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INTRODUCTION GÉNÉRALE

1 Présentation de la thèse

1.1 Contexte

Cette thèse s'inscrit dans le programme de recherche de l'Institut National de Développement des Pêches (INDP) au Cap-Vert. Elle a été appuyée par une bourse d'études dans de cadre du Programme Canadien de Bourse de la Francophonie (PCBF) pour la période 2002-2007. Du point de vue scientifique, cette thèse a permis une meilleure compréhension du fonctionnement de l'écosystème marin de l'archipel du Cap-Vert, s'intéressant aux divers processus physiques et biologiques qui déterminent la dynamique et la structure des populations démersales de l'archipel. Les résultats obtenus nous permettent d'espérer, à moyen et long terme, des améliorations dans la gestion des pêcheries, dans la conservation des ressources marines et dans l'efficacité de la recherche. Les financements de base ont été assurés par l'INDP, le PCBF et l'Université du Québec à Rimouski (UQAR) à travers l'Institut de Science de la Mer de Rimouski (ISMER).

Les travaux de recherche ont été dirigés par Jean-Claude Brêthes, professeur et chercheur à l'UQAR – ISMER et codirigés par Bruno Zakardjian et Jean-Marie Sévigny professeurs associés l'UQAR – ISMER. Considérant l'ampleur des travaux de laboratoires, les opérations en mer et l'échantillonnage, l'ensemble des travaux de terrain a été appuyé par une équipe de techniciens de l'INDP au Cap-Vert et du GIP Mercator-Océan à Ramonville (Toulouse – France).

1.2 Structure de la thèse

La présente thèse est structurée en six parties qui commencent par une introduction générale suivie de quatre chapitres qui exposent les principaux résultats. Ces chapitres sont présentés sous forme d'articles rédigés en anglais. Une conclusion générale reprend et synthétise les résultats les plus importants. Le thème directeur est de chercher à comprendre comment se structure un écosystème d'archipel en analysant plus spécifiquement la communauté exploitée de poissons démersaux des îles du Cap-Vert. Elle fait appel à plusieurs approches, écologiques, morphométriques et hydrodynamiques, qui visent à se compléter afin de disposer d'une vue d'ensemble de cet écosystème particulier.

Le premier chapitre, publié dans la revue Marine Ecology (Medina *et al.* 2007), décrit l'organisation spatiale de la communauté des poissons démersaux de l'archipel, en utilisant les données de la pêche artisanale. Un indice de distance écologique est calculé à deux niveaux d'organisation (espèce et communauté) à partir de la dominance relative des espèces. Il est mis en relation avec un facteur d'isolement physique qui combine la distance entre les îles et la bathymétrie. Les populations démersales présentent une structure géographique par île et groupes d'île en fonction de l'isolement physique. L'isolement est plus marqué en saison chaude, de mai à novembre, qu'en saison froide, de décembre en avril, où cet isolement est plus faible.

Le deuxième chapitre, à soumettre pour publication, se situe dans la suite du premier. À partir des mêmes données de la pêche, il analyse la dynamique d'occupation de l'espace selon une démarche géostatistique. Deux niveaux d'organisation sont étudiés, la communauté et l'espèce. La dynamique apparaît contrainte par la disponibilité de l'espace

habitable. Un modèle de variation différentielle de la densité est associé aux îles présentant des plateaux insulaires relativement larges. Une dynamique à densité proportionnelle est associée aux îles confinées par l'exiguïté de leurs plateaux. Au niveau des espèces, la dynamique spatiale est proportionnelle, indépendamment du modèle observé au niveau de la communauté. À ces deux niveaux, l'occupation de l'espace est indépendante de la densité et semble être principalement contrainte par des facteurs environnementaux.

Le troisième chapitre, soumis à *Journal of Fish Biology*, cherche à vérifier si la structure écologique observée pouvait se traduire par des variations phénotypiques des espèces. La forme du poisson *Cephalopholis taeniops* a été analysée. Les résultats révèlent une variation allométrique significative de la forme du corps selon des patrons qui varient d'une île à l'autre. Les variations inter-îles de la forme du corps sont nettement plus grandes que les variations intra-îles selon des modèles ontogénétiques globalement différents. L'isolement physique, défini dans le premier chapitre, est significativement corrélé avec la divergence morphologique entre populations des différentes îles.

Pour comprendre les différences observées entre les îles, le chapitre 4 présente les résultats d'une modélisation hydrodynamique. Ils montrent un patron de circulation à l'intérieur de l'archipel, dominé par des courants et des structures de circulation tourbillonnaire à petite échelle responsables des mélanges nord-sud et est-ouest. Dans ce chapitre, nous proposons des indices de connectivité hydrodynamique calculés pour différents niveaux de profondeur. Ces indices sont ensuite appliqués dans l'archipel pour estimer les variations mensuelles et annuelles de rétention locale, d'importation et d'exportation entre les îles et les pertes de particules (que nous inférons au niveau des

larves) en dehors de l'archipel. Ces indices sont utilisés dans un contexte multidimensionnel pour étudier la connectivité hydrodynamique de l'écosystème et les relations avec la distance, la bathymétrie et les traits phénotypiques.

Une discussion générale, basée sur les résultats des chapitres précédents, présente les populations démersales des plateaux insulaires de l'archipel du Cap-Vert comme une grande metacommunauté constituée essentiellement de trois metapopulations – la metapopulation des îles du Nord, la metapopulation des îles de l'Est et la metapopulation des îles du Sud. Chaque metapopulation est constituée d'un ensemble de populations typiques de chaque île ou îlot à l'intérieur de laquelle il peut exister des échanges dont l'intensité et l'échelle dépendent du degré de fragmentation de l'écosystème. Les échanges par migration d'adultes et de juvéniles peuvent se produire entre populations qui se trouvent sur les mêmes plateaux à des profondeurs inférieures à 100 m, tandis que des échanges de gamètes, œufs et larves peuvent se produire par effet hydrodynamique à des échelles spatiales supérieures.

Finalement une conclusion générale replace les principaux résultats en fonction des objectifs et hypothèses de recherche. La thèse termine de façon ouverte vers des perspectives de recherches, inspirées des défis méthodologiques et scientifiques. Ces défis, ayant pris forme le long des cinq dernières années d'études et de recherche, dépassent le cadre de la thèse mais représenteront des suites intéressantes pour faire évoluer les connaissances sur le fonctionnement d'un écosystème océanique insulaire tropical.

2 Problématique

2.1 Considérations générales

Les tendances actuelles dans la gestion des ressources naturelles favorisent une approche écosystèmique qui tient compte d'une vision plus large, plus dynamique, mais aussi plus complexe de l'écosystème, par rapport à une vision compartimentée de ses différentes composantes, comme le propose la « théorie de la pêche » classique. Les deux approches souffrent toutefois des mêmes limitations, liées à la variabilité spatio-temporelle des multiples facteurs du milieu et de leurs interactions. Cependant l'avancement récent des connaissances sur l'écosystème et son fonctionnement, plus particulièrement des relations entre les organismes et l'environnement, incluant l'activité prédatrice de l'homme par la pêche, ouvrent des voies à l'adoption de politiques d'exploitation et de conservation des ressources mieux ajustées aux cycles naturels des espèces et à leur variabilité spatio-temporelle.

Dans une situation idéale de prise de décision, on viserait une approche de gestion qui s'intéresserait aux différentes échelles spatiales, locales et régionales, et aux différentes échelles temporelles, à court, moyen et long terme. On chercherait donc à préserver les composantes biotiques et abiotiques des écosystèmes. Cependant, souvent la méconnaissance de l'écosystème conduit à des scénarios où les approches durables sont freinées par des pratiques où l'on privilégie les bénéfices à court terme et à petite échelle, au détriment des avantages à long terme et à plus grande échelle.

En milieu marin, l'appréhension et la maîtrise des échelles de variation spatiale et temporelle représentent une condition indispensable à la compréhension de la dynamique et

de la structure des populations. Cette variabilité est présente dans toutes les phases du cycle de vie des individus (gamètes, œufs, larves, juvéniles et adultes) en raison de différents phénomènes : dérive, rétention, migration, advection et diffusion, induits et contrôlés par des facteurs biotiques et abiotiques. Parmi ces facteurs, la littérature scientifique, issue d'importants programmes internationaux de recherche océanographique, met en évidence le rôle de l'hydrodynamisme dans la variabilité des populations de poissons à travers des phénomènes de dérive et de rétention pendant la phase pélagique de développement (Werner *et al.* 1997; Van der Veer *et al.* 1998; Jager 2001; Shank & Halanych 2007) induits par des processus physiques dont le vent assume une importance déterminante (Nielsen *et al.* 1998). D'autres facteurs liés au comportement des individus dans l'occupation de l'habitat jouent un rôle important dans leur distribution spatiale à petite ou grande échelle, à court et à long terme (MacCall 1990; Fréon & Misund 1999).

La définition appropriée du concept de stock, du point de vue biologique ou du point de vue de la gestion, et l'estimation du degré d'échange entre les membres d'un stock demeurent encore un défi scientifique important pour les biologistes et les gestionnaires des pêches (Begg *et al.* 1999a). En effet, il n'est pas encore possible de cartographier directement l'étendue et la direction de la dispersion larvaire (Thresher 1999) ce qui rend particulièrement difficile leur rattachement à un stock donné ainsi que le suivi de leur recrutement. Pour ces raisons, il existe dans la littérature des nombreuses études portant sur l'identification des stocks, leurs dynamiques et leurs structures, basées sur une multitude de techniques et d'approches qui fait appel à plusieurs disciplines dont la génétique, la biochimie, la chimie, la biométrie, la parasitologie et la science halieutique.

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2.2 Structure des populations

Du point de vue de la biodiversité, les populations marines tendent à se structurer et se distribuer dans l'espace en fonction des conditions favorables du milieu et cherchent à adapter leurs stratégies de développement – reproduction, croissance, dispersion, migration - aux cycles naturels de l'environnement. Ainsi, le succès dans l'occupation de l'espace se fera en fonction de la capacité des espèces à s'adapter par le biais d'un équilibre entre le coût de ces stratégies et leur valeur écologique. Cela se fait toujours dans une logique d'optimisation de l'utilisation des ressources du milieu de façon à augmenter la cohésion et la stabilité des communautés (Legendre & Legendre 1998). C'est ainsi que la distribution des espèces en fonction des régimes hydrologiques et des caractéristiques intrinsèques des populations conduit à des situations d'isolement écologique et génétique, plus ou moins accentué, dont le degré de stabilité des communautés est à la base de la diversité de structures des populations marines. Des patrons écologiques dans la distribution et l'abondance des espèces sont donc liés aux caractéristiques des habitats, aux mécanismes de dispersion, aux capacités de colonisation, aux flux geniques et au pool génétique (Sinclair 1988; Bailey 1997).

2.2.1 Unité génétique et unité de gestion

La maîtrise de cette complexité écologique est fondamentale dans la compréhension de la dynamique des populations et dans la gestion des pêcheries (Sinclair 1988; Bailey 1997; Booke 1999). La définition de stock comme unité de base de la gestion est un concept important qui est en évolution depuis de nombreuses années. Déjà en 1957, Marr

(in Begg & Waldman 1999) faisait une différence entre stock et sous-population, en considérant celle-ci comme l'entité génétique la plus petite capable de s'autoalimenter. Le stock serait la population ou une portion de la population dont tous les membres sont caractérisés par des similarités non héritées induites par l'environnement, pouvant comprendre des membres de plusieurs sous-populations différentes. Cette définition traduit le point de vue de la gestion et se base plutôt sur la similarité des paramètres de production de la population comme les taux de natalité, de croissance et de mortalité (Chadwick 1990) et se réfère à un groupe arbitraire d'une certaine espèce, suffisamment grand pour s'autoreproduire, disponible pour l'exploitation dans une aire donnée (Laurec & Le Guen 1981; Milton & Shaklee 1987).

Du point de vue biologique, la population est l'unité génétique d'une espèce pourvue du même capital génétique, vivant dans une aire suffisamment restreinte pour que tous les membres soient capables de se rencontrer et se reproduire (Chadwick 1990; Bailey 1997). La notion ainsi retenue implique la mono-spécificité, mais elle est plus restrictive que celle d'espèce, de sous-espèce ou de race géographique, car l'écosystème considéré peut être choisi d'étendue plus réduite (Laurec & Le Guen 1981). Les sous-populations peuvent diverger génétiquement soit par mutation, soit par dérive génétique et sélection naturelle favorisant l'adaptation aux environnements locaux. Elles peuvent converger à travers des processus d'homogénéisation par flux géniques, mouvements de gamètes, d'individus ou de populations. Swain & Foote (1999) présentent le stock comme étant une population locale adaptée à un environnement particulier et portant des différences génétiques par rapport à d'autres groupes en conséquence de cette adaptation. Ces auteurs introduisent ainsi la

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notion de stock génétique pour le distinguer d'un stock phénotypique, caractérisé par des différences entièrement induites par l'environnement. Cependant, selon les situations, les différents concepts peuvent représenter les mêmes entités. Malgré ces nombreuses définitions suivant des points de vue différents, actuellement, la prémisse principale qui supporte le concept moderne de stock est, en général, l'existence d'un marqueur génétique ou phénotypique qui se maintient dans le temps, sans trop de variation selon les différents outils d'identification (Booke 1999, Palsbøll *et al.* 2006).

2.2.2 Concept de metapopulation

Une population naturelle occupant une aire suffisamment étendue peut être composée de plusieurs populations locales (Laurec & Le Guen 1981; Bailey 1997). On parle alors de metapopulation, une entité plus vaste ayant la population locale comme unité spatiale à l'intérieur de laquelle se produisent la plupart des interactions (Diadov 1998). Harrison (1991) considère essentiellement cinq types de metapopulations (Figure 1) selon les différents degrés de dépendance et d'interaction: A) metapopulation de Levins – les populations locales ont toutes la même taille et interagissent dans un habitat fragmenté sur l'aire de distribution; B) metapopulation centre-satellite – les habitats sont fragmentés à l'intérieur de l'aire de distribution, mais il y a seulement une population plus grande qui est la source des populations satellites; C) metapopulation fragmentée – les habitats sont continus le long de l'aire de distribution des espèces, mais il y a une agrégation des populations locales; D) metapopulation non équilibrée – semblable au modèle de

metapopulation de Levins, mais il n'y a pas de mouvement entre les populations locales; E) un modèle mixte entre metapopulation centre-satellite et metapopulation fragmentée.

Considérant cette complexité, le concept de structure géographique est fondamental dans la compréhension de la dynamique des populations. L'identification des stocks est une composante intégrante de leur évaluation pour la gestion des pêcheries et la protection des espèces menacées (Bailey 1997; Begg *et al.* 1999a; Begg & Waldman 1999; Shaklee *et al.* 1999). La plupart des méthodes d'évaluation des stocks modélisent la dynamique d'une population isolée et estiment que les paramètres de production sont homogènes (Laurec & Le Guen 1981; Brêthes 1990, 1992; Cadrin & Friedland 1999). Cependant, des résultats erronés peuvent se produire si le modèle est appliqué sur plusieurs populations isolées ou seulement sur une portion de la population, en assumant une seule population (Bailey 1997; Begg *et al.* 1999; Fréon & Misund 1999). Des erreurs dans la reconnaissance d'une structure de population d'espèces exploitées peuvent conduire à la surexploitation ou à l'extinction des populations moins productives. Aussi, pour des populations en phase de récupération, la non-identification de taux différentiels de production réduit les possibilités de pronostic du recrutement ce qui est un paramètre nécessaire à la définition des politiques de conservation et gestion (Ruzzante *et al.* 1999).

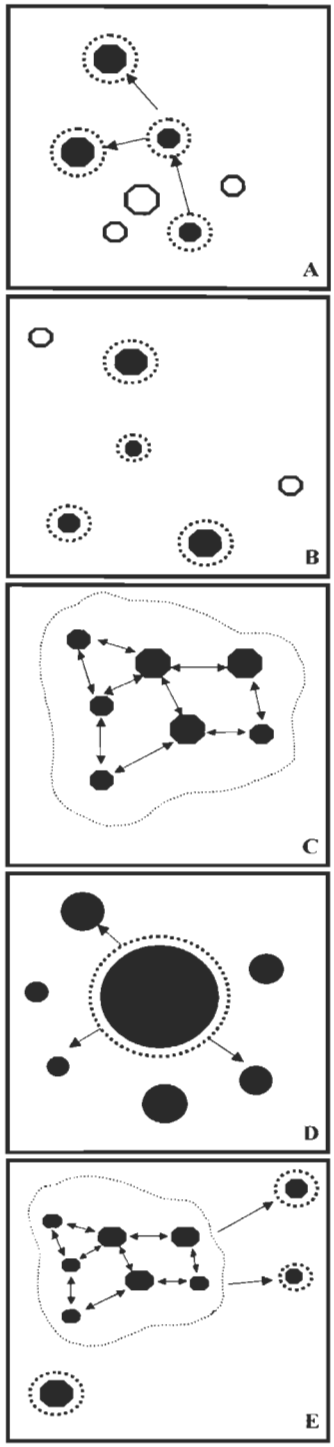

Figure 1 Différents types de metapopulations selon Harrison (1991) : A - metapopulation de Levins; B - metapopulation centre-satellite; C - metapopulation fragmentée; D - metapopulation non équilibrée; E - metapopulation mixte (modèle mixte entre B et C). Les flèches indiquent des migrations entre les populations. ○ – habitats inoccupés ; ● – habitats occupés

2.2.3 Quelques études sur la structure des populations marines

Des études récentes sur les espèces et les écosystèmes marins mettent l'accent sur la structure des populations par des techniques d'identification de stocks (Schweigert 1981; Wood *et al.* 1988 ; Begg *et al.* 1999a, 1999b; Begg & Waldman 1999; Cadrin & Friedland 1999; Letcher & King 1999; Swain & Foote 1999; Thresher 1999; Oliva & Ballón 2002) et sur leur dynamique spatio-temporelle (Bailey 1997; De Vries *et al.* 2002; Smith *et al.* 2002; Miller & Shanks 2004; Nielsen *et al.* 2005; Treml *et al.* 2007). La dynamique est fortement liée à des phénomènes de migration, dispersion ou rétention de larves, juvéniles et adultes, conditionnés par l'hydrodynamisme (Sinclair 1988; Werner 1997; Burke *et al.* 1998; Nielsen *et al.* 1998; Van der Veer *et al.* 1998; Jager 2000) et par des facteurs de comportement.

Ruzzante *et al.* (1999) présentent une revue de la structure génétique des populations de morue (*Gadus morhua*) dans l'Atlantique du Nord Ouest ainsi que des affinités entre les populations de larves de la même espèce à Terre-Neuve et dans le golfe du Saint-Laurent. Leurs résultats suggèrent l'existence de différences significatives entre les populations de morue à l'échelle des bancs et des baies, confirmées par l'existence d'un patron spatio-temporel dans la ponte. Cette séparation est associée à des barrières au flux génique entre des agrégations voisines, liées à une circulation tourbillonnaire induite par la topographie.

Diadov (1998), dans une étude sur les populations de flétan (*Reinhardtius matsuurae*) au nord du Pacifique, démontre que des groupes provenant des zones à circulation stable étaient génétiquement plus différents que ceux habitant des zones géographiques plus éloignées et connectées par des courants marins. Avec des résultats qui expliquent les

structures de population décrites auparavant par Harrison (1991), il démontre ainsi l'existence de deux metapopulations de cette espèce dans le Pacifique Nord : d'une part, une composée par des populations des eaux à circulation stable qui entraînent les œufs et les larves pélagiques et, d'autre part, une composée par une agrégation de populations satellites locales liées à une population centrale par des courants qui assurent les échanges d'œufs et de larves.

De Wolf *et al.* (2000) ont étudié la structure et le flux génique à grande échelle des populations d'une espèce de mollusque gastéropode (*Littorina stiata*) dans la région de la Macaronésie (archipels des Açores, de Madère, des Canaries et du Cap-Vert). Bien qu'ils n'aient pas trouvé de différences génétiques significatives entre les populations des quatre archipels, ni à l'échelle macro-géographique, ni à l'échelle micro-géographique, ils ont remarqué que le nombre de locus présentant des allèles hétérogènes augmente avec la distance géographique (Figure 2). La présence significative d'allèles privés (26,6 % au Cap-Vert et 6,6 % aux Açores) semble révéler un patron géographique qui corrobore des résultats d'études antérieures sur la même espèce (De Wolf *et al.* 1998a, 1998b) selon lesquelles les populations du Cap-Vert présentent un degré de variabilité morphologique et génétique plus élevée que celles du reste de la Macaronésie.

