes and squids at night (Norris *et al.*, 1994; Dolar *et al.*, 2003). Vertical distribution of the prey items summarized from published literature indicate that spinner dolphins forage in the upper 200 meters and probably occasionally as deep as 400 meters (Dolar *et al.*, 2003). Melon-headed whales are oceanic predators, mostly feeding on mesopelagic fishes and cephalopods throughout their range (reviewed in Brownell *et al.*, 2009). When considering the vertical distribution of these prey groups, melon-headed whales probably forage in the upper 700 meters (Young, 1978). Like spinner dolphins, melon-headed whales seem to feed at night during vertical migrations of their preys, while they rest and socialize during daytime near oceanic islands (Brownell *et al.*, 2009). Therefore, the two species may share some similar features of habitat and resource use, although at Moorea, melon-headed whales do not use inshore and nearshore waters like spinner dolphins do. This possible overlap was confirmed in this study, as stable isotope signatures were not significantly distinguishable. Note that this absence of significant difference could be due to small sample size for melon-headed whales. However, around the island of Mayotte (with similar habitats to those around Moorea) in the south-western Indian Ocean, stable isotope analyses on skin samples revealed significant differences in $\delta^{13}C$ and $\delta^{15}N$ values with similar sample size than in our study (Gross *et al.*, 2009). Melon-headed whales were characterised by significantly higher $\delta^{13}$C and $\delta^{15}$N values (Gross *et al.*, 2009). In our study, $\delta^{13}$C signatures were very similar between spinner dolphins and melon-headed whales, suggesting they prey on species with similar $\delta^{13}$C signatures or even similar prey. This could suggest that their prey are not limited quantitatively, allowing the two species to feed on similar resources without deleterious competition for one or the other. However, despite no statistical evidences, some differences in the $\delta^{15}$N values suggest that melon-headed whale has a higher trophic level, and may probably feed on prey of higher trophic position (probably larger prey). The feeding ecology of the rough-toothed dolphin is poorly known, but it is known to feed on cephalopods (Aguiar dos Santos & Haimovici, 2001), deep water fishes (Miyazaki & Perrin, 1994) and occasionally on coastal prey (Shallenberger, 1981). Foraging on flying fishes and other surface fish has been regularly observed off Moorea (Oremus & Poole, personal observations). In the eastern tropical Pacific, rough-toothed dolphins regularly feed on dolphin fish (*Coryphaena hippurus*; Pitman & Stinchcomb, 2002). Short-finned pilot whales are deep-water cephalopod predators (Hernandez-Garcia & Martin, 1994). Recent evidence suggests that short-finned pilot whales can dive to depths reaching 1,000 meters on occasion (Aguilar Soto *et al.*, 2008). Based on the available literature, making comparisons of the diet of the rough-toothed dolphin and the short-finned pilot whale appears highly hazardous, given the limited existing information. However, the latter seem to feed deeper in the water column. In our results, the rough-toothed dolphin and the short-finned pilot whale were not statistically different in their stable isotope signatures. However, *S. brenadensis* had lower $\delta^{13}$C and $\delta^{15}$N signatures than those in short-finned pilot whales. The later may feed on more carbon-enriched prey. As there is a bottom-surface gradient of $\delta^{13}$C, with higher carbon values from the sea bottom than at the surface (Hobson, 1999), higher $\delta^{13}$C values observed in short-finned pilot whales could be due to their preference for prey occurring deeper in the water column, in closer proximity to bottom organic matter sources. This is consistent with published literature describing general ecology, prey preferences and diving behaviour of short-finned pilot whales (Aguilar Soto *et al.*, 2008; Hernandez-Garcia & Martin, 1994). The lower $\delta^{15}$N values observed in the rough-toothed dolphin may be attributed to its preference for preys of a lower trophic position than those consumed by pilot whales. Overall, when looking at biometrical data of predators from our study (Jefferson *et al.*, 2008), we observe that there is a correlation between trophic position and body size. Larger predators have a higher trophic level in this delphinid community, which is consistent with many other species communities.

Difference in feeding ecology between genders has rarely been documented in delphinids (Desportes & Mouritsen, 1993). From our dataset, we did not observe statistically significant gender-specific variations of stable isotope signatures. In other words, the feeding niches of delphinids from Moorea may not differ according to sex. However, some segregation processes may be not detected through the use of stable isotopes, and traditional dietary analyses may answer this question. Detailed studies of diving behaviour may also contribute to assessing gender-specific variation in feeding strategies. However, at least for short-finned pilot whales, our sample size was small, which could conceal potential differences related to sex. Indeed, it is known that males in sexually dimorphic species such as long-finned pilot whales feed on larger prey, and potentially have a higher trophic level (Desportes & Mouritsen, 1993). Nevertheless, no detailed studies of the diet of short-finned pilot whales have been published, and such gender-specific variation is unknown in this species.

## Conclusions

When conventional dietary studies cannot be undertaken, such as around Moorea where dead animals from strandings and bycatch are unavailable, the use of stable isotopes can be recommended to assess trophic relationships in a community of cetacean predators, especially delphinids. The delphinids around Moorea seem to have different feeding niches, although statistical analyses do not always show significant differences among species. To complement the interpretation of these first results, documenting accurate data on local carbon sources and reference levels of nitrogen by analysing the isotopic content of particulate organic material that constitute the basis of the local food webs and/or of a range of putative prey taxa from coastal to oceanic habitats, would help in characterizing the three-dimensional isoscape (Jaeger, 2009) in which this assemblage of sympatric dolphins dwells. Additionally, any information on the diet, diving behaviour, activity budget and micro-scale spatial distribution of the four dolphin species constituting this community would considerably improve the potential for interpreting stable isotope data.