Exadactylos *et al.* (1998), en étudiant la structure d'une population de sole commune (*Solea solea*) dans deux environnements à flux génique élevé (Océan Atlantique - Grande-Bretagne et la Méditerranée - Grèce), suggèrent que la fragmentation génétique des populations est le résultat d'un processus évolutif comme la dérive génétique ou l'effet d'extinction/sélection.

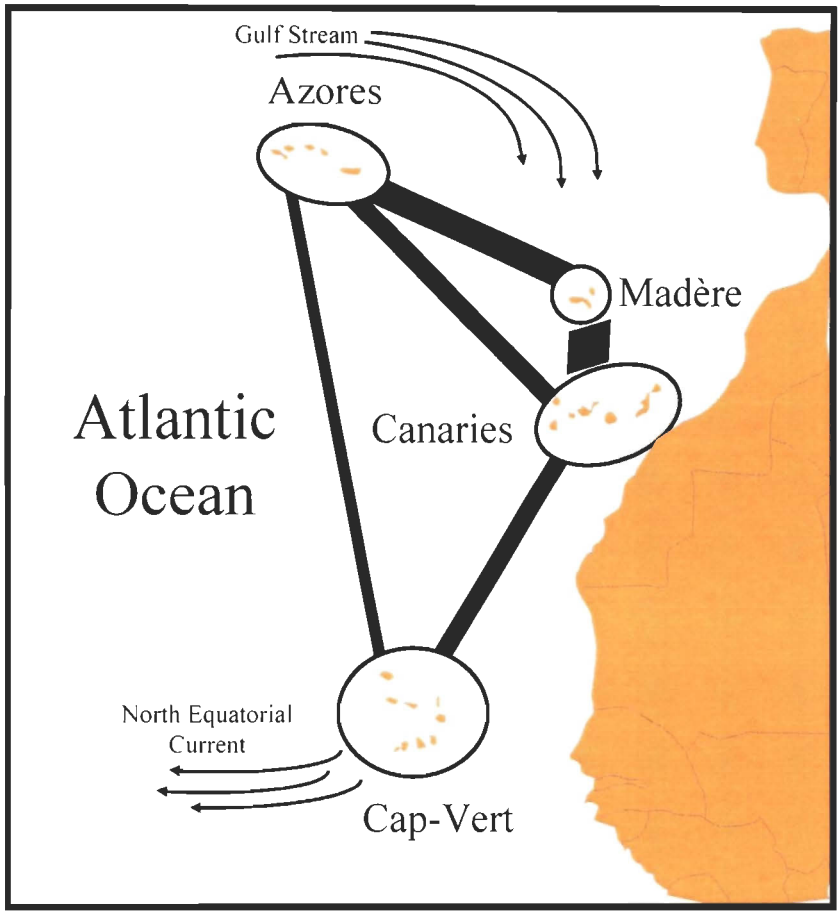

Figure 2 Représentation graphique de l'intensité de flux génétique (lignes épaisses) entre les différents archipels de la Macaronésie, basée sur la fréquence d'allèles privés (adapté de De Wolf *et al.* 2000).

Une étude plus récente sur la même espèce (Chardron 2004), entre le golfe de Gascogne (France) et le Pertuis d'Antioche (Grèce) confirme une divergence génétique significative entre les populations, et postule sur l'effet d'un isolement géographique dans un contexte de succession de périodes glaciaires associées à des régressions et transgressions marines. Lors des périodes de régression, les deux océans ainsi que leurs populations respectives furent totalement isolés les unes des autres.

Ces études suggèrent donc que les mécanismes évolutifs et écologiques peuvent jouer un rôle combiné dans la structure génétique des populations d'une espèce.

Burke *et al.* (1998) ont étudié l'influence des facteurs environnementaux sur les premiers stades de développement du Cardeau Hirame (*Paralichthys* sp.) une espèce de poisson, dans les baies de Wakasa (Kyoto, Japon) et Onslow (Caroline du Nord, EUA). Ils ont remarqué que les larves dans la baie de Onslow subissent un transport sélectif avec le courant de marée. Selon ces auteurs, les larves de cette population présentent un rythme endogène d'activité lié au cycle des marées. Des résultats semblables ont été obtenus par Jager (2001) sur une population de la même espèce dans l'estuaire de Ems (mer de Waden, Pays-Bas). Les concentrations larvaires montrent des variations très marquées avec la marée, sur toutes les échelles temporelles et présentent une distribution fragmentée dans l'espace. Les variations hydrodynamiques, induites par les variations des conditions des vents, représentent des sources de variabilités importantes dans le transport et la rétention larvaire et donc dans l'immigration au niveau des pouponnières.

Nielsen *et al.* (1998), dans une étude du transport des premiers stades de développement de la plie (*Pleuronectes platessa*) induit par le vent le long de la côte du

Danemark (Shagerrak – Kattegat), ont aussi démontré le rôle des processus physiques dans la médiation des échanges géographiques d'œufs et larves de poissons. En utilisant le vent comme un indice de transport, ils concluent que le transport des masses d'eau et l'influence des conditions de vent sont des facteurs importants dans l'approvisionnement des pouponnières en larves. D'autres études ont évalué l'impact de la variabilité interannuelle de l'hydrodynamisme sur le transport des œufs et des larves de plie au sud de la mer du Nord (Van der Veer *et al.* 1998). Les résultats de ces études, issus d'un modèle de simulation, démontrent que la variabilité interannuelle du transport larvaire, à partir des lieux de ponte, est élevée et augmente avec la distance. Ces auteurs estiment une échelle de corrélation spatiale de 500 km pour le recrutement et concluent que, pour les espèces marines, ces fluctuations ne peuvent être expliquées que par l'influence du vent et de la température de l'eau, les seuls facteurs qui présentent des échelles de corrélation suffisamment grandes. Le modèle suggère que seule la variabilité de la circulation hydrodynamique, induite par le vent, explique la variabilité interannuelle de l'intensité d'immigration des larves dans la mer de Wadden.

Nielsen *et al.* (2005) ont étudié la structure de population des juvéniles de morue (*Gadus morhua*) dans une zone de transition entre la mer du Nord et la mer Baltique et ont observé que les juvéniles et les adultes de la même région géographique était génétiquement groupés, appuyant ainsi l'hypothèse selon laquelle la structure des populations de poissons marins est maintenue grâce à la rétention larvaire. Dans le cas de la morue, la localisation précise de la ponte ne serait pas définie en fonction du courant résiduel qui relie les lieux de ponte avec ceux d'alimentation, mais plutôt par la

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recirculation à travers laquelle la distribution discontinue des œufs et des larves est maintenue pendant quelques mois (Sinclair 1988; Ruzante *et al.* 1999).

Plus récemment, Miller & Shanks (2004), dans une étude sur la dispersion des larves de *Sebastes melanops* et sur les implications en terme de structure de population pour la définition de réserves marines, postulent que la distance de dispersion larvaire peut être considérablement plus courte (<120 km) que celle prévue par les modèles de dispersion passive, ce qui suppose des aspects comportementaux qui ne sont pas pris en compte dans les modèles physiques.

C'est ainsi que cet aspect dynamique de la structure des populations marines attire encore de plus en plus l'attention des biologistes et écologistes, dans une perspective pluri et interdisciplinaire qui couple la modélisation des comportements des premiers stades des cycles de vie et la modélisation des processus hydrodynamiques dominants. La modélisation de la dispersion larvaire passive dans des systèmes estuariens, océaniques ou insulaires par des approches lagrangiennes stochastiques (Ribergaard *et al.* 2004; Engie & Klinger 2007) ou eulériennes d'advection-diffusion (Treml *et al.* 2007), illustre bien l'importance de cet aspect dynamique dans la compréhension des structures des populations marines.

2.2.4 Méthodes d'étude de structures de populations

L'étude de la structure des populations marines fait appel à plusieurs techniques, méthodes et disciplines dont on mentionne les plus utilisées, dans un but illustratif.

Marqueurs génétiques. Les différences génétiques entre individus, stocks et populations sont des indicateurs de certification du degré d'isolement reproductif, un mécanisme fondamental de structuration des différences entre groupes taxonomiques (Begg & Waldman 1999). L'utilité, la résolution et l'efficacité des différentes techniques sont très variables selon la nature du problème que l'on cherche à étudier (Sunnucks 2000). Parmi les différentes techniques, la variation de protéines ou enzymes par électrophorèse permet d'obtenir une expression indirecte des différences entre des groupes, dans la fréquence des allèles au niveau des nucléotides. Cependant, le fait que la même protéine puisse être codée par des séquences multiples de nucléotides représente une limitation à son utilité. Cette méthode a déjà été utilisée dans une étude de la différentiation de *Littorina stiata* à travers la variation de l'estearase et de la myoglobine (De Wolf *et al.* 1998b). Une autre technique cherche à mettre en évidence des variations de l'ADN mitochondrial. Il s'agit d'une molécule circulaire cytoplasmique, héritée, qui contient entre 16 000 et 20 000 paires de bases. La transmission héréditaire est du type haploïde et quasi exclusivement maternelle, montrant des différences ancestrales. Différentes régions de la molécule ont déjà été utilisées pour séparer différents stocks, mais le pouvoir de discrimination semble limité à un nombre restreint de locus spécifiques (Møller 1968; Jamieson & Otterlind 1971; Cross & Payne 1978; Dahle & Jørstad 1993; cités par Ruzzante *et al.* 1999) et de telles différences ne semblent pas s'exprimer lorsqu'un plus grand nombre de locus nucléaires est analysé. Il semble que des analyses basées sur ce marqueur génétique montrent généralement des faibles différentiations à l'échelle microgéographique de l'aire de distribution des espèces. En effet, certaines régions de la molécule sont plus variables que

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d'autres (ex. zones de réplication) et donc peuvent être plus puissantes pour discriminer les populations. La variation de l'ADN nucléaire semble être actuellement la technique la plus robuste en terme de discrimination. Des séquences de base d'ADN nucléaire (microsatellites) présentent un énorme potentiel (supérieur à trois millions de paires de nucléotides) en tant que marqueur dans presque tout individu (Begg & Waldman 1999). Bien que l'ADN soit diploïde et donc, toutes les recombinaisons possibles représentent les deux sexes. Malgré que l'interprétation de situation de polyploïdie puisse devenir compliquée dans certaines situations, beaucoup d'études montrent que des microsatellites d'ADN nucléaires sont très abondants et largement distribués dans le génome eucaryote et présente un niveau élevé de polymorphisme (Ruzzante *et al.* 1999). En laboratoire, il est actuellement relativement facile de générer des amplifications à partir de quantités minimes de tissu frais ou conservé, ce qui rend les microsatellites de l'ADN nucléaire des instruments importants en tant que marqueurs génétiques pour l'identification de stock. Actuellement il semble que c'est la technique plus largement utilisée (Daniel *et al.* 2006; Valentin 2006).

Marqueurs chimiques. Les otolithes sont des structures composées essentiellement de Ca et d'éléments traces présents dans la niche écologique du poisson. En assumant que les structures calcifiées des poissons, à quelques exceptions près, ne sont pas susceptibles de dissolution ou résorption et que ces tissus continuent à croître au cours de la vie des individus, elles représentent des enregistrements permanents de l'influence des facteurs endogènes et exogènes sur la matrice Ca-protéine. Cette hypothèse assume que des différences dans l'environnement auquel la population a été exposée, ont affecté les

éléments traces des structures calcifiées, résultant en une composition chimique spécifique pour chaque population qui permet ainsi de les distinguer (Thesher 1999). Étant possible d'analyser des portions sélectionnées d'otolithes, il est possible d'associer ces signatures à un stade particulier de croissance de l'espèce (Begg & Waldman 1999). Cette approche semble relativement utile lorsqu'il existe des signaux environnementaux marqués. Cependant, les résultats issus de ces analyses sont souvent difficiles à interpréter en raison de l'effet combiné de l'influence physiologique, ontogénique et environnementale sur le dépôt des éléments traces, en plus des problèmes liés à l'échantillonnage a posteriori et à la contamination. Cette méthode a déjà été utilisée, par exemple, dans l'étude de la structure de population de morue, (Campana *et al.* 1994; Campana & Gagné 1995).

Marqueurs parasitiques. Des stocks de poissons peuvent présenter des différences en terme de composition spécifique et d'abondance en parasites à cause des différences biogéographiques dans leur tolérance environnementale, la différente disponibilité d'hôtes intermédiaires et les différents paramètres vitaux des populations. Les meilleurs marqueurs de cette catégorie doivent être des parasites à cycle de vie directe, de façon à ce que l'infection soit impossible s'il n'y a pas un contact étroit entre poissons infectés et poissons non infectés (Oliva & Ballón 2002). En absence de différence qualitative, des différences quantitatives peuvent indiquer la présence de populations ou stocks différents à travers l'étude simultanée de plusieurs groupes de parasites par des analyses statistiques multivariées. La prévalence et l'intensité parasitiques sont donc des variables importantes (Wood *et al.* 1988; Oliva & Ballón 2002). Cette approche, qui a déjà été utilisée, par exemple, dans la discrimination de stocks de merlu du Chili - *Merluccius gayi gayi* (Oliva

& Ballón 2002), exige des connaissances considérables sur la biologie des parasites et peut être biaisée par des variations importantes à l'intérieur du stock, liées à l'adoption de différents styles de vie (Begg & Waldman 1999).

Marqueurs morphologiques. Parmi ces marqueurs, les caractères méristiques, analysés à partir du dénombrement de structures anatomiques (rayons des nageoires, branchiospines, écailles et nombre de vertèbres) ont déjà été utilisé dans l'identification de différentes populations de poissons, dont le hareng du Pacifique (Schweigert 1981) et le saumon rouge (Wood *et al.* 1988). Cette technique suppose que les caractères méristiques sont établis très tôt dans le développement ontogénique de l'individu, souvent même avant l'éclosion ou au niveau des gamètes, et reflètent l'effet de l'environnement (salinité, lumière, oxygène dissous, vents, température, etc.) pendant cette période de développement (Nielsen *et al.* 1998; Swain & Foote 1999). La plupart des caractères demeurent stables tout le long de la vie du poisson, ce qui permet de séparer différents stocks à travers des analyses statistiques multivariées. Cependant, puisque ces caractères ont aussi une base génétique, il peut s'avérer difficile de distinguer l'effet de l'environnement (Begg & Waldman 1999). Une deuxième méthode dans cette catégorie, représentée par la géométrie morphométrique (Rohlf 1999; Adams *et al.* 2004; Zelditch *et al.* 2004). Contrairement aux caractères méristiques, il s'agit de données continues qui requièrent des ajustements ou corrections par rapport à la taille des différents spécimens, car elles changent avec la croissance de l'individu. Il s'agit aussi de caractères déterminés par l'influence combinée de facteurs environnementaux et génétiques. Cette méthode s'est révélée robuste dans des études sur la variation de forme du corps de poissons, aussi bien intrapopulation (Swain & Foote 1999;

Loy *et al.* 2000; Neves & Monteiro 2003; Trapani 2003) qu'entre populations (De Vries *et al.* 2002; Klingenberg *et al.* 2003), ou entre espèces (Cavalcanti *et al.* 1999; Langerhans *et al.* 2003; Hankison *et al.* 2006). Elle a aussi été utilisée sur des crustacés (Cadrin & Friedland 1999; Tseng *et al.* 2001). Cette méthode est utilisée pour étudier la forme du corps en tout ou en partie (Cadrin & Friedland 1999; Swain & Foote 1999). Dans cette dernière utilisation, on étudie souvent des structures comme les écailles et otolithes (*sagitta*, *lapillus* et *asterisci*) qui fournissent des informations importantes pour la distinction des stocks de poissons. Les avancées récentes dans le domaine du traitement d'image vidéo et digitale empruntent à ces techniques, ainsi qu'à celles décrites précédemment, une utilité notable dans l'identification de stocks.

Paramètres vitaux de la population. Les paramètres vitaux de la population incluent la croissance, la survie, l'age à la maturité, la fécondité, la distribution et l'abondance. Ils sont l'expression phénotypique de l'interaction entre la génétique et l'environnement, et représentent différents modes de vie. Des différences entre ces paramètres sont utilisées pour identifier des entités de gestion séparées en supposant que les variations phénotypiques sont dues à des influences génétiques et environnementales, ce qui représente une évidence d'isolement géographique ou reproductive. Bien que l'utilité de ces paramètres diminue avec la complexité des stocks et l'historique des pêcheries, leur applicabilité augmente avec le nombre de paramètres examinés. Ces méthodes offrent des informations de base pour la reconnaissance et la délimitation initiale des aires géographiques représentatives de stocks individuels de poissons (Begg *et al.* 1999a). Elles ont été récemment utilisées dans l'analyse de la stabilité temporelle des paramètres vitaux

des populations de morue de l'Atlantique (*Gadus morhua*), de l'églefin (*Melanogrammus aeglefinus*) et de la limande à queue jaune (*Limanda ferruginea*) dans l'Océan Atlantique (Begg *et al.* 1999b).

Marquage et recapture. Le marquage de poissons peut aussi être utilisé dans l'étude de la structure des stocks. Les meilleurs résultats sont obtenus lorsque l'on procède au marquage de stocks supposés distincts, au moment où ils se trouvent géographiquement séparés, de façon à déterminer par la suite leur degré de mélange. Une autre approche consiste à procéder au marquage des stocks mixtes et évaluer par la suite leur degré de séparation géographique (Begg & Waldman 1999). Ces techniques exigent un temps considérable et leur efficacité dépend largement de la représentativité du marquage et des efforts de recapture.

2.3 Les écosystèmes marins insulaires

L'importance de facteurs biotiques et abiotiques varie non seulement en fonction du mode de vie adopté par l'individu au cours d'un stade donné de son développement, mais aussi selon les écosystèmes. Dans les écosystèmes insulaires, des interactions multiples entre de nombreux facteurs physiques du milieu comme la bathymétrie, la topographie, la morphologie des côtes, l'étendue des plateaux et la distance géographique, liés à des patrons très variables de circulation océanique à petite et à grande échelle, sont à l'origine d'une diversité écologique qui influence la structure et la dynamique des populations marines.

Pour les espèces à reproduction sexuée qui colonisent les plateaux peu profonds autour des îles océaniques, la conclusion intuitive est celle selon laquelle les populations

marines sont auto-soutenues ce qui conduit à déduire qu'il doit exister des mécanismes favorisant la rétention des larves (Sinclair 1988). Ces mécanismes de rétention semblent être à la fois une association entre des processus physiques et des manifestations de comportement actif des espèces (Burke *et al.* 1998; Sinclair 1988; MacCall 1990; Fréon & Misund 1999) liées à la nage et à des stratégies de reproduction où la période de ponte est ajustée aux manifestations plus favorables à la rétention d'œufs, de larves et de juvéniles. Les discontinuités physiques représentent un facteur dominant dans la rétention de la phase pélagique du cycle de vie des espèces dans un espace particulier de l'océan, permettant ainsi la persistance de la population (Sinclair 1988). Dans ces environnements marins particuliers, la structure, l'abondance et la richesse des populations sont clairement une fonction des frontières spatiales.

Des observations en Atlantique Nord dans le bassin des Canaries, où se trouvent les archipels des Açores, des Canaries, de Madère et du Cap-Vert, ont démontré que les îles et les pics sous-marins jouent un rôle important dans la circulation océanique tourbillonnaire (Richardon & Tychensky 1998; Simmons & Nof 2000). Ces structures induisent des forces suffisantes pour produire la scission des anneaux océaniques, provoquant des phénomènes de transfert d'énergie, de mouvement, de salinité et de température à de petites échelles dissipatives. La circulation tourbillonnaire est importante dans les processus de dispersion et mélange (Hamner & Hauri 1981; Robinson 1983; Rissik *et al.* 1997) et pourraient favoriser une rétention mécanique d'œufs et larves autour d'îles et récifs coralliens. Ce phénomène, connu comme « effet de masse d'île » depuis Doty & Oguri (1956) est souvent

associé à des concentrations de production primaire (Hamner & Hauri 1981; Sander 1981; Boden 1988 ; Palacios 2002 ; Sasamal 2006).

Les îles, les chaînes d'îles et les pics sous-marins sont des structures topographiques qui fonctionnent comme des zones frontières entre des bassins océaniques. Le bilan de vorticité qui doit s'établir après contact des masses d'eau avec ces structures, induit des patrons de circulations et des mélanges turbulents autour des îles ou pics sous-marins (Spall 2000). Les mouvements ascendants ou descendants des masses d'eaux produisent respectivement une diminution et augmentation de la vorticité relative et il en résulte la formation de tourbillons anticycloniques et cycloniques. La Figure 3 présente des observations de ces phénomènes dans l'Atlantique Nord, enregistrées en 1994 par Richardson & Tychensky (1998) dans la région de la Macaronésie. La dynamique des figures anticycloniques reste toujours liée au pic sous-marin tandis que celle des figures cycloniques peut, en fonction de la vitesse du courant incident, être entretenue par les premiers ou dériver en aval du pic sous-marin (Kamenkovich 1986).

La formation d'ondes de front à grande échelle et leur évolution vers des anneaux cycloniques et anticycloniques a été observée dans des images satellites infrarouges pendant des phénomènes de résurgence pouvant être associés à la topographie des fonds et à la géométrie des côtes (Tseng & Ferziger 2001). La structure de ces anneaux qui se forment dans des zones de résurgences et se propagent dans la direction du vent peut être modifiée par des perturbations côtières.

Toutes ces caractéristiques physiques des îles, associées à des patrons de circulations aussi particuliers et à une fragmentation géographique plus ou moins significative, sont à l'origine de l'hétérogénéité que l'on observe dans les écosystèmes marins insulaires.

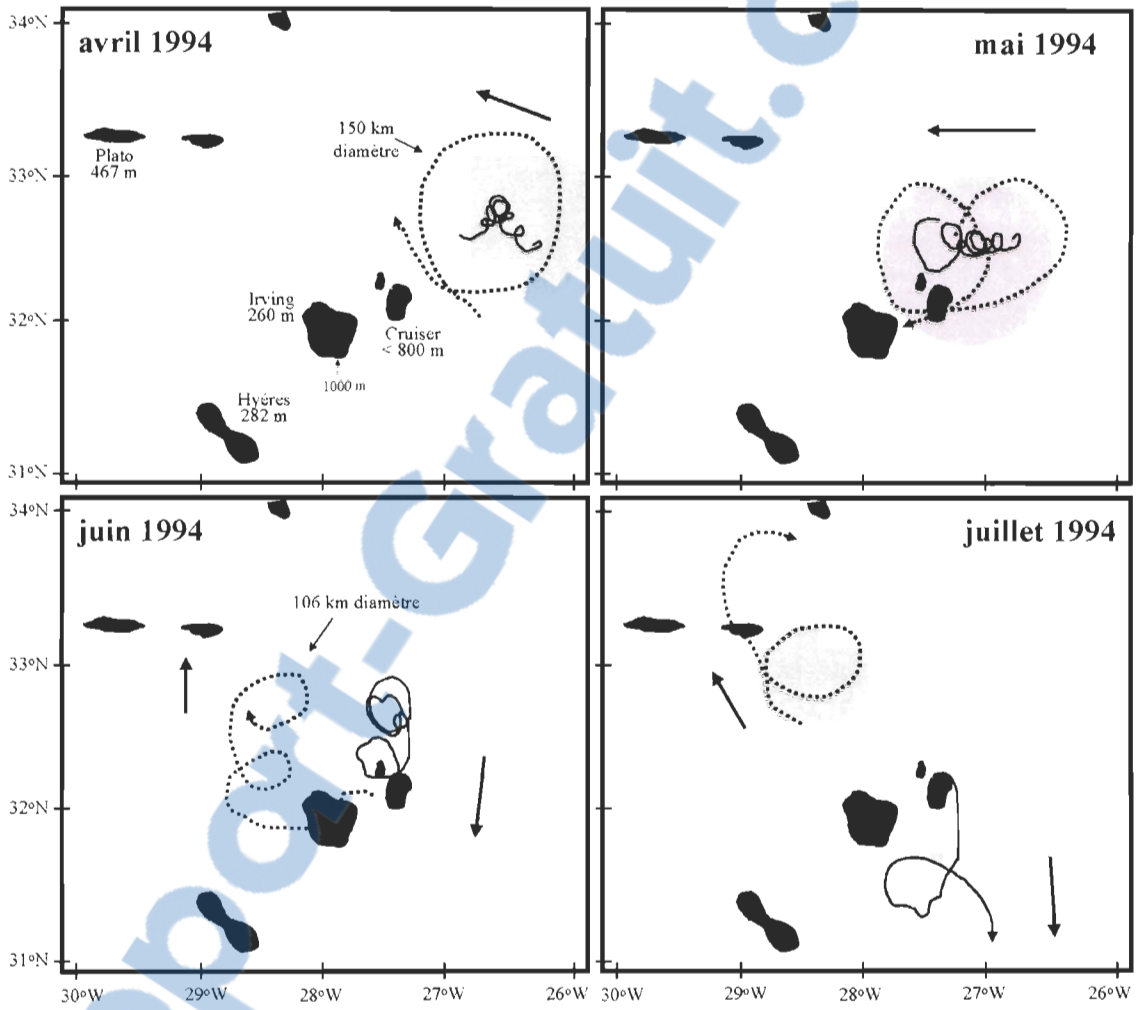

Figure 3 Scission d'anneaux méditerranéens en Atlantique Nord dans la région de l'archipel des Azores après contact avec une chaîne de pics sous-marins entre avril et juillet 1994. La circulation tourbillonnaire atteint les îles en avril et soubis une cision en un anneaux cyclonique (flèches pointilées) vers le nord et un anticyclonique (flèches continues) vers le sud. (adapté de Richardson & Tychensky 1998)

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L'expression plus ou moins forte de cette hétérogénéité dépend de plusieurs facteurs dont la distance entre les îles, l'étendue, la profondeur et la topographie des plateaux insulaires et le régime hydrologique dominant.

La dispersion est le processus biophysique qui tend à contraindre les effets de la fragmentation dans la structure et la dynamique spatio-temporelle des populations marines. C'est le niveau d'équilibre entre ces deux phénomènes dans un écosystème qui détermine le degré de connectivité entre les populations marines. Ce concept prend de plus en plus d'importance au niveau de l'écologie marine insulaire où, dans un contexte de pression anthropique croissante, l'exploitation durable des ressources requiert des stratégies efficaces de conservation. Les efforts de recherche se penchent actuellement donc sur la compréhension des mécanismes qui contrôlent la dispersion larvaire, le rôle des processus physiques et le comportement des organismes.

2.4 L'archipel du Cap-Vert

2.4.1 Structure et formation géologique

L'archipel du Cap-Vert se trouve entre les parallèles 14° 50 et 17° 20 N et entre 22° 40 et 25° 30 de longitude W, à 620 km de la côte occidentale africaine, 2 500 km du Brésil et à 5 100 km du sud-ouest de la Grande-Bretagne. Composé par dix îles et cinq îlots principaux, tous d'origine volcanique, l'archipel s'intègre, avec ceux des Açores, de Madère et des Canaries dans la région biogéographique de la Macaronésie (Figure 4).

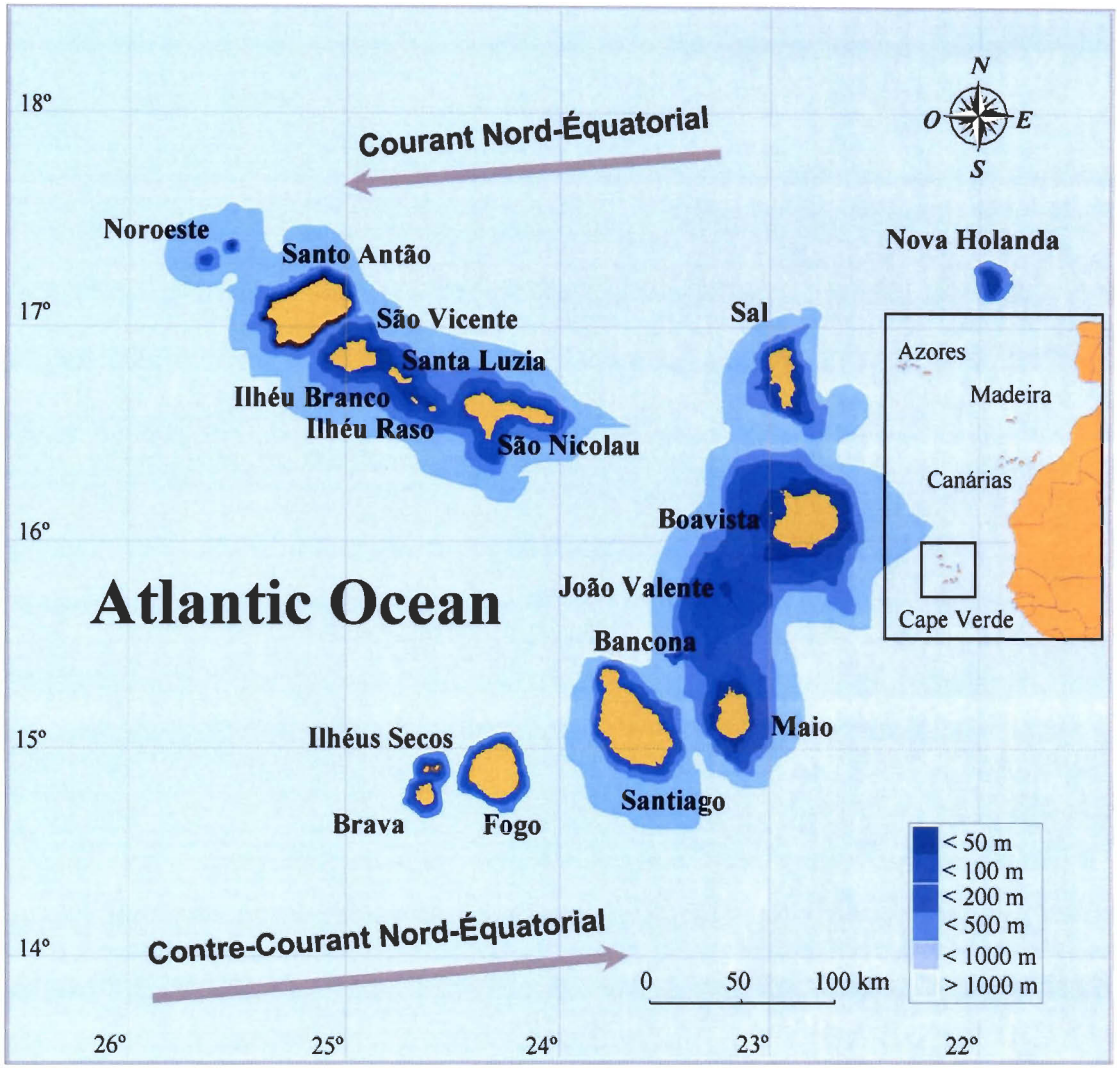

Figure 4 Carte de l'archipel du Cap-Vert et sa localisation dans la région biogéographique de la Macaronésie avec trois autres archipels (Azores, Madère et Canaries). Les flèches représentent les deux principaux systèmes de courants à grande échelle qui affectent l'archipel.

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La formation géologique des îles est associée à l'évolution d'activités magmatiques insérée sur des formations sédimentaires pendant le tertiaire et le quaternaire. Sal, Boavista et Maio présentent une origine similaire et sont considérées les plus âgées de l'archipel, avec un relief plus doux, des grandes régions planes et quelques cônes volcaniques. Les autres îles semblent être plus récentes, ayant été formées à partir de successions volcaniques dans le quaternaire. Aux îles de Fogo et Brava, les plus récentes, il y a encore des manifestations volcaniques et sismiques fréquentes.

2.4.2 Géomorphologie côtière et topographie des fonds

La géomorphologie côtière est très variée, avec une ligne de côte d'environ 1 020 km et une Zonne Économique Exclusive (ZEE) de 734 265 km2. Les îles présentant plusieurs baies. Les distances entre elles sont très variées, pouvant aller d'environ 6 km entre l'île de Brava et les îlots Grande à 270 km entre les îles de Santo Antão et Maio. La profondeur et l'étendue des plateaux insulaires sont aussi très variées. On peut passer d'une profondeur de 55 m entre l'île de Brava et les îlots Grande à plus de 3 990 m entre les îles de São Vicente et Fogo.

La surface du plateau diminue brusquement jusqu'à la profondeur de 200 m et la pente reste relativement faible jusqu'à 1 000 m (Bravo de Laguna 1985; Menezes *et al.* 2001). La cartographie des fonds marins de l'archipel montre d'importants pics sous-marins qui s'élèvent jusqu'à des profondeurs variant entre 660 m (sud-ouest de l'archipel) et très proche de la surface (Nova Holanda – nord-est de l'île de Sal), plus ou moins éloignés des îles et qui sont utilisés comme des bancs de pêche importants.

La position géographique des îles (l'axe majeur) par rapport aux vents et courants dominants varie de quasi parallèle (île de Sal) à quasi perpendiculaire (île de São Nicolau) ou incliné (îles de Santo Antão et Santiago). Cette caractéristique géomorphologique, associée à la forme générale des îles (quasi ronde – île de Boavista, Fogo et Brava; oblongue – îles de Santiago; rectangulaire – îles de Sal, Maio et Santo Antão; losange – île de São Vicente) et à la topographie des côtes contribuent à une hétérogénéité environnementale typique des systèmes insulaires. De plus la nature volcanique des îles induit une considérable variabilité des fonds marins entre essentiellement sableux (îles de Boavista et Maio), rocheux (îles de Santo Antão, São Nicolau, Santiago, Fogo et Brava) ou sableux-rocheux (îles de São Vicente, Santa Luzia et Sal), en relation avec différentes formations coralliennes et pics sous-marins.

2.4.3 Le climat

L'archipel se trouve en pleine zone sahélienne sous la dominance des vents alizés du nord-est, entre les hautes pressions sub-tropicales de l'Atlantique et les basses pressions équatoriales du front inter-tropical. Un groupe d'îles, nommé localement "Barlavento" (Santo Antão, São Vicente, Santa Luzia, Îlots Raso et Branco, São Nicolau, Sal et Boavista) est localisé du côté au vent et un autre groupe nommé "Sotavento" (Îles de Maio, Santiago, Fogo, Brava et Îlots Grande, de Cima et Luis Carneiro), est du côté sous le vent.

Le climat est de type tropical sec, caractérisé par une saison froide et sèche, de décembre en mars, une saison de transition, avril et mai, et une saison chaude et humide, de juillet à novembre. Les pluies sont torrentielles, irrégulières et se concentrent entre les mois

d'août et septembre (60 % à 90 % de la précipitation annuelle totale) en fonction de la topographie et de l'altitude (De Brum Ferreira 1989). Ces variations temporelles se traduisent aussi dans les variations temporelles de l'activité de pêche au cours de l'année (Medina 1995).

2.4.4 Circulation océanique et structure thermique des masses d'eaux

Les îles et les eaux voisines se trouvent sous forte influence de la circulation océanique à grande échelle, sur le bord sud de la circulation anticyclonique sub-tropicalel de l'Atlantique Nord (Courant Nord-Équatorial) et sur la limite nord du Contre-Courant Équatorial qui peut atteindre la latitude de 10° Nord (Lázaro *et al.* 2005). Ces deux systèmes de courants océaniques subissent des variations saisonnières qui affectent la circulation de la couche superficielle jusqu'à 200 m de profondeur, et leur frontière peut s'établir au niveau des îles pendant certaines périodes de l'année (Stramma & Siedler 1988; Stramma & Schott, 1999). L'archipel est sous l'influence des deux masses d'eaux centrales de l'Atlantique Nord et Sud (NACW et SACW), la transition entre elles se faisant au sud du parallèle 20° N (Hernandez-Guerra *et al.* 2001).

La température moyenne de l'air varie de 22°C à 27°C entre les saisons froides et chaudes respectivement. La température de la mer suit celle de l'air, avec une variation en période froide entre 21°C et 22°C et, en période chaude, entre 23°C et 27°C. La distribution des températures est caractérisée par une forte stratification dans les premiers 100 m. La couche de mélange de surface varie entre 25 et 40 m, avec des températures de 25 °C. À partir de cette couche s'établit la thermocline avec un gradient thermique d'environ 0,1°C/m

sur 100 m de profondeur. À la base de cette thermocline, la température baisse à des valeurs de l'ordre de 15 à 16 °C. À partir de 100-150 m le gradient diminue considérablement et la température atteint des valeurs de 10 °C à 500 m et de 6 °C à 1 000 m (Marques *et al.* 1997).

2.4.5 Problèmes de gestion et conservation des ressources halieutiques

Les ressources halieutiques sont très importantes pour le développement socio-économique du pays. Il est donc nécessaire de bien connaître la structure et la dynamique spatio-temporelle des populations marines ainsi que les processus et phénomènes océanographiques qui influencent cette structure.

Au cours des dernières années, des études menées par l'Instituto Nacional de Desenvolvimento das Pescas (INDP) montrent que certains stocks d'espèces démersales subissent des déclins accentués et à des rythmes différents selon des patrons spatio-temporels aussi différents (Dias 1992; Carvalho *et al.* 1999; Medina *et al.* 2002; Oddsson & Monteiro 1998, 1999). Les langoustes côtières se trouvent en situation de surexploitation, voire d'effondrement autour de certaines îles (Santiago et Sal) ou encore en situation d'équilibre dans d'autres (Maio et Boavista). Ce diagnostic semble indépendant des distances entre les îles et des patrons d'effort de pêche car la tendance à l'effondrement des stocks persiste, depuis environ une quinzaine d'années, sans qu'il ait eu les rétablissements attendus à la suite d'une réduction ou d'une absence d'activité de pêche. Ce diagnostic est aussi valable pour les poissons démersaux dont les stocks se trouvent à des niveaux exploitables assez différents d'une île à l'autre depuis plus d'une dizaine d'années. On ne sait

pas si cette situation est liée à des différences dans la dynamique des populations, à des rythmes différents d'exploitation, à des changements environnementaux ou à des effets combinés de plusieurs de ces facteurs.

À partir de plusieurs études sur l'état des pêcheries au Cap-Vert (Strömme *et al.* 1982; Magnússon & Magnússon 1987; Dias 1992; Carvalho 1994; Reis 1997; Oddsson & Monteiro 1998, 1999; Carvalho *et al.* 1999; Monteiro 1999; Medina *et al.* 2002a, 2003; Tariche *et al.* 2002) et compte tenu de la diversité écologique et océanographique présente dans l'archipel, on peut déduire une forte hétérogénéité spatio-temporelle dans la distribution des ressources. Toutefois, le degré de mélange entre sous-populations, processus par lesquels la dynamique des populations locales dépend (croissance *in situ* et colonisation), et le degré de mouvements entre populations, demeurent des questions encore non résolues.

3 Objectifs de recherche

L'objectif général de cette thèse est de définir et de modéliser le fonctionnement d'un écosystème marin insulaire tropical en matière de structure et dynamique des populations démersales, en tenant compte de principales variables qui influencent la variation spatiale et temporelle de la distribution et de l'abondance des espèces.