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## Résumé

L'étude de l'écologie des communautés et de la ségrégation écologique revêt une importance particulière, notamment pour ses apports en biologie évolutive mais aussi pour ses applications dans le domaine de la conservation. La présente étude s'intéresse à la ségrégation écologique des delphinidés de l'île de Mayotte (Canal de Mozambique, sud-ouest de l'océan Indien) à deux échelles : la communauté d'espèces (approche interspécifique) et les communautés d'individus (approche intra-spécifique). Autour de cette île, une communauté diversifiée de delphinidés se partage l'espace et les ressources, et ce à de très faibles échelles spatiales. Sur treize espèces observées, au moins cinq sont observées régulièrement et ont donc été étudiées : le grand dauphin de l'Indo-Pacifique (*Tursiops aduncus*), le dauphin à long bec (*Stenella longirostris*), le dauphin tacheté pantropical (*Stenella attenuata*), le péponocéphale (*Peponocephala electra*) et le dauphin de Fraser (*Lagenodelphis hosei*). Chez les espèces vivant en sympatrie, des mécanismes de ségrégation devraient s'observer selon les trois dimensions principales de la niche écologique : l'espace, la ressource et le temps. A l'échelle interspécifique, les analyses de l'habitat défini par les caractères physiographiques associés à chaque observation, de l'utilisation des ressources exprimée par les isotopes stables du carbone et de l'azote et des budgets d'activités montrent que les delphinidés occupent des niches écologiques distinctes. Parallèlement, certaines espèces jumelles peuvent constituer des associations poly-spécifiques, les mettant apparemment en situation de compétition pour les ressources et les habitats. Il a été montré que ces associations, notamment chez les delphinidés du genre *Stenella*, n'avaient pas de signification trophique, mais constituaient plutôt une stratégie de vigilance contre les prédateurs. Le dernier volet de l'étude s'intéresse à la ségrégation intra-spécifique et à la structure de population à fine échelle, notamment chez le grand dauphin de l'Indo-Pacifique, la principale espèce de delphinidé à vivre dans les eaux intérieures du lagon. La combinaison d'approches dont les échelles sont emboitées : de l'échelle évolutive populationnelle (structure génétique) à l'échelle de la vie de l'individu (domaine vital), a permis de démontrer que l'unique groupe panmictique de Mayotte se segmentait en communautés (définies par des ensembles d'individus ayant un domaine vital commun). Au moins deux communautés ont été identifiées, utilisant des domaines distincts, formant des groupes sociaux stables mais non constitués d'individus apparentés. L'ensemble de l'étude montre que la ségrégation écologique s'observe aux échelles inter- et intra-spécifiques chez les delphinidés, et que celle-ci ne peut être mis en évidence que par des approches multi-échelles et transdisciplinaires.

Mots clés : ségrégation écologique, delphinidés, diversité, habitat, ressource, variations temporelles, communautés, isotopes stables, associations poly-spécifiques, lutte anti-prédateur, fonctionnement social, structure de populations.

## Abstract: Ecological segregation within a community of tropical delphinids: habitat, resource use and social structure

The study of communities and ecological segregation is of primary importance, especially for its contribution to the field of evolutionary biology and its applications to conservation. The present study aims to assess ecological segregation of tropical delphinids of the island of Mayotte (Mozambique Channel, SW Indian Ocean) at two scales: interspecies and intra-species level. Around Mayotte, a diverse community of delphinids can be found within a restricted range. Thirteen species have been recorded, among which five species regularly occur: the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*), the spinner dolphin (*Stenella longirostris*), the pantropical spotted dolphin (*Stenella attenuata*), the melon-headed whale (*Peponocephala electra*) and the Fraser's dolphin (*Lagenodelphis hosei*). In species living in sympatry, segregation mechanisms should be observed along the three main dimensions of the ecological niche: habitat, resource and time. In inter-specific comparisons, analyses of habitat defined by physiographic variables at sighting locations, resource use expressed as carbon and nitrogen stable isotope signatures, and activity budgets revealed that each species occupies its own ecological niche. At the same time, sibling species form mixed-species associations that place them in situation of apparent competition for habitats. It has been shown that these mixed-species associations, especially among dolphins of the genus *Stenella*, do associate for anti-predator vigilance rather than for trophic benefits. Finally, the last approach of this study aims to investigate fine scale population structure and intra-species segregation in the Indo-Pacific bottlenose dolphin, the main delphinid occurring in the inner lagoon. The combination of approaches over temporal scales: from the genetic population structure to the community characteristics at individual life-scale (home range), showed that a single panmictic group of Indo-Pacific bottlenose dolphins was segmented into communities (defined by a common home range). At least two bottlenose dolphin communities were found, using a common home range and within which genetically unrelated individuals are preferentially associated. The whole study underlines that ecological segregation can be observed inter- and intra-specifically in delphinids, and this segregation can only be assessed by using multi-scale and multidisciplinary approaches.

Keywords: ecological segregation, delphinids, diversity, habitat, resource, temporal variations, communities, stable isotopes, inter-species associations, anti-predator vigilance, population structure, social structure.