Plus spécifiquement, on cherchera à:

1. Analyser l'importance de la fragmentation induite par la distance géographique et par la bathymétrie dans la structure spatio-temporelle et la variabilité écologique des communautés de poissons démersaux dans l'archipel;

2. Analyser la dynamique spatiale des populations démersales exploitées, c.-à-d. la relation entre leurs variations locales de densité et d'abondance, en ayant recours à des concepts théoriques en écologie spatiale, tout en tenant compte des différentes échelles spatio-temporelles (îles, saisons et années) et des différents niveaux d'organisation écologique (espèce et communauté);
3. Vérifier jusqu'à quel point la fragmentation d'habitat résultant de la persistance de conditions d'isolement physique ou écologique entre les îles se traduit en isolement effectif des populations;
4. Définir et valider un modèle hydrodynamique de connectivité de l'écosystème marin de l'archipel, tenant compte des objectifs antérieurs et de l'essentiel des phénomènes et processus océanographiques dominants;

4 Hypothèses de recherche

La problématique générale présente l'archipel du Cap-Vert avec ses caractéristiques géologiques, géographiques et hydrodynamiques. Il s'agit ainsi d'un écosystème insulaire océanique tropical, où les données environnementales et celles provenant de l'activité de pêche, nous permettent de supposer un certain isolement écologique entre les îles ou groupes d'îles. Cet isolement peut s'exprimer dans la structure et la dynamique des populations marines qui composent la faune de l'archipel. En effet, l'existence d'un patron géographique dans la structure des populations peut être liée à des patrons historiques ou récents de barrières entre populations locales, à l'isolement géographique, à la fragmentation de l'habitat ou aux gradients environnementaux, qui tendent à maintenir les

populations sans contacts (Bailey 1997). Cela rejoint les constats de Sinclair (1988) selon lesquels les discontinuités physiques représentent une possibilité de rétention de la phase pélagique du cycle de vie des espèces dans un espace particulier de l'océan, permettant ainsi la persistance de la population. Dans ces environnements marins particuliers, la structure, l'abondance et la richesse des populations sont clairement une fonction de la limite spatiale. Ainsi, les hypothèses de recherche qui ont guidé cette thèse sont fondées sur les éléments suivants:

1. La fragmentation des habitats se traduit par une structure spatiale des populations démersales, propre à chaque île ou groupe d'îles;
2. L'isolement écologique induit une différentiation morphologique entre les individus de même espèce habitant chaque île ou groupe d'îles;
3. Le régime hydrologique dans l'archipel contribue à l'isolement génétique et écologique des îles.

5 Démarche méthodologique

À l'exception de quelques travaux récents (Stobberup 2006) l'archipel du Cap-Vert, parmi ceux qui composent la région biogéographique de la Macaronésie, est jusqu'à présent, celui qui a reçu le moins d'attention scientifique au niveau de l'écologie marine. En raison de cela, et tenant compte de la complexité de la problématique qui guide cette initiative de recherche, nous avons adopté une démarche méthodologique pluri- et interdisciplinaire. Ainsi, nous avons pu optimiser les opportunités de recherche existantes et les possibilités techniques offertes par plusieurs disciplines, à liens directs ou indirects avec

l'océanographie dont la biologie halieutique, l'écologie marine, la géométrie morphométrique et l'océanographie physique. Cette démarche a été appuyée par des approches d'analyses statistiques multidimensionnelles qui ont permis d'accéder à un maximum possible d'information scientifique visant l'illustration de la problématique et la vérification des hypothèses de recherche. La Figure 5 A-C, représente un schéma la démarche méthodologique structurée selon trois étapes, à savoir: 1ère étape - Caractérisation de l'archipel par une typologie spatio-temporelle des îles, à partir des données de la pêche commerciale sur les espèces les plus abondantes et plus largement distribuées; 2e étape - Caractérisation phénotypique de l'archipel basée sur une espèce suffisamment abondante et largement distribuée sur toutes les îles; 3e étape - Caractérisation hydrodynamique de l'archipel à partir des possibilités de modélisation offertes par des modèles océanographiques opérationnels couvrant l'océan Atlantique Nord.

La Figure 5-D, résume l'intégration de résultats de ces trois étapes distinctes, mais complémentaires, pour répondre à la problématique de recherche. Cela a résulté dans la définition de la structure et la dynamique spatio-temporelle des populations démersales de l'archipel du Cap-Vert, à partir de 1) une structure écologique et dynamique spatiale, issues de données halieutiques; 2) une structure phénotypique issue de la géométrie morphométrique sur la forme du corps d'une espèce et 3) une structure de population révélée par l'hydrodynamisme et la connectivité entre les îles.

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5.1 Caractérisation typologique des îles (1ère étape)

L'existence d'un système statistique des pêches, en place dans l'archipel depuis plus de 20 ans et couvrant toutes les îles à la longueur de l'année, permet l'exploitation d'une base de données potentiellement représentative de l'évolution spatiale et temporelle des populations exploitées par la pêche artisanale. En effet, il s'agit d'une activité principalement côtière, pratiquée avec la ligne à main sur des barques artisanales en bois, ouvertes, de taille standard entre 3 et 6 m en moyenne, propulsées généralement par un moteur hors-bord de 15 HP. En raison des limitations techniques (capacité de stockage, équipements de communication, etc.), les unités de pêche n'ont pas d'autonomie en mer et, de ce fait, les opérations de pêches se déroulent au cours d'une période de 24 heures, dans un secteur limité (*ca* 10 km) autour des îles. Dans un tel écosystème tropical, la pêche démersale est multispécifique et non ciblée où la totalité des captures est débarquée dans 85 ports de pêche et vendue sur les marchés locaux. En raison de ces caractéristiques de la pêche d'artisanale, on ne s'attend pas à une variation de la puissance de pêche entre les barques.

Parmi les espèces commercialement importantes, nous avons sélectionné les plus abondantes. D'une part, un tel choix méthodologique assure la disponibilité de données pour les espèces à l'étude et évite le problème de données manquantes, ce qui augmente la puissance des analyses statistiques. D'autre part, il est reconnu que les espèces dominantes déterminent les caractéristiques biologiques principales des communautés démersales tandis que les espèces non ciblées semblent demeurer relativement inchangées, en dépit d'une activité de pêche intensive à long terme (Colvocoresses & Musick 1984; Greenstreet

& Hall 1996; Jin & Tang 1996). En fait, l'interprétation de la structure de la communauté basée sur des données de pêche commerciale peut être erronée parce que ces données ne sont ni aléatoires ni exhaustives et on ne peut pas assumer que les communautés exploitées fonctionnent naturellement. En fait, la pêche commerciale résulte d'une interaction complexe entre plusieurs facteurs liés à des stratégies de pêche (Salthaug & GodØ 2001); même dans la situation d'une pêche mixte (Ketchen 1964; Chadwick & O'Boyle 1990), les données ne représentent pas toutes les espèces des communautés exploitées. Cependant, dans le système à l'étude, les pêcheurs échantillonnent la densité de poissons autour des îles selon un processus invariable dans le temps et sans une stratégie de pêche prédéfinie. Dans ce cas où les stratégies de pêche ne changent pas, des données de capture par unité d'éffort (CPUE) peuvent être employées pour construire une série chronologique comparable d'indices d'abondance (Petitgas 1998). Ainsi, les patrons mensuels et annuels de variation de ces indices sur les principaux fonds de pêche peuvent être indicatifs de la complexité d'une population et permettre l'évaluation des variations spatiales et temporelles de son abondance (Begg & Waldman 1999).

La figure 5-A présente un diagramme de la démarche méthodologique qui a guidé la caractérisation typologique de la première étape de ce projet de recherche. Dans un premier temps, à partir de l'échantillonnage de la pêche artisanale réalisée de façon systématique par l'INDP dans le cadre du système national des statistiques de pêches au Cap-Vert, nous avons extrait des données brutes de débarquements et efforts de pêche concernant environ 1354 barques sur 260 sites de pêches à la longueur de l'année, et cela pendant une période de sept ans (1996 – 2002). Ces données ont été ensuite triées par espèce, mois, île et site de

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pêche, permettant d'établir une série spatio-temporelle de CPUE. Cette série a ensuite été utilisée dans la conception d'indices de distances écologiques. Dans un deuxième temps, nous avons établi un indice d'isolement physique entre les îles, à partir de la distance géographique et de la bathymétrie moyenne entre elles.

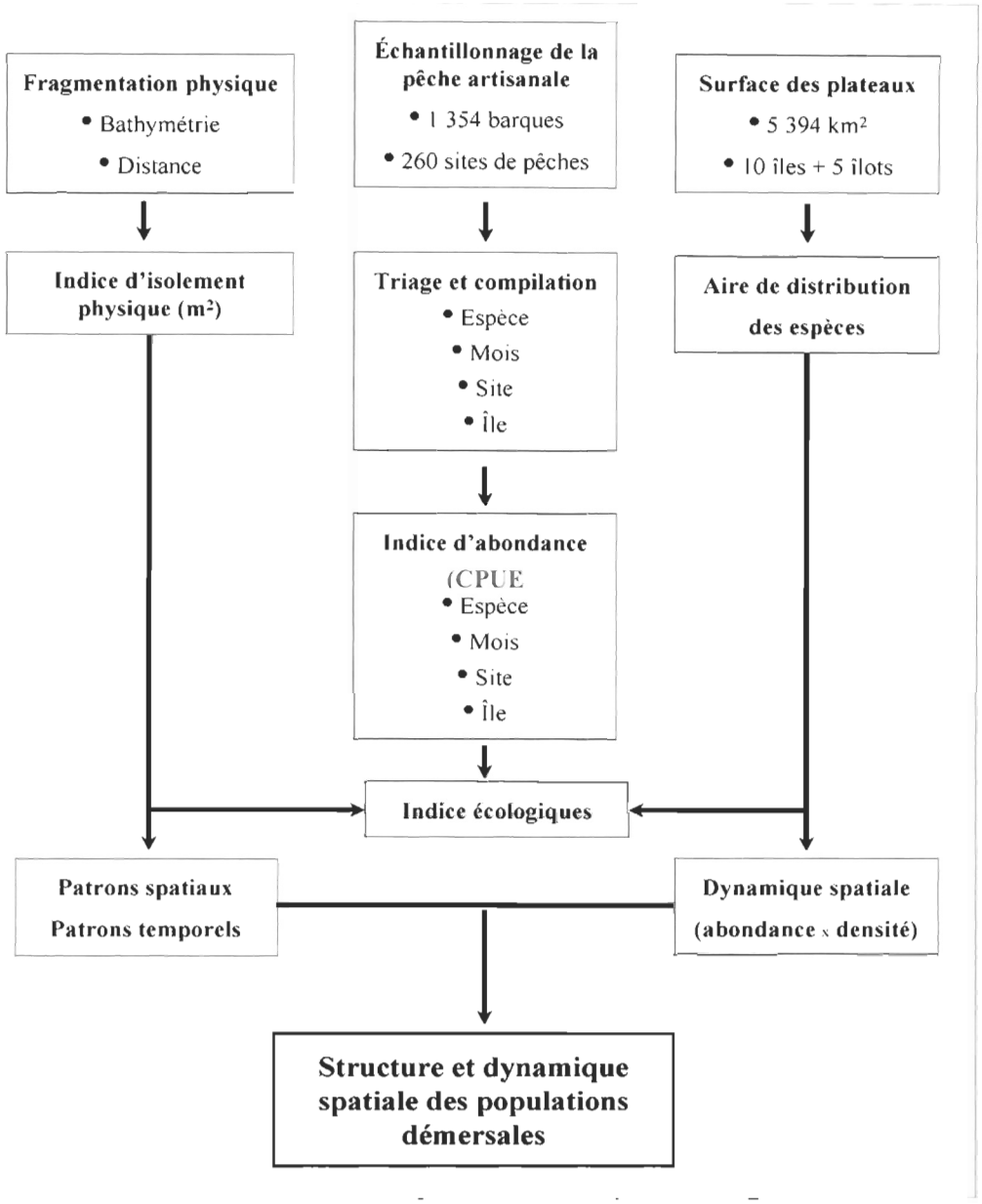

Figure 5-A Diagramme schématique de la première étape de recherche visant la caractérisation typologique de l'archipel du Cap-Vert à partir des données de pêche artisanale.

Finalement, ayant recours à des analyses statistiques multidimensionnelles (ordination et groupement) combinées avec des modèles statistiques linéaires (GLM – ANOVA et ANCOVA), nous avons étudié la relation entre ces indices écologiques, d'une part pour en déduire des patrons spatio-temporels dominants et, d'autre part, avec de l'information sur les aires de distribution des espèces, pour étudier leur dynamique spatiale. L'analyse de ces deux aspects de la distribution et de la dynamique des populations nous a permis d'établir une première structure écologique et dynamique spatio-temporelle des populations démersales exploitées dans l'archipel.

5.2 Caractérisation phénotypique des îles (2^{e} étape)

La figure 5-B présente un diagramme qui résume la démarche méthodologique de caractérisation phénotypique basée sur la variation de forme du corps des individus dans l'archipel, réalisée sur 574 individus de *Cephalopholis taeniops* (Mérou à point bleu). Il s'agit d'une espèce démersale, un téléostéen à développement larvaire pélagique, protogyne hermaphrodite (Siau 1994) avec un sex-ratio nettement en faveur des femmelles dans la population. Elle est largement distribuée dans l'océan Atlantique Est, du Sahara Occidental jusqu'en Angola, y compris le Cap-Vert et les îles de São Tomé et Principe, habitant des fonds sableux et rocheux. Bien qu'elle s'avère être une espèce adéquate pour les objectifs de recherche que nous poursuivons, en raison de sa forte abondance et sa large distribution, elle présente cependant des difficultés particulières liées à son comportement reproducteur et à son développement ontogénétique.

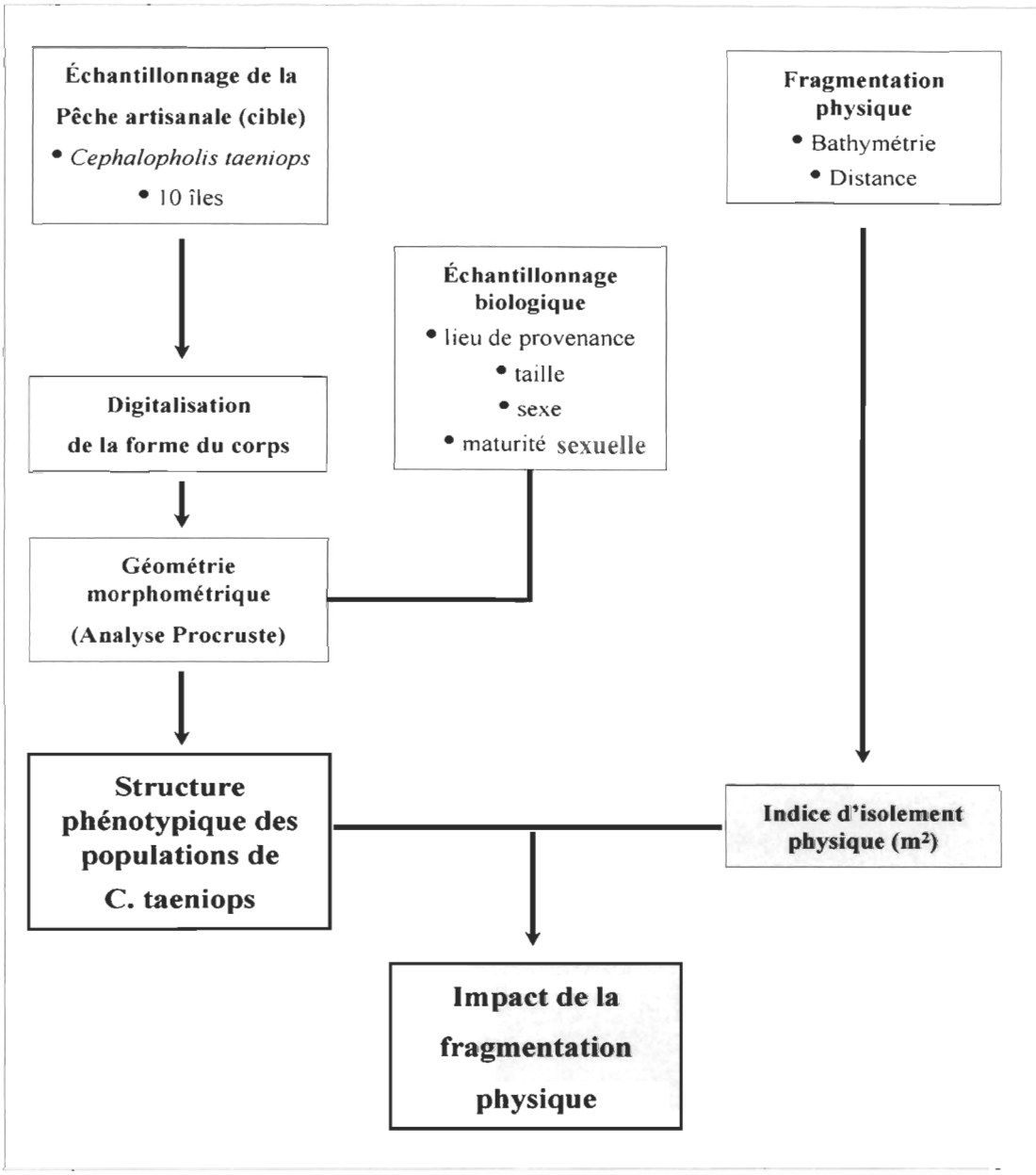

Figure 5-B Diagramme qui résume la démarche méthodologique pour la caractérisation phénotypique de l'archipel.

En effet, les espèces du genre *Cephalopholis* sont caractérisées par hermaphrodisme protogyne où les individus présentent les deux sexes, simultanément ou séquentiellement (Siau 1994; Nakai & Sano 2002; Liu & Sadovy 2004). En changeant de femelle fonctionnelle en mâle fonctionnel, tout au long de son cycle de vie un individu peut suivre différentes voies selon un processus monandrique ou diandrique. Tandis que dans des espèces monandriques, tous les mâles sont dérivés exclusivement des femelles fonctionnelles par le changement de sexe (c.-à-d. mâle secondaire), chez les diandriques, quelques mâles se différencient directement à partir des stades juvéniles par différentiation sexuelle (c.-à-d. mâle primaire). Selon ces complexités biologiques, la signification adaptative des modèles ontogénétiques et sexuels peut être fonctionnelle ou liée à leur développement. De ce fait, analyser des différences morphométriques chez ces espèces devient aussi intéressant que particulièrement troublant exigeant de la démarche d'analyse une évaluation préalable de la nature des variations de forme.

Pour cette étude un échantillon de 574 spécimens a été capturé par la pêche artisanale sur sept îles, en août 2003 et juin 2004, spécifiquement aux fins de cette étude. Suivant une démarche typique d'analyse en géométrie morphométrique (Chapitre 3 de cette thèse), nous avons pu établir une structure phénotypique des populations de l'espèce dans l'archipel. Cette structure phénotypique de *C. taeniops* a ensuite été étudiée en relation avec l'indice d'isolement physique établi lors de la première étape et cela nous a permis d'évaluer l'impact de la fragmentation physique sur la structure des populations marines de l'archipel.

5.3 Caractérisation hydrodynamique de l'archipel (3e étape)

L'étude porte sur un environnement assez hétérogène, variable et relativement vaste où les connaissances actuelles des processus biologiques et océanographiques, à l'échelle de l'île, sont très limitées. Nous avons donc commencé cette étape du projet de recherche par une étude préalable des modèles de prévisions océanographiques à l'échelle de l'océan Atlantique, pouvant permettre une application à la région, après les ajustements d'échelles spatio-temporelles nécessaires. Parmi les modèles existants, deux se sont révélés adéquats à la problématique de modélisation hydrodynamique à l'échelle d'île et archipel. Le ROMS[1] (Regional Ocean Modeling System) est un modèle numérique régional destiné à simuler des courants, des écosystèmes, des cycles biogéochimiques et la dynamique sédimentaire dans des régions côtières (Shchepetkin & McWilliams 2005). Mercator-Océan[2] est un système opérationnel de prévision océanographique (Madec *et al.* 1998) de portée internationale, permettant de décrire à tout instant, l'état de tous les océans.

La figure 5-C présente un diagramme de la démarche méthodologique suivie pour la caractérisation hydrodynamique de l'archipel. À la suite d'une étude préalable du prototype Mercator (PSY2V2) à haute résolution pour l'océan l'Atlantique Nord et la Méditerranée (Siefridt *et al.* 2002; Lellouche *et al.* 2005) nous avons extrait deux ans (2004 et 2005) de prévisions journalières des principales variables qui décrivent l'état de l'océan couvrant le

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[1] - développé conjointement par l'Université de la Californie à Los Angeles (UCLA), l'Université Rutgers à New Jersey et l'Institut de Recherche pour le Développement (IRD) en France.

[2] - développé par six institutions de recherche et développement en France (Centre National d'Études Spatiales – CNES; Institut de Recherche pour le Développement - IRD; Centre National de Recherche Scientifique – CNRS; Institut Français de Recherche pour l'Exploitation de la Mer – IFREMER; Service Hydrographique et Océanographique de la Marine – SHOM et METEO France) et opéré par un groupe d'intérêt public basé à Ramonville, Toulouse

domaine dans l'océan Atlantique Nord entre 13° et 19° de latitude et entre 20° et 28° de longitude ouest, c.-à-d. environ 55 000 km^2

Les prévisions opérationnelles de Mercator étaient déjà validées dans plusieurs régions de l'Atlantique Nord, de la Méditerranée et du Pacifique (http://www.mercator-ocean.fr/), que ce soit directement dans l'étude des processus océanographiques ou en fournissant les conditions limites à des modèles régionaux. Cependant, les questions scientifiques qui ont guidé la recherche dans le cadre de cette thèse, se rapportent à des échelles spatiales beaucoup plus petites, c.-à-d. île et archipel. Ainsi, en 2004 nous avons effectué une expérience préliminaire de validation des prévisions Mercator pour la région d'étude (Chapitre 4 de cette thèse). Les résultats nous ont permis de suivre une approche de modélisation en utilisant les prévisions Mercator. D'une part, à travers des analyses en Fonctions Empiriques Orthogonales (EOF), nous avons identifié et décrit les principaux patrons spatio-temporels de la circulation entre les îles et, d' autre part, nous avons étudié la connectivité hydrodynamique à l'intérieur de l'archipel par Modélisation Lagrangienne Stochastique (LSM) de dérive passive de particules. Les résultats de ces deux exercices de modélisation nous ont permis ensuite d'établir et de caractériser une structure hydrodynamique des populations marines à vie larvaire pélagique.

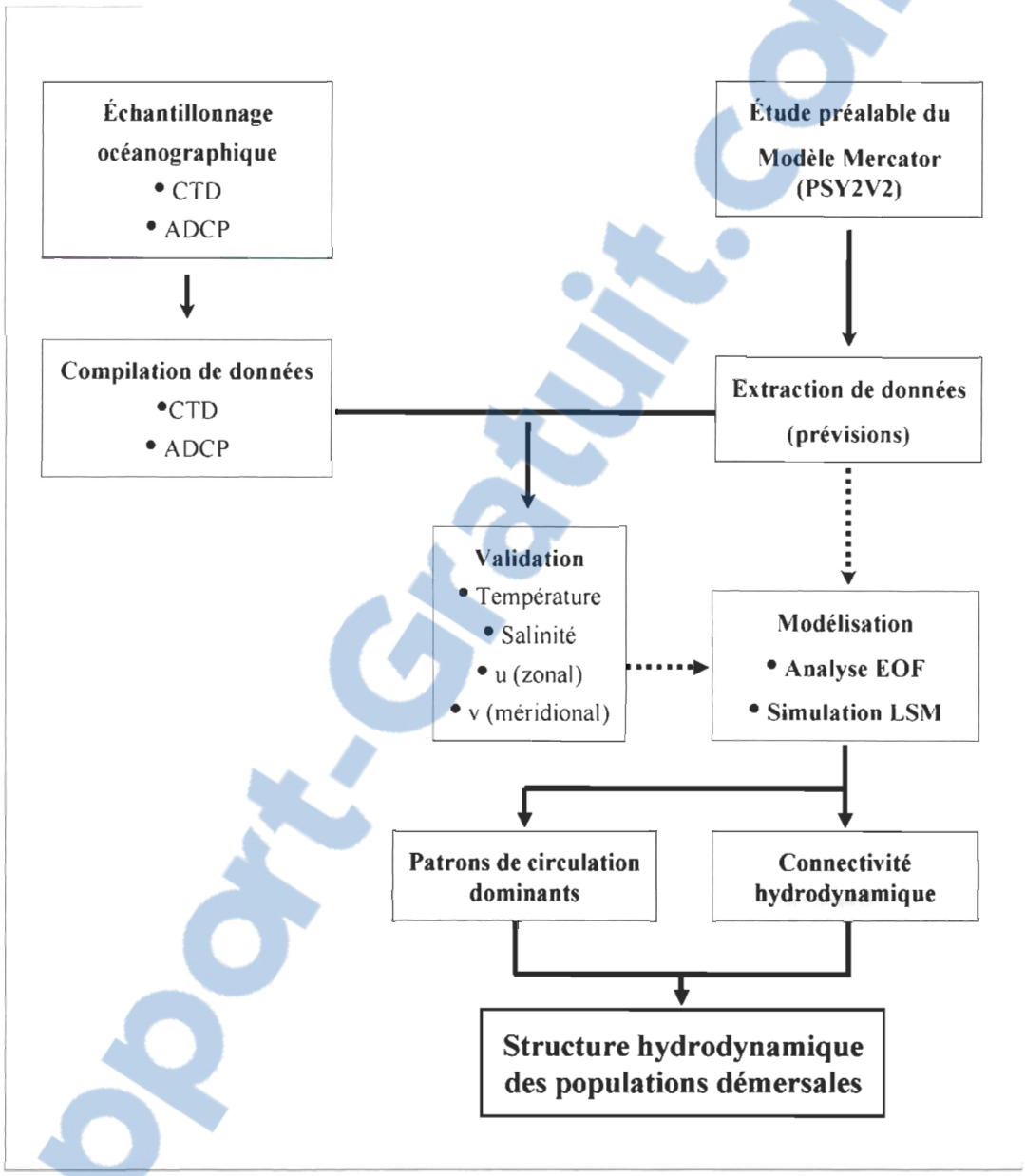

Figure 5-C Diagramme qui résume la démarche de modélisation pour la caractérisation hydrodynamique de l'archipel du Cap-Vert.

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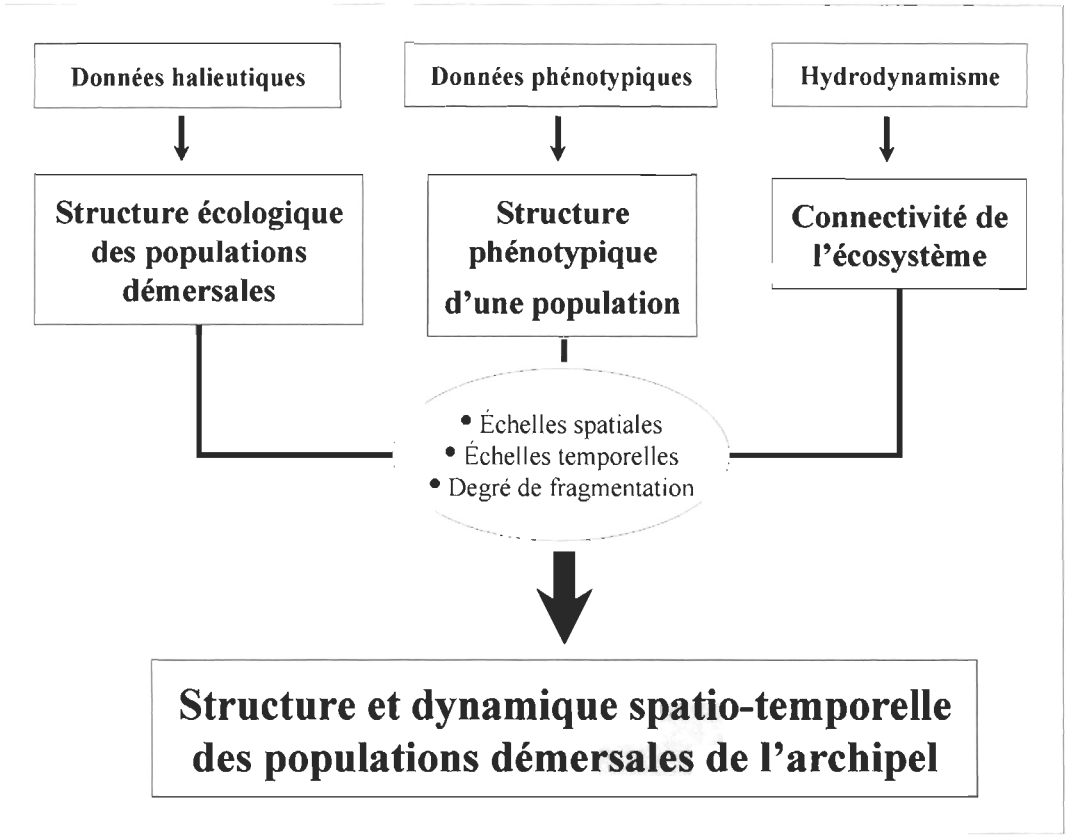

Figure 5-D Diagramme intégrant les résultats des trois étapes de recherche conduisant à l'accomplissement des objectifs de recherche fixés.

CHAPITRE 1

HOW GEOGRAPHIC DISTANCE AND DEPTH DRIVE ECOLOGICAL VARIABILITY AND ISOLATION OF DEMERSAL FISH COMMUNITIES IN AN ARCHIPELAGO SYSTEM (CAPE VERDE, EASTERN ATLANTIC OCEAN)

Article publié dans *Marine Ecology*

Medina A., Brêthes J-C, Zakarjian B & Sévigny J-M (2007) How geographic distance and depth drive ecological variability and isolation of demersal fish communities in an archipelago system (Cape Verde, Eastern Atlantic Ocean). *Marine Ecology*, **28**, 404-417.

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Résumé

Le Cap Vert est un écosystème océanique tropical, très fragmenté et dispersé, avec des îles physiquement isolées par la distance et la profondeur. Pour comprendre comment cet isolement affecte la variabilité écologique dans l'archipel, nous avons réalisé un projet de recherche sur la structure de communauté de 18 espèces de poissons commercialement les plus importantes. Un indice de distance écologique basé sur la dominance relative des espèces (D_i) est développé à partir des captures pas unité d'effort (CPUE) obtenues d'une longue série de données de la pêche d'artisanale. Deux mesures de distance écologique entre les îles sont calculées : au niveau des espèces, ΔD_i, et au niveau de communauté, ΔD (somme des ΔD_i). On propose un facteur d'isolement physique (I_{db}) combinant la distance (d) et la bathymétrie (b). Une analyse de covariance démontre que le facteur d'isolement est positivement corrélé avec ΔD_i et ΔD, suggérant que I_{db} peut être considéré comme facteur d'isolement écologique. L'effet de I_{db} change avec la saison et les espèces. Cet effet est plus fort en été (mai à novembre) qu'en hiver (décembre à avril) qui semble être plus instable. Les espèces réagissent différemment à I_{db}, indépendamment des saisons. Une analyse en composantes principales (PCA) sur la moyenne mensuelle (ΔDi) pour les 12 îles et les 18 espèces, complétée par une analyse hiérarchique ascendante (AHC), révèle un modèle géographique d'organisation des îles selon I_{db}. Les résultats indiquent que la structure écologique des communautés démersales de poissons de l'archipel du Cap-Vert, dans le temps et dans l'espace, peut être expliquée par un facteur d'isolement géographique. L'approche analytique utilisée ici est prometteuse et pourrait être envisagée dans d'autres systèmes d'archipel.

Mots clés: Système d'archipel, biogéographie, distance géographique, bathymétrie, variabilité écologique, facteur d'isolement, indice de dominance relative, analyse multivariée, structure de communauté de poissons.

Abstract

Cape Verde is a tropical oceanic ecosystem, highly fragmented and dispersed, with islands physically isolated by distance and depth. To understand how isolation affects the ecological variability in this archipelago, we conducted a research project on the community structure of the 18 commercially most important demersal fishes. An index of ecological distance based on species relative dominance (D_i) is developed from Catch Per Unit Effort, derived from an extensive database of artisanal fisheries. Two ecological measures of distance between islands are calculated: at the species level, ΔD_i, and at the community level, ΔD (sum of ΔD_i). A physical isolation factor (I_{db}) combining distance (d) and bathymetry (b) is proposed. Covariance analysis shows that isolation factor is positively correlated with both ΔD_i and ΔD, suggesting that I_{db} can be considered as an ecological isolation factor. The effect of I_{db} varies with season and species. This effect is stronger in summer (May to November), then in winter (December to April), which appears to be more unstable. Species react differently to I_{db}, independently of season. A principal component analysis (PCA) on the monthly (ΔD_i) for the 12 islands and the 18 species, complemented by an agglomerative hierarchical clustering (AHC), shows a geographic pattern on island organization, according to I_{db}. Results indicate that the ecological structure of demersal fish communities of Cape Verde archipelago, both in time and space, can be explained by a geographical isolation factor. The analytical approach used here is promising and could be tested in other archipelago systems.

Key words: Archipelago system, biogeography, geographic distance, bathymetry, ecological variability, isolation factor, relative dominance index, multivariate analysis, fish community structure.

1.1 Introduction

The concept of geographical structure in marine ecosystems is fundamental for understanding population dynamics, for fisheries management, and for the implementation of conservation measures. The geographical structure of populations generally results from spatial distribution patterns that are related to historic or current barriers between local communities, such as geographic distance, environmental patchiness and environmental gradients that tend to keep populations from mixing freely (Bailey 1997). The geographic structure is often naturally fragmented, with a large habitat area subdivided into habitat patches. This has a major impact on population dynamics, community structure and ecosystem diversity.

Habitat fragmentation tends to reduce the area of habitat patches and decreases the long-term survival probability of populations and communities. In such habitats, population sizes decrease and have a higher probability of going extinct due to environmental or demographic stochasticity and to an increasing vulnerability to external influences (Saunders *et al.* 1991). Several authors refer to empirical knowledge about the evolutionary and adaptive mechanisms underlying the response of populations and communities to fragmentation (Wiens *et al.* 1993; Diffendorfer *et al.* 1995) and analyze the effects of such phenomena according to spatial scale (Andreassen *et al.* 1998). On one hand, small-scale fragmentation is mainly related to patchy populations characterized by specific life-history and behavioural characteristics like intrinsic growth rate, reproduction, food competition and social organization. On the other hand, large-scale habitat fragmentation affects

metapopulation dynamics through processes such as exchange rates between local populations, connectivity, speciation, resource turnover and environmental pressures.

Physical isolation by geographic distance has been proposed to drive genetic isolation and population structure (Wright 1943), not only in marine systems like coral reefs and archipelagos (De Wolf *et al.* 1998a, 2000; Planes & Fauvelot 2002; Duda & Rolán 2005), but also in terrestrial ecosystems for birds (Wiggins *et al.* 1998), mammals (BjØrnstad *et al.* 1998), and plants and invertebrates (Zschokke *et al.* 2000). Wright (1943) initially introduced the concept of isolation by distance in an island population structure model where organisms' dispersal ability is constrained by distance and where gene flow is most likely to occur between neighbouring populations (Planes & Fauvelot 2002). In parallel, the vertical dimension associated with bathymetry plays a varied and complex role in ecosystem fragmentation through its interaction with hydrodynamic processes such as wind-driven circulation, turbulent mixing processes and buoyancy forces, as described by Werner *et al.* (1997), Jirka (2001) and Johnston & Merrifield (2003). Such mechanisms play major roles in population and community structure of archipelago systems. These systems are usually characterized by a rich endemic marine biodiversity due to their isolation from continents. They often represent unique ecosystems with clearly established spatial limits. Marine species may respond to various aspects of the habitat's fragmentation that influence species richness, abundance, and distribution as well as biomass (Öhman & Rajasuriya 1998). In species with limited dispersal capacity, isolation by distance can occur.

The Cape Verde archipelago is a tropical oceanic ecosystem that is highly fragmented and dispersed, with islands and group of islands physically isolated by depths often greater than 3000 m. Geographic distance and bathymetry, along with other physical factors, likely induce various degrees of isolation between islands. Understanding how isolation in such a naturally fragmented ecosystem affects the overall ecological variability is a key issue for a better understanding of the Cape Verde marine population dynamics, community structure and biodiversity. Such understanding is necessary for planning sustainable marine exploitation. By using an extensive database of artisanal fisheries, the present work analyses how geographic distance and depth affect spatial and temporal structure and variability of exploited demersal fish communities of Cape Verde archipelago. It also examines how physical isolation explains the ecological variability among demersal fish communities in an archipelago system that has, until now, received little scientific attention.

1.2 Material and Methods

1.2.1 Site description

The Cape Verde archipelago is one of the four oceanic archipelagos belonging to the large biogeographic region of Macaronesia, which also includes Madeira, the Azores and the Canary Islands in the eastern Atlantic Ocean (Figure 1.1). With 4 033 km^2 of land, 1 020 km of coastline and an exclusive economic zone of 734 265 km^2 (Bravo de Laguna 1985), this archipelago is made up of ten volcanic islands and some islets. Seamounts also

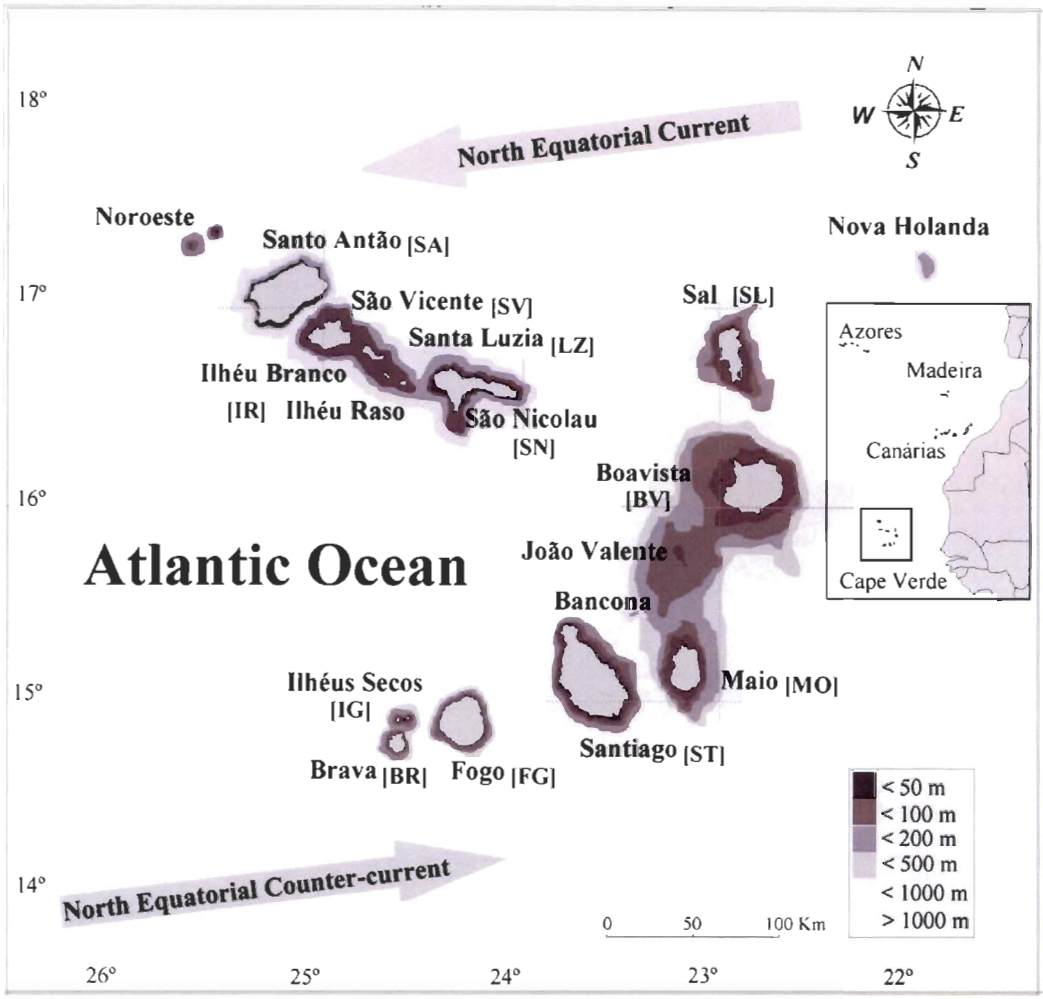

Figure 1.1

- Localisation de l'archipel du Cap-Vert dans la région biogéographique de la Macaronésie.
- Location of the Cape Verde archipelago in the biogeographic region of Macaronesia.

come close to the sea surface (Noroeste, Nova Holanda, Bancona and João Valente). The insular shelf slope is steep until 200 m depth and then less pronounced down to 1000 m (Bravo de Laguna 1985). There are a large variety of geographic distances and average depths between islands. The physical environment is largely under the influence of dominant winds. A group of islands, named locally "Barlavento" (Santo Antão [SA], São Vicente [SV], Santa Luzia [LZ], Ilhéus Raso and Branco [IR], São Nicolau [SN], Sal [SL] and Boavista [BV]), are located windward of the northeasterly trade winds. Another group, named "Sotavento" (Maio [MO], Santiago [ST], Fogo [FG], Brava [BR], Ilhéus Grande, de Cima and Luis Carneiro [IG]; the island abbreviations are used in Figure 1.5), are leeward of those winds.

Two main seasons are recognized during the year: a warm one from May to November and a cold one from December to April. The warm season is divided into a dry period between May and July, under the influence of Harmattan wind and dust from the Sahara, and a wet period from August to September, which is influenced by northeasterly Trade Winds from the Azores anti-cyclone and by southwesterly Trade Winds from the Santa Helena anti-cyclone. When rains occur on land, they are torrential, irregular and concentrated in the wet period (90%) according to topography and altitude (De Brum Ferreira 1989). Sea-surface temperature follows the average air temperature, varying from 18°C to 27°C during the year.

The islands are also under the strong influence of large-scale oceanic circulation, being on the southern boundary of the North Atlantic's northern anti-cyclonic circulation

and on the northern limit of the equatorial counter-current. These two systems of oceanic currents present seasonal variations that affect the circulation of the surface layer down to 200 m depth (Stramma & Siedler 1988).

1.2.2 Data source

The work presented here is based on the artisanal fishery database compiled by the Instituto Nacional de Desenvolvimento das Pescas (National Institute for Fisheries Development from Cape Verde, INDP). That database provides information about fishing boats, fishermen, fishing ground locations, trip date and duration, species identification and catches, from 1996 until the present. The database is supplied by a sampling plan which combines a stratified and a three-stage sampling design for units of unequal sizes as described in Medina (1995).

We used data collected from January 1996 to December 2002 (INDP 1996:2002). Each landing site was visited six times a month, and all active boats were sampled at each visit providing data on time at sea (in hours), fishing location and catch per fishing trip (in kilograms) for each species. Knowing the distance between landing ports and fishing sites as well as the average boat speed, time at sea was corrected to provide an estimate of the effective fishing time. Species abundance index was estimated as Catch Per Unit Effort (*CPUE*). For each island, monthly average *CPUE* for each species was estimated boat-by-boat as:

$$CPUE = \frac{\sum_{i=1}^{n} \frac{C_i}{f_i}}{n} \qquad (1)$$

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where C and f are respectively the catch (kg) and the fishing effort (h) of boat i, and n is the total number of observations during a month. Artisanal fishing is mainly coastal, practised with hand lines on artisanal wooden and opened boats of standard size between 3 and 6 m, propelled by an outboard engine of 15 HP. Because of technical limitations (storage capacity, communication facilities, etc) fishing units do not have autonomy at sea and thus fishing operations are carried out within a period of 24 hours in a limited range area (*ca* 10 km) around islands. In such a tropical ecosystem, demersal fisheries are multi-species; no particular commercial species is targeted and the whole catch is landed at 85 artisanal fishing ports, and sold on local markets. Due to these characteristics of the artisanal fishery, we do not expect variation in fishing power between boats, therefore, no standardization of *CPUE* was necessary. Since original data were expressed in weight, we used biomass of catches rather than number of individuals. This procedure could lead to biases when estimating dominance of larger than average individuals. However, in the structuring of the communities, each individual has an ecological cost proportional to its biomass (*i.e.* the part of the resources that it takes) as well as an ecological value (*i.e.* its contribution to the stability of the system). Very often, catch samples of demersal fish contain individuals of different lengths and at different stages of maturity and so they represent different ecological cost and value in the structuring of communities. Therefore, according to previous authors, the use of biomass units is recommended (Wihm 1968; Dickman 1968; Lyons1981; Jin & Tang 1996; Legendre & Legendre 1998).

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Winters & Wheeler (1985) present a general criticism in interpreting *CPUE* data as an abundance index without prior information on population spatial distribution. However, in this research we worked at an island scale. Thus, despite these general criticisms and precaution, we assume that the spatial distribution of *CPUE* of 1 354 standard artisanal boats fishing all year round on the 260 fishing sites dispersed on a cumulative shelf area of 5 394 km^2 (Bravo de Laguna 1985) over seven years, actually reflects the spatial distribution of demersal species and is representative of changes in the area occupied by demersal fish communities. As stated by Greenstreet & Hall (1996), examining fisheries data from a multi-species perspective is important because, for example, exploited species may be replaced by ecologically similar species differing only in their sensitivity to exploitation. So, for the purpose of this work, such a procedure seems quite adequate according to the nature of data available and the peculiarities of the fishery and ecosystem being studied.

1.2.3 Species selection

For the purpose of this study, the 18 most abundant species were selected (Table 1.1) from about 40 commercially important demersal fish. On one hand, such a choice warrants the availability of data for all species under study, and avoids missing values, which enhance the robustness of statistical analyses. On the other hand, dominant species determine the main biological characteristics of demersal communities and the non-target assemblages appear to remain relatively unchanged, despite long-term intensive fishing activity (Colvocoresses & Musick 1984; Greenstreet & Hall 1996; Jin & Tang 1996).

Tableau 1.1 Liste des principales espèces de poissons démersaux signalés dans la base de données de la pêche artisanale de l'INDP et sélectionnés pour la présente recherche.

Table 1.1 List of the main demersal fish species reported in the INDP artisanal fisheries database and selected for the present research.

INDP database code	Scientific name	English name	Local name
253	*Bodianus scrofa*	Barred hogfish	Bedja
259	*Lethrinus atlanticus*	Atlantic emperor	Bica de rocha
260	*Epinephelus marginatus*	Dusky grouper	Mero
268	*Apsilus fuscus*	African forktail snapper	Fatcho de fundo
270	*Lutjanus agennes*	Gorean snapper	Goraz
322	*Pseudupeneus prayensis*	West African goatfish	Salmonete
369	*Galeoides decadactylus*	Lesser African threadfin	Barbo
380	*Parapristipoma humile*	Guinean grunt	Papagaio
385	*Pomadasys incisus*	Bastard grunt	Besugo
394	*Priacanthus arenatus*	Atlantic bigeye	Façola
402	*Scarus hoefleri*	Guinean parrotfish	Bidião
452	*Scorpaena scrofa*	Largescaled scorpionfish	Fanhama
457	*Cephalopholis taeniops*	African hind	Garoupa
465	*Mycteroperca rubra*	Mottled grouper	Badejo
470	*Serranus atricauda*	Blacktail Comber	Manelinho
528	*Viridentex acromegalus*	Bulldog dentex	Bentelha
606	*Acanthurus monroviae*	Monrovia doctorfish	Barbeiro
699	*Seriola dumerili*	Greater amberjack	Esmoregal

Doubtful and false identifications were excluded from the data set, and only data corresponding to the identification level of species were considered.

1.2.4 Ecological indices

There is much ecological literature that focuses on the concept of species richness, seeking common approaches and frameworks for measuring population, community and ecosystem variability. All methods aim at reducing the high dimensionality of species abundance data to summarize community structure and each one is sensitive to specific aspects of structural variation. No single measure is therefore adequate to capture all community properties. Thus, according to ecological aspects that one seeks to highlight at a species, community or ecosystem level, it is often of interest to find the approach best adapted to the objectives of the research, able to provide the most robust conclusions. Ecological distance measures allow subsequent ordination methods, statistical approaches widely used in ecology to depict community structure and respective variation in space and time (Legendre & Legendre 1998; McCune & Grace 2002).

For the purposes of the present study, we considered each island as a finite community with several ecological niches characterized by a particular species richness, equitability and community structure. Therefore, based on the nature of the data available (fishery commercial data), we introduced an ecological index D_i based on species relative dominance between pairs of islands. Dominance is recognized as an important parameter of community structure that integrates the majority of the mathematical formulations of diversity indices and ecological distance measures (Frontier 1983; Legendre & Legendre

1998; Mouillot & Lepretre 2000). To assess the ecological distance between two islands *1* and *2*, we defined a relative dominance (D_i) of each species (i) in each island as the proportion of its biomass B_i at each island related to the total abundance of all species in the two islands:

$$D_i = \frac{B_i}{B_1 + B_2} \tag{2}$$

where B_1 and B_2 represent the total biomass of all species in each island. As stated by Legendre & Legendre (1998) species are basic units in the theory of the ecological niche each representing a genetic pool that shares ecosystem suitability and, in doing so, they are structured in communities. We assumed then that the value of D_i over space and time might be an indicator of variation in ecosystem suitability as perceived by a particular species and is an imprint of the community structure. The contribution of each species to the ecological distance between communities from two islands is the absolute value ΔD_i:

$$\Delta D_i = \frac{\left|B_{i,1} - B_{i,2}\right|}{B_1 + B_2} = \left|D_{i,1} - D_{i,2}\right| \tag{3}$$

Then we define an index of ecological distance between two islands, ΔD as the sum of ΔD_i for the n species recorded on the two islands:

$$\Delta D = \sum_{i=1}^{n} \Delta D_i \tag{4}$$

ΔD became a particular expression of Steinhaus's coefficient (Legendre & Legendre 1998). It varies between zero and unity respectively from identical to completely different community structure.

1.2.5 Effect of distance and bathymetry

In order to better understand how geographic distance and bathymetry can be integrated to explain ecological variability among islands, we propose a conceptual co-variation model for the most probable scenarios (Figure 1.2). In some cases, geographic distance may strengthen the bathymetric effect (positive covariance) by inflating isolation and variability between ecosystems (Figure 1.2 A and B). In other cases, geographic distance may counteract the bathymetric effect (negative covariance) either by reducing isolation and ecological variability between ecosystems (Figure 1.2 C) or by increasing isolation (Figure 1.2 D). Furthermore, particular situations exist where one of those variables masks the positive or negative effect of the other. This is the typical situation of suppressor variables, first introduced by Horst (1941) and widely reported in the scientific literature (Lancaster 1999; Mackinnon *et al.* 2000; Lynn 2003). Despite considerations about the deleterious effect of colinearity between independent variables and the recommended statistical procedures to exclude one of them from computations (Zar 1984), the computation of a first-order partial correlation has been recommended (Jolicoeur 1997; Legendre & Legendre 1998) in order to better describe the relationships between variables. It is then possible to distinguish between a positive (Figure 1.2 E and 1.2 F) or negative (Figure 1.2 G and 1.2 H) effect.

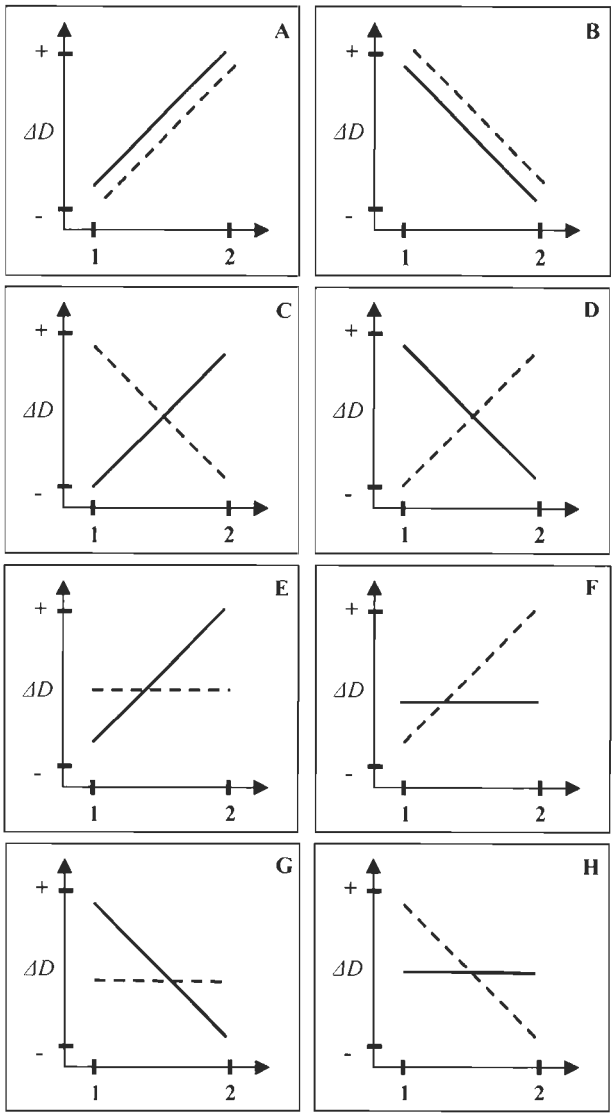

Figure 1.2

- Modèle conceptuel pour expliquer l'effet de la distance géographique (---) et de la bathymétrie (—) sur la dominance relative des espèces (D_i), et la variation de la structure des communautés entre les îles de l'archipel. Pour une espèce potentiellement dominante, D_i entre les îles 1 et 2 peut être influencée par une covariance positive (A et B), une covariance négative (C et D), une corrélation partielle positive (E et F) ou une corrélation partielle négative (G et H).

- Conceptual model to explain the effect of geographic distance (---) and bathymetry (—) on species relative dominance (D_i) and community structure variation among islands in an archipelago system. For a potentially dominant species, D_i between islands 1 and 2 may be affected by positive covariance (A and B), negative covariance (C and D), partial positive correlation (E and F) or partial negative correlation (G and H).

In the present work, the shortest geographic distances between pairs of islands (d), expressed in kilometers (km), were obtained by direct measurement on the Cape Verde archipelago map published by the United Kingdom Hydrographic Office (1989). Distances (d) vary from 6 km, between Brava Island and Secos islets, to 270 km, between Santo Antão and Maio islands. Average isobaths, expressed in meters (m), were obtained from Bravo de Laguna (1985) and data issued by IOC, IHO & BODC (2003). The mean depth between pairs of islands (b) was then calculated and it varies from 55 m between Brava Island and Secos islets to 3990 m between São Vicente and Fogo islands.

We investigated the relationship between species relative dominance (D_i), the geographic distance (d) and the average bathymetry (b). Islands were first compared two by two. A time series of D_i was calculated for each island, over the entire period and for all species. The two series of D_i were compared by a Pearson correlation analysis. A pair of islands was then characterized by (1) the correlation coefficient between D_i, (2) the geographical distance (d), and (3) the average bathymetry (b) between those islands. For the entire system, those parameters are represented in three square matrices that were compared by a series of Mantel tests (Dietz 1983; Smouse *et al.* 1986; Oden & Sokal 1992), which provided total and partial correlations between those three matrices. In order to meet conditions of normality, D_i values were log_2 transformed. Missing values and double zeros were excluded from computations.

Finally, to integrate mutual influence of distance and depth, we computed a physical isolation factor (I_{db}) as:

$$I_{db} = d \times b \quad (5)$$

Computed values of I_{db} varied from 0.33 km^2 between Brava island and Secos islets to 846 km^2 between Sal and Brava islands. In order to prevent scale measures effects, for statistical analysis I_{db} data were normalized.

1.2.6 Spatial and temporal variability

Firstly, we tested main effects on ΔD_i of year (Y, 7 levels), month (M, 12 levels) and species (S, 18 levels) with a three fixed-factor ANOVA without replication. Secondly, we investigated ecological variability between islands at two levels of organization (species and communities) with a series of analyses of covariance (ANCOVA). In a preliminary step, we carried out an ANCOVA between ΔD_i as the dependent variable and I_{db} as covariates for two factors (18 species levels - S, and 12 months levels – M) as independent qualitative variables. That analysis allowed us to define species groups and seasons. Next, we computed an ANCOVA between ΔD and I_{db} for those species groups (C: two levels) and for seasons (P: two levels).

Multivariate analyses were used to illustrate the spatial organization of the demersal fish community in the archipelago. The matrix of monthly average ΔD_i, with the 12 islands as observations and the 18 species as descriptors, was analysed with a PCA based on the Pearson correlation coefficient. To complement this analysis, we performed an agglomerative hierarchical clustering (AHC) for the same data matrix. Although single

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linkage is widely used as an agglomerative method to complement PCA (Legendre & Legendre 1998), we used a complete linkage method because we were mainly interested in a better contrast between islands or island groups. Finally, a complementary analysis of islands and species in the space of the first two PCA axes enabled us to study the variability between islands and the correlations between species in addition to the relationships between islands and species. For all statistical tests the null hypothesis was analyzed for an α error of 0.05. All statistical calculations were made with the XLSTAT-Pro v.7.5.3 software.

1.3 Results

1.3.1 Relationships between D_i, d and b

Linear correlations were not significant between D_i and d and between D_i and b but, highly significant between d and b (Mantel tests, Table 2). Partial correlation was highly significant as well between D_i and d and between D_i and b. It suggests that d and b interact as suppressor variables, masking a larger and significant correlation between each one of them and D_i.

Positive partial correlation between D_i and d, on one hand, and negative partial correlation between D_i and b, in the other hand, shows that, for potentially dominant species, distance and depth do not affect community structure in the same way (Table 2). Increasing the geographic distance while average depth remains constant will increase D_i (positive partial correlation); reciprocally, increasing the average depth while geographic distance remains constant will decrease D_i (negative partial correlation).

Tableau 1.2 Corrélations linéaires et partielles de première ordre (en gras) à partir d'un test de Mantel entre trois matrices symétriques [corrélation *r* entre log_2D_i], [distance géographique *d*] et [bathymétrie moyenne *b*]. Les tests ont été réalisés avec un nombre exhaustive de permutations

Table 1.2 Linear and first-order partial correlations (in bold) from a Mantel test computed between three symmetrical matrices [*r* correlation between log_2D_i], [geographical distance *d*] and [average depth *b*]. Tests were performed for an exhaustive number of permutations.

Matrix	Linear correlation	Partial correlation	*p*
$\log_2 D_i$ x b	0.156	-	0.11
log_2D_i x *d*	0.077	-	0.441
b x *d*	0.945	-	< 0.0001
log_2D_i x *d*| *b*	-	**0.779**	**< 0.0001**
log_2D_i x *b*| *d*	-	**- 0.698**	**< 0.0001**

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1.3.2 Relation between ΔD_i, ΔD and I_{db}

Results indicate that ΔD_i is highly related to species, year and month (ANOVA, S: $F_{17,\ 7845} = 473.23$, $p<0.001$; Y: ($F_{7,\ 7845} = 37.181$, $p<0.001$; M: $F_{11,\ 7845} = 233.626$; $p<0.001$). Monthly patterns are consistent between years (interactions between Y and M: $F_{66,\ 7845} = 0.917$, $p = 0.484$ *n.s.*). Despite a year effect, no particular trend was observed in the time series. However, S and Y show significant interaction ($F_{187,\ 7845} = 7.295$, $p = 0.000$) illustrating the existence of a strong monthly pattern in ΔD_i, common to all species.

Following these results, to assess relationships between ΔD_i and I_{db}, further analyses were carried out on an "average year", calculated from monthly averaged ΔD_i. We observe a significant effect of month and species on the covariance between ΔD_i and I_{db} (Table 1.3, upper panel). By evaluating the significant amount of information brought by each variable and parameter to the model *i.e.* their degree of statistical sifnificance, we distinguish two seasons (P_1: January, February, March, April and December; P_2: May, June, July, August, September, October and November) and two discrete species group (C_1: 253, 259, 270, 322, 369, 402, 606; C_2: 260, 268, 380, 385, 394, 452, 457, 465, 470, 528, 699; see species' identifications in Table 1.1).

Then, ΔD was computed between islands for the two defined seasons (2 levels - P_1 and P_2) and species groups (2 levels - C_1 and C_2), and its spatial and temporal variability was studied by further ANCOVA (Table 1.3, lower panel). Results indicate a significant covariance between ΔD and I_{db}, which is different between seasons and between species groups. It is particularly interesting to note that using seasons (P) and species groups (C) instead of month (M) and species (S) does not cause any significant deviation from the general covariation model, which shows the robustness of our approach.

Tableau 1.3 Résultats d'une ANCOVA entre ΔD_i (niveau espèce) et ΔD (niveau communauté) comme variables dépendantes et I_{db} comme co-variable. Le panneau supérieure du tableau montre des effets du mois (M) et de l'espèces (S). Le panneau inférieur montre des effets de la saison (P) et du groupe d'espèces (C).

Table 1.3 Results from the ANCOVA between ΔD_i (species level) and ΔD (community level) as dependent variables and I_{db} as covariates. The upper panel of the table shows months (M) and species (S) effects. The lower panel shows season (P) and species group (C) effects.

Dependent variable	Source	*df*	Sum of squares	Mean square	Fisher's F	*p*
ΔD_i ($r^2 = 0.619$)	I_{db}	1	163.988	166.351	5626.995	< 0.0001
	M	11	43.046	3.272	134.279	< 0.0001
	S	17	34.009	2.282	68.644	< 0.0001
	M x S	187	3.737	0.019	0.686	0.999
	$M \times I_{db}$	11	0.409	0.040	1.276	0.231
	$S \times I_{db}$	17	0.331	0.019	0.668	0.837
	Error	4742	138.196	0.029		
ΔD ($r^2 = 0.806$)	I_{db}	1	2.224	2.224	265.634	< 0.0001
	P	1	1.711	1.711	204.324	< 0.0001
	C	1	0.530	0.530	63.356	< 0.0001
	P x C	1	0.019	0.019	2.267	0.135
	$P \times I_{db}$	1	0.007	0.007	0.795	0.374
	$C \times I_{db}$	1	0.033	0.033	3.962	0.049
	Error	122	1.022	0.008		

On one hand, a main seasonal effect and the absence of interaction between P and I_{db} reveal an important influence of I_{db} on the ecological distance ΔD between islands, not varying from one season to another. On the other hand, a significant interaction between species groups and I_{db} suggests that those groups do not follow the same pattern. Species seem to behave differently in the same season.

The whole statistical analysis led us to a general covariance model illustrating the influence of I_{db} on ΔD between islands. The ecological distance between islands varies between two seasons, being higher during the warm than the cold season (Figure 1.3 A, Table 1.4). Within each season one group of species (C_1) was less sensitive to the isolation factor (I_{db}) than the other one (C_2) (Figure 1.3 B, 1.3 C and Table 1.4). The seasonal pattern is illustrated by the variation of the ecological distance index ΔD averaged by month from January to December (Figure 1.4); the index is lower during the cold season. According to the standard deviation, ΔD seems to be more stable during the warm season.

1.3.3 Island and community structure

Results of the PCA and of the AHC, illustrated by a Wroclaw diagram, show a clear geographic pattern of monthly average species' ΔD_i. Islands are grouped according to degree of physical isolation and ecological similarities (Figure 1.5) and species are assembled according to their contribution to the ecological distance between islands. Moreover, a superposition of the two factorial spaces (islands and species) in the PCA led us to recognize a significant association between islands and species (Figure 1.6).

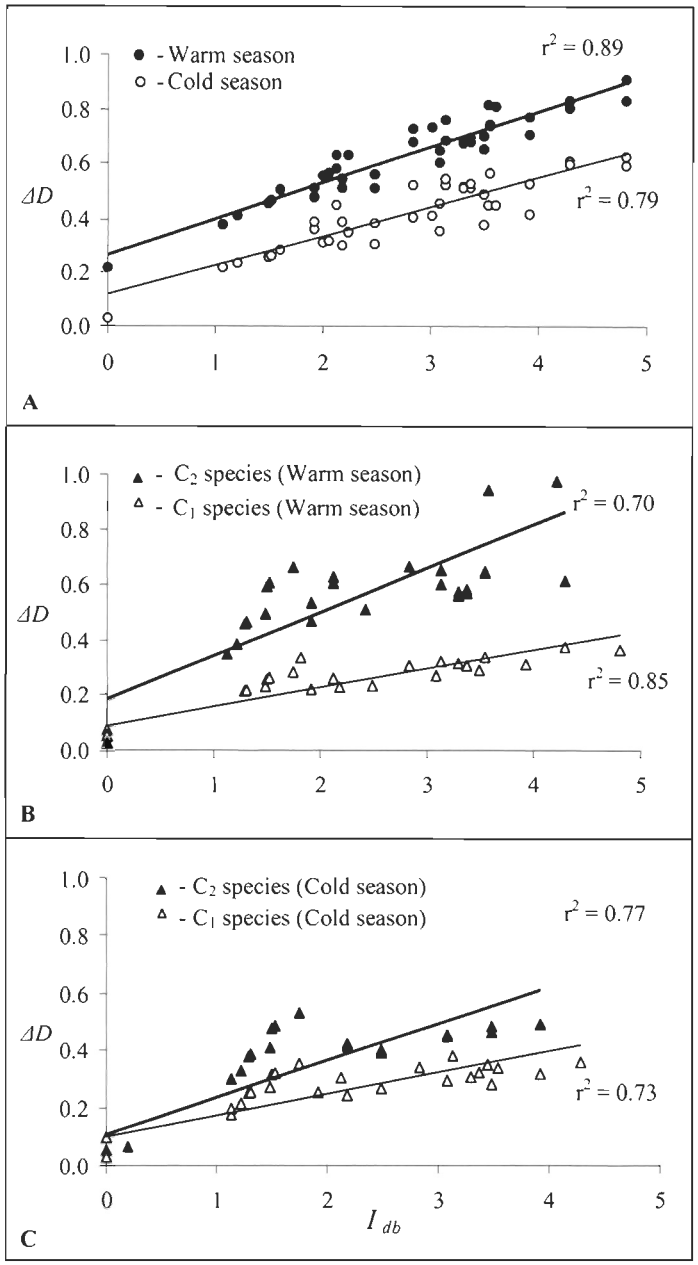

Figure 1.3

- Modèles de covariance entre la variation de la structure des communautés (ΔD) et l'isolement physique (I_{db}) entre les îles du Cap-Vert selon des patrons temporels différents en deux saisons: froide de décembre à avril et chaud de mai à novembre (A) et des groupes d'espèces montrant deux niveaux de sensibilité (B et C).

- Covariance models between community structure variation (ΔD) and physical isolation (I_{db}) among Cape Verde islands according to temporal patterns with two different seasons: cold from December to April and warm May to November (A) and species groups showing two levels of sensitivity (B and C).

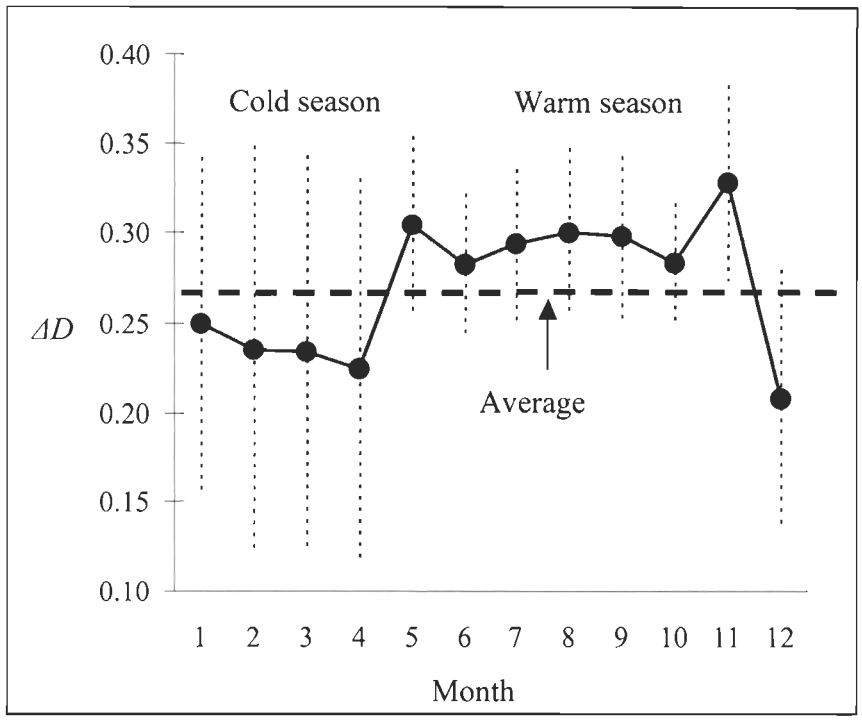

Figure 1.4

- Variation mensuelle de la distance écologique (ΔD). Deux saisons principales sont illustrées: froide, de décembre à avril, plus variable, avec un faible niveau de ΔD et une tendance négative; chaude, de mai à novembre, avec un niveau plus élevé de ΔD et apparemment plus stable. Les barres d'erreur représentent l'écart type.

- Monthly variation of ecological distance (ΔD). Two main seasons are illustrated: cold, from December to April, more variable, with lower level of ΔD and a negative trend; warm, from May to November, with a higher level of ΔD and apparently more stable. Error bars are standard deviation

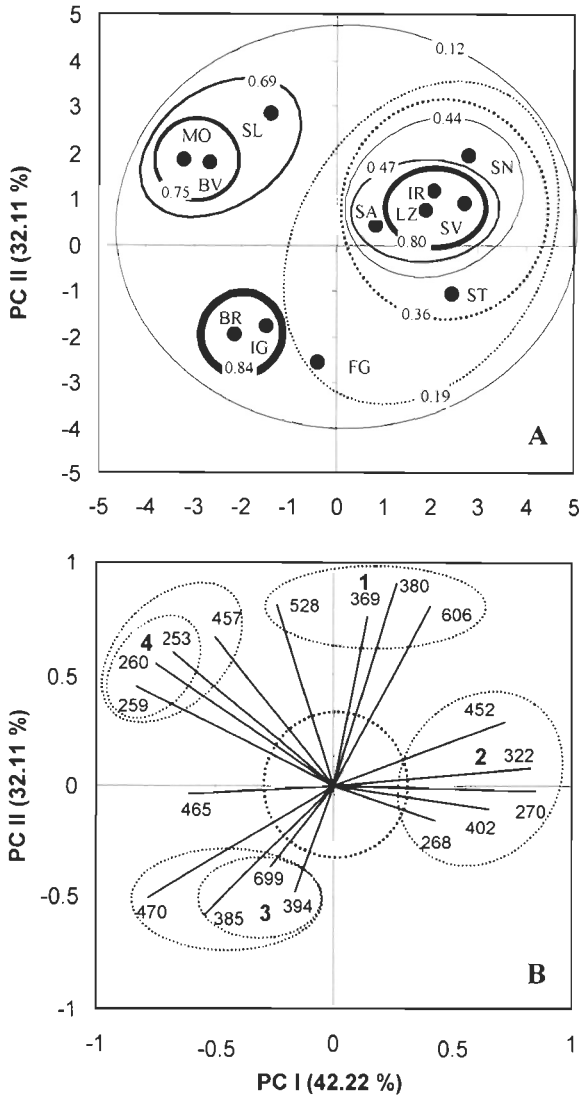

Figure 1.5

- Patrons spatiaux entre les îles du Cap-Vert déterminés par Analyse en Composantes Principales (ACP) et Groupement Agglomératif Hiérarchique (GAH) sur une matrice de corrélation de Pearson entre les ΔD_i des 18 espèces de poissons. A) Structure des îles en fonction de deux premiers axes et diagramme de Wroclaw pour différents niveaux de similarité entre les îles (voir texte). B) Corrélation entre les espèces selon les deux premiers axes. Le cercle au centre (rayon = 0.333) représente la contribution équilibrée des espèces aux deux axes. Les chiffres en gras représentent des assemblages de poissons, les autres chiffres représentent les codes des espèces (voir le tableau 1.2).

- Spatial patterns among Cape Verde islands determined by PCA and HAC computed with a Pearson correlation matrix between ΔD_i from 18 demersal fishes. A) Island structure according to the first two axes and a Wroclaw diagram drawn for different levels of similarity between islands (see text). B) Species correlation according to the two first axes. The central circle (radius 0.333) represents the balanced contribution of species to the two axes. Numbers in bold represent fish assemblages, other numbers represent species codes (see table 1.2).

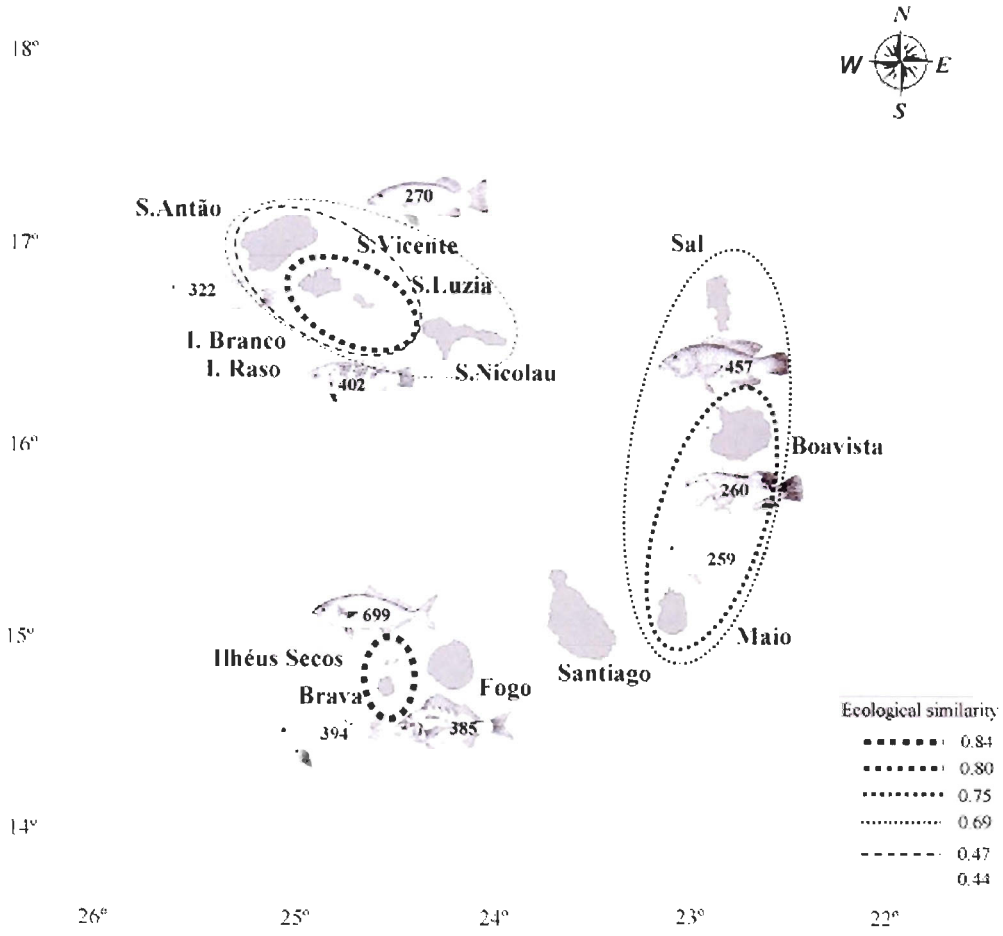

Figure 1.6

- Carte de similarité écologique dérivée de l'analyse ACP entre les populations de poissons démersaux du Cap-Vert montrant un patron de variabilité écologique induit par le facteur d'isolement physique (distance géographique et profondeur moyenne). Pour simplifier l'illustration, seulement les espèces les plus discriminantes sont représentées (voir la figure 1.5 et le tableau 1.1). Celles de l'assemblage 1 sont associées aussi bien aux îles du Nord qu'àu îles du Sud.

- Map of ecological similarity derived from PCA analysis among demersal fish populations from Cape Verde Islands showing pattern of ecological variability, driven by a physical isolation factor (geographic distance and average depth). For illustration purpose, only the most discriminating species are represented (see Figure 1.5 and table 1.1). Species from assemblage 1 are associated to the northern islands as well as to the southern ones.

At a high similarity level (≥ 0.80), a group is formed by Brava and the Secos islets, in the southern part of the archipelago, and another one by São Vicente, Santa Luzia and Raso islet in the northern part. Those two island groups are well correlated but, in an opposite way, explaining 42.2 % of the total variance. Such a correlation seems to be related to two different species assemblages. While the northern group appears to be more associated with *Apsilus fuscus* - 268, *Lutjanus agennes* - 270, *Pseudupeneus payensis* - 322, *Scarus hoefleri* - 402 and *Scorpaena scrofa* – 452 (assemblage 1), the southern group is better characterised by *Serranus atricauda* - 470, *Pomadasys incisus* -385, *Priacanthus arenatus* -394 and *Seriola dumerili* –699 (assemblage 3). In the east, Sal, Boavista and Maio form another group at 0.69 similarity, but Maio and Boavista are more strongly linked, with a higher similarity (0.75). This group appears to be associated with *Bodianus scrofa* - 253, *Lethrinus atlanticus* -259 and *Epinephelus marginatus* – 260 (assemblage 4). *Cephalopholis taeniops* - 457 is weakly linked to this assemblage and seems well correlated with Sal Island. This later islands-species association explains 32.1% of the total variance. In almost complete contrast to assemblage 3, species from assemblage 1 (*Parapristipoma humile* -380, *Galeoides decadactylus* - 369, *Virididentex acromegalus* - 528 and *Acanthurus monroviae* - 606) can be considered intermediate between assemblage 2 and 4 in structuring the northern and eastern islands groups. At lower similarities, Santo Antão and São Nicolau tend to be linked with the northern group, while Santiago and Fogo islands remain isolated. The species *Mycteroperca rubra* (465) is strongly and negatively correlated with assemblage 2, but is not associated with any assemblage.

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1.4 Discussion

A large variety of ecological indices are used to assess ecological variability and community structures. In the present research, we used an ecological index based on species relative dominance that also measures species contribution to community structure variation between two islands. Such contribution is measured by the relative dominance of each species on the total species biomass of the two communities. This approach was the most appropriate given the nature of the available data. In fact, interpreting community structure based on commercial fisheries data can be distorted because these data are neither random nor exhaustive and fished communities cannot be assumed to function naturally. In fact, commercial fisheries result from a complex interaction among several factors related to fishers' strategy (Salthaug & Godø 2001). Even in the situation of a mixed fishery (Ketchen 1964; Chadwick & O'Boyle 1990), the data do not represent all species from exploited communities. However, in the system under study, artisanal fishermen sample the fish density around islands in a time invariant process without definite fleet tactics. In such a case where fishing process does not change, CPUE data can be used to construct a time series of comparable abundance indices (Petitgas 1998). The monthly and annual variation patterns of these indices on the main fishing grounds can be indicative of a population's complexity and allow the assessment of spatial and temporal variations in abundance (Begg & Waldman 1999). Thus the use of classical approaches, either synthetic measurements like the Shannon-Weaver, Simpson, Hill and McIntosh indices (Frontier 1983; Legendre & Legendre 1998) or analytical procedures like rank-frequency diagrams (Frontier 1983;

Mouillot & Lepretre 2000), are not very useful in such a situation because of their sensitivity to species richness. The approach we propose in the present study to assess community structure variation has the advantage of being mainly sensitive to species abundance distribution rather than to species richness and so is useful in a context where only fisheries data are available.

The relationship among species relative dominance, geographic distance and average depth allow us to highlight an important ecological feature of the species–habitat dynamics in the Cape Verde archipelago that may be applicable to similar systems. Depth and distance are partially correlated with species relative dominance but in opposite ways, which led us to propose a niche effect associated with variation in shelf area and thus, in space availability. On one hand, increasing geographic distance with a constant average depth means more space available and thus improves general suitability of the habitat for potentially dominant species in a particular area. Consequently D_i will increase. On the other hand, an increase in the average depth for the same geographic distance would decrease the space available and reduce general habitat suitability. As a result, D_i will decrease because a species has less space available to express its dominance. From the ecological point of view, since space availability is the physical support of biotic and abiotic conditions within which the species can exist, such aspects seem to be important for the dynamics of species use of space and are related to ecosystem resource partitioning. Hence, it seems to be an important factor structuring demersal fish assemblages. This rationale corresponds to the MacArthur (1957) hypothesis about environment structure and relative abundance of birds in an equilibrium or near-equilibrium population. However the

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present study considers two spatial scales: (1) at an island scale, niches seem to be continuous and non-overlapping and (2) at an archipelago scale, niches are obviously discrete.

The rate of expansion and contraction of a population within a distribution area is unlikely to be uniform since habitat conditions will be less favourable at the extremes than at the centre (Winters & Wheeler 1985). In terms of the amount and arrangement of favourable habitats, the spatial correlation between geographic distance and depth is particularly important in determining the overall suitability of the environment (Hiebeler 2000). In a heterogeneous and naturally fragmented landscape like the Cape Verde archipelago, this is particularly important for theoretical studies on the dynamics of population abundance and density (MacCall 1990; Petitgas 1998; Hiebeler 2000).

The computation of a physical isolation factor based on geographic distance and average depth between islands allows the integration of their effects and mutual interactions into a single variable whose covariance was tested against community structure variation indices. The rejection of the null hypothesis with such an approach has suggested that, for the Cape Verde archipelago, physical isolation is an important factor that drives ecological isolation among islands. Such ecological isolation varies through the year according to two distinct seasons that are separated by different wind and temperature regimes. The shorter cold season from December to April seems to be more unstable and shows lower ecological variability than the warmer one, from May to November, which appears to be more stable. This observation leads us to formulate the hypothesis that, in the Cape Verde archipelago, ecological isolation between islands is affected by different hydrodynamic regimes between

cold and warm seasons. This dynamic process would be regulated, *inter alia*, by the correlation between the average depth and the distance between islands. Although this assumption will have to be validated by knowledge of oceanic circulation around Cape Verde islands, such information does not yet exist. However, it is well known that wind and temperature variations favour turbulent mixing processes in the water column as well as near the bottom (Spall 2000; Jirka 2001; Johnston & Merrifield 2003) and in archipelago systems, these process are frequently related to jet current flows between islands (Xie *et al.* 2001).

For the species considered, physical isolation does not affect their relative dominance with the same intensity during the same season. We could distinguish between more sensitive species, dominated by Seranidae (*C. taeniops*, *S. atricauda*, *M. rubra* and *E. marginatus*) and Haemulidae (*P. humile* and *P. incisus*), followed by six other families, each one represented by a single species, and less sensitive species, represented by seven families with one species each. These differences in behaviour can be related to interactions between spatial and temporal features affecting their distribution. Species with coastal and shallow distributions throughout the year are expected to be less sensitive that those with a broader and deeper distribution. However, these demersal fishes are mostly sedentary and reef-associated, colonizing rocky or sandy bottoms on the coastal zones around islands. Thus, at least at the juvenile stage, such different behaviours with respect to ecological isolation would be complex to understand. However, species dispersal capability can vary with development stage. Thus, we hypothesize that the main significant interactions between physical and hydrodynamic features, that affect species dispersal and distribution,

probably occur during spawning or early life stages. For the Cape Verde archipelago, no information exists about flows of energy, materials, or organisms across island boundaries. This is a major aspect of the theory of island biogeography (MacArthur & Wilson 1967), and its generalisation in neutral theory (Hubbell 1997, 2001). Aside from the recent debate on these theories, both supportive (Volkov *et al.* 2003; Hubbell 2006) and critical (McGill 2003; Wootton 2004), the main assumption of ecological equivalence in communities constrained by dispersal and recruitment seems to limit the applicability of such theories in very heterogeneous and dynamic systems like coral reefs (Dornelas *et al.* 2006) or archipelagos such as Cape Verde. However, future research on this matter can contribute understanding of ecological variability in the context of functional ecology and the design of appropriate conservation and management strategies.

Community structure shows a geographic pattern according to the physical isolation factor, which suggests that demersal communities are affected by geographic distance and depth. Similar results have been found recently for the genetic structure of gastropod populations (*Conus* sp.) in the Eastern Cape Verde islands (Duda & Rolán 2005). These authors found that species from Boavista and Maio islands are genetically more similar to each other than they are to species from Sal islands. In fact, the migration of species between Boavista and Maio has apparently been more common than between Sal and Boavista. This phenomenon seems to be facilitated by stronger ecological isolation (I_{db}) between the two later islands. Despite the importance of oceanographic influences on larval dispersal and their consequences for population connectivity (Werner *et al.* 1997; Cowen 2002), we believe that the long-term persistence of such physical isolation between islands

might be at the origin of important speciation processes, resulting in high marine biodiversity at the genetic, specific, taxonomic, ecological and functional levels (Medina *et al* 2002 b).

Because there has been no other scientific research on the population structure among the Cape Verde islands related to how fishing affects genetic resources and biodiversity, we suggest that, for conservation and management purposes, populations from spatially distinct islands or islands groups, as identified in the present study, should be considered as discrete management units. As stated by Stephenson (1999), aside from the debate on the basic premise behind the modern concept of a stock (Booke 1999; Swain & Foote 1999), this is particularly important as part of a precautionary approach to fisheries management (FAO 1995) and to topical discussions of the potential value of Marine Protected Areas.

Several physical and geographical features are common among archipelagos from the large biogeographic region of Macaronesia (Cape Verde, Madeira, Azores and the Canary Islands). It would be interesting to test the approach we propose here in a broader context in order to study ecological variability and demersal population structure in the context of archipelago systems. However, the spatial and temporal patterns of the hydrodynamic features that are expected to influence ecological isolation must be included in such a research program.

Among significant scientific questions to be addressed related to geographic distance, depth and ecological isolation in the study area, it will be of great interest to investigate the population spatial dynamics of the main demersal species on the insular

shelf and how they can be related to seasonal and annual variations in population abundance. In order to prevent and control the unknown effect of fishing, it would be desirable to combine commercial fisheries and survey data (Fox & Starr 1996; Petitgas *et al*. 2003; Verdoit *et al.* 2003). Furthermore, to address how such ecological isolation affects population genetic structure and dynamics, more data are needed on the population genetics of marine species in the archipelago. Although recent research has begun to address this issue (De Wolf *et al.* 1998 a, b, c, d, 2000; Duda & Rolán 2005), these studies were mainly concerned with molluscs. Because of the ecological complexity of such tropical oceanic systems, it will be advantageous to direct research efforts toward a greater diversity of *taxa*.

CHAPITRE 2

DENSITY-INDEPENDENT HABITAT SELECTION AS A COMMON SPATIAL DYNAMICS FOR MARINE DEMERSAL SPECIES IN ARCHIPELAGOS SYSTEMS. THE CASE OF CAPE VERDE ISLANDS (EASTERN ATLANTIC OCEAN)

Article à soumettre

Résumé

À partir des données de pêche artisanale, le présent travail vise à analyser la dynamique spatiale des populations exploitées de poissons démersaux dans l'environnement fragmenté de l'archipel du Cap-Vert. Il analyse la dynamique spatiale à deux niveaux d'organisation, espèces et communauté, représentée par l'assemblage de 18 espèces les plus abondantes. Des courbes d'agrégation géostatistiques sont employées pour étudier la relation entre la densité et l'abondance locale des populations. Elles sont calculées à l'échelle des îles pour des années et des saisons présentant des abondances contrastées. De telles courbes sont interprétées à la lumière de quatre principaux modèles conceptuels en écologie de poissons marins. Au niveau de l'assemblage, les résultats montrent deux types de dynamique: un modèle de densité différentielle est associé aux îles présentant un plateau relativement large; un modèle de densité proportionnelle est observé dans les îles confinées par l'exiguïté de leur plateau. Les résultats obtenus au niveau de l'espèce indiquent l'existence d'une dynamique à densité proportionnelle, indépendamment du modèle observé au niveau de l'assemblage. Aux deux niveaux, la dynamique spatiale est indépendante de la densité et semble être principalement conditionnée par des facteurs environnementaux. Dans un tel écosystème fragmenté, l'abondance et la distribution de populations sont fortement contraintes par l'exiguïté des plateaux insulaires et donc la distribution libre idéale des poissons n'est pas susceptible de se produire. Les espèces tendent à maximiser leur niche écologique dans les situations où la disponibilité de l'espace est un facteur critique. Ces résultats recommandent des précautions spéciales de gestion, en particulier dans les régions où la dynamique spatiale est caractérisée par une variation différentielle de la densité locale, car la concentration exagérée des flottilles de pêche artisanale sur des bancs de pêche particuliers pourrait produire des perturbations importantes de l'écosystème par une surexploitation locale.

Mots clés: Système d'archipel, assemblages de poissons démersaux, courbes d'agrégation géostatistique, dynamique spatiale, sélection d'habitats, indice de sélectivité de l'espace.

Abstract

Based on artisanal fisheries data, the present work aims to analyze the spatial dynamics of exploited demersal fish populations in the fragmented environment of Cape Verde archipelago. It analyses the spatial dynamics at two organisation levels, single-species and fish community, represented by the assemblage of 18 most abundant species. Geostatistical aggregation curves are used to study the relationships between local density and population abundance. They are computed at islands scales for years and seasons of contrasting abundance levels. Such curves are interpreted in the light of four key conceptual models in marine fish ecology. At the assemblage level, the results show two types of dynamics: a differential density model is associated with islands presenting a relatively wide shelf area, a proportional density dynamic is found in islands confined by the narrowness of their shelf. Results obtained at species level reveal the existence of proportional density dynamics, independently of the model observed at assemblage level. At both levels, spatial dynamics are density-independent and appear to be mainly constrained by environmental factors. In such a fragmented ecosystem, population abundance and distribution are strongly constrained by the insular shelf tightness and an ideal free distribution of fish is not likely to occur. Species tend to maximise their ecological niches in situations where space availability is a critical factor. Those results point out special management precautions, particularly in regions where spatial dynamics are characterized by a differential variation of local density since the exaggerated concentration of the artisanal fishing fleets on particular fishing grounds could generate important perturbations of the ecosystem by local overfishing.

Key words: Archipelago system, demersal fish assemblages, geostatistical aggregation curves, spatial dynamic, habitat-selection, space selectivity index.

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2.1 Introduction

It is known that fishing success depends on fisher's behaviour but also obviously depends on fish abundance and distribution (Swain & Sinclair 1994; Gauthiez 1997). Therefore, understanding strategies of space occupation by marine populations and communities represents a key issue for stock assessment and management. Those strategies are also important factors to be considered for stock unit's identification in relation to exploitation and conservation policies (Fréon & Misund 1999).

Relationships between the spatial distribution of populations and their abundance have often been the basis of studies on biogeography of marine fishes. Several approaches analyze those relationships by calculating dispersion indices and by means of geometrical analyses. Those approaches aim to provide information on underlying mechanisms of habitat selection (Fréon & Misund 1999). Among those mechanisms, density-dependent habitat selection has been described for pelagic (MacCall 1990; Fréon & Misund 1999) and demersal (Swain & Wade 1993; Swain & Morin 1996; Petitgas 1998) fish populations as an application of the theory of the ideal free distribution. This theory assumes that individuals have a complete knowledge of their environment, they are free to move between habitats and adopt the foraging strategy that maximizes their net energy intake per unit of time. At low abundance, only the best habitats should be occupied. As abundance increases, individuals should begin to occupy marginal habitats as profit rate in the best habitats decreases due to competition. As a result of such a behaviour, population range should expand as population size increases. Thus, if distribution range is proportional to population size, catchability will increase as abundance decreases (Winters & Wheeler

1985; Crecco & Overholtz 1990; MacCall 1990; Swain & Wade 1993; Swain & Sinclair 1994; Swain & Morin 1996; Atkinson *et al.*1997; Swain & Benoît 2006).

Murawski & Finn (1988) studied species distribution in relation to environment, using a spatial dispersion index based on individuals' average distance from the mean geographical position of the population. Swain & Wade (1993) and Swain & Sinclair (1994) developed abundance-independent indices of spatial distribution, based on the estimation of an area for which density values exceed a definite threshold, either in absolute or relative value. Atkinson *et al.* (1997) used a statistical bivariate ellipse to describe changes in the geographical position of Northern Cod (*Gadus morhua*) catches.

Petitgas (1998) developed a geometrical analysis with distribution indices based on geostatistical aggregation curves to study the spatial dynamics of young Hake (*Merluccius merluccius*) in the Bay of Biscay and pelagic fishes on the Senegalese continental shelf. That author described conceptual models for marine fish distribution, comparing the geographic patterns of density at different population sizes and the relative rate of changes in local density.

In the majority of studies related to mechanisms by which species occupy their habitat, spatial scale is of crucial importance, as biological and physical processes interact differently at different scales (Mason & Brandt 1999; Shepherd & Litvak 2004). Spatial scale is of crucial importance in the understanding of the ecology of very heterogeneous environments. In fact, in those systems, multiple mechanisms may generate a large variety of patterns that are scale-dependent which may vary across different spatial and temporal scales. Archipelago systems appear to be particular cases of such heterogeneous

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environments. They are naturally fragmented by physical factors and present various degrees of ecological isolation and variability between islands (Medina *et al* 2007). In those archipelagos, depth and geographical distance are isolation factors that can play a significant role in space availability, determining the overall suitability of the environment (Hiebeler 2000; Shepherd & Litvak 2004). Despite their ecological interest, such systems have received limited scientific attentions on studies of population spatial dynamics.

Cape Verde archipelago represents a tropical oceanic ecosystem, highly fragmented and very dispersed. Based on artisanal fisheries data and using theoretical concepts of spatial dynamics, the present work aims to analyze the spatial and temporal distribution of exploited demersal fish populations on insular shelves. We studied the relationship between local density and population abundance by means of geostatistical aggregation curves proposed by Petitgas (1998) at different space-time scales (islands, years and seasons) for different ecological organization levels (species and species assemblage). Different graphical configurations of such curves were finally interpreted in the light of conceptual models in marine fish ecology.

2.2 Material and Methods

2.2.1 Site description

The present research was carried on in the Cape Verde archipelago, one of the four oceanic archipelagos belonging to the large biogeographic region of Macaronesia, which also includes Madeira, Azores and Canary Islands in the Eastern Atlantic Ocean (Figure 2.1).

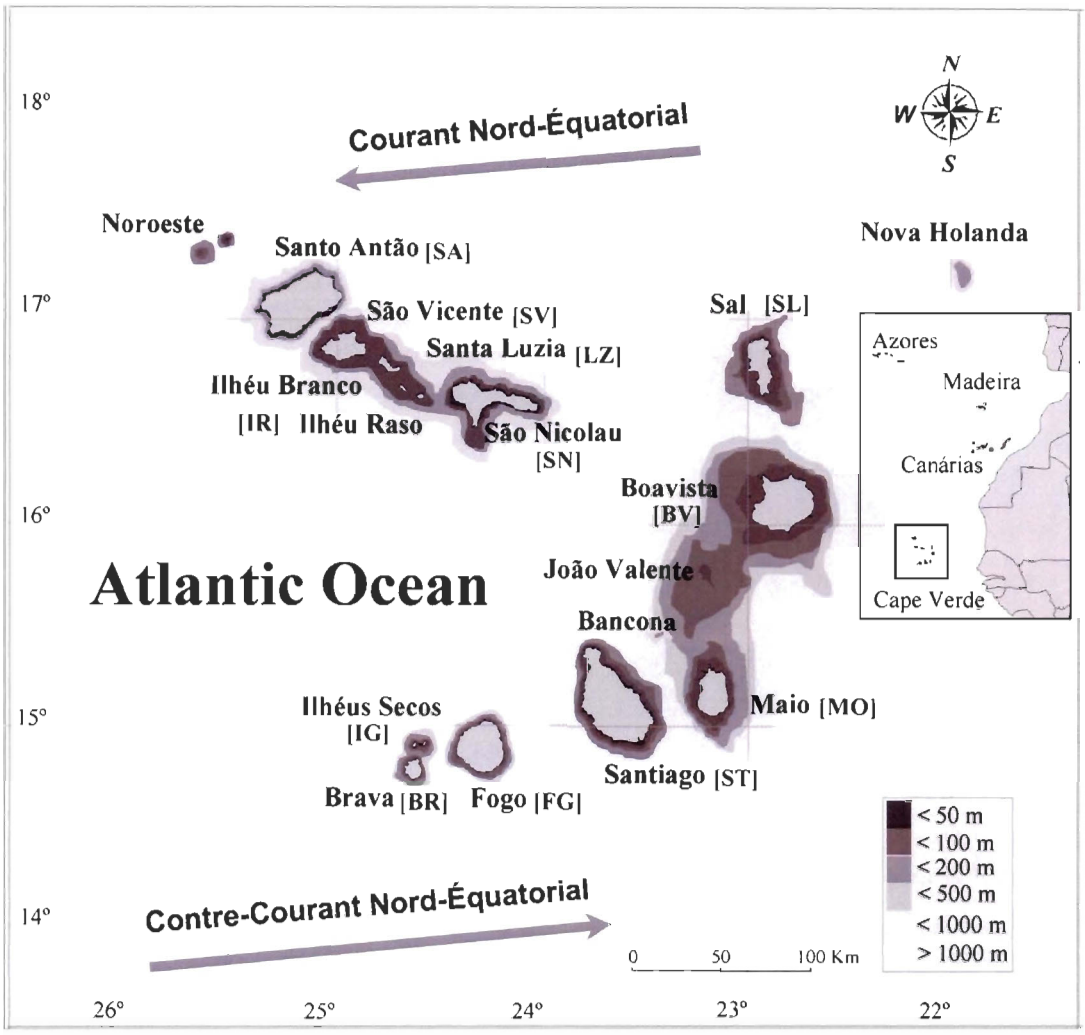

Figure 2.1

- Localisation de l'archipel du Cap-Vert. La carte insérée représente la localisation de l'archipel du Cap-Vert dans la région biogéographique de la Macaronésie (*In :* Medina *et al.* 2007).

- Location of the Cape Verde archipelago. Insert map represents location of Cape Verde archipelago within Macaronesia biogeographic region (from Medina *et al.* 2007).

The Cape Verde archipelago is composed by ten volcanic islands, several islets and some seamounts close to the sea surface. It represents 4 033 km^2 of land, 1 020 km of coast line and a insular shelf of 5 394 km^2 down to 200 m depth (Bravo de Laguna 1985). The physical environment is largely under the influence of dominant winds and large-scale oceanic circulation, being on the southern boundary of the North Atlantic's northern anti-cyclonic circulation and on the northern limit of the equatorial counter-current (Stramma & Siedler 1988). A group of islands and islets, named locally "Barlavento" (Santo Antão [SA], São Vicente [SV], Santa Luzia [LZ], Ilhéus Raso and Branco [IR], São Nicolau [SN], Sal [SL] and Boavista [BV]), are located windward of the northeasterly trade winds. Another group, named "Sotavento" (Maio [MO], Santiago [ST], Fogo [FG], Brava [BR], Ilhéus Grande, de Cima and Luis Carneiro [IG]; the island abbreviations are used in the text), are leeward of those winds. Sea-surface temperature follows the average air temperature, varying from 18 °C to 27 °C during the year. Two main seasons are recognized: a warm one from May to November and a cold one from December to April. During warm season, a dry period can be identified between May and July, under the influence of Harmattan wind and dust from the Sahara, and a wet period from August to September. The wet period is influenced by northeasterly Trade Winds from the Azores anti-cyclone and by southwesterly Trade Winds from the Santa Helena anti-cyclone. When rains occur, they are torrential, irregular and concentrated in the wet period (90%) according to topography and altitude (De Brum Ferreira, 1989).

2.2.2 Methodological approach

The present work is based on geostatistical aggregations, or concentration curves, which are statistical tools of current use in mining science. They describe the relation between the mineral tonnage and the mineral content of a definite surface. Geostatistical tools have increasingly been used in fisheries and marine ecology, either to optimise sampling strategies (Petitgas 1996) and stock assessment (Petitgas 1993; Fernandes & Rivoirard, 1999), or to map distributions and spatial patterns of fishes (Simard *et al.* 1992; Petitgas 1998; Barange *et al.* 2005; Stelzenmüller *et al.* 2006). Mathematical formulations were originally proposed by Matheron (1981) and were further adapted by Petitgas (1998) to fisheries data.

In such an approach, two kinds of data are necessary: species' abundance on the fishing grounds and area of species' distribution. As described below, abundance data were obtained from the artisanal fishery database compiled by the *Instituto Nacional de Desenvolvimento das Pescas* (Cape Verde National Institute for Fisheries Development, INDP). Data on spatial distribution of demersal species were taken in reference to the cumulative surface of insular shelf, as limited by the isobath of 200 m, the depth limit of their maximum abundance.

2.2.2.1 Artisanal fisheries

Artisanal fishery is mainly coastal, practised with hand lines on wooden and opened crafts of standard size between 3 and 6 m, propelled by an outboard engine of 15 HP. Because of technical limitations (storage capacity, communication facilities, etc.), fishing

units do not have a large autonomy at sea and thus, fishing operation are carried out within a period of 24 hours in a limited range area (*c.* 10 km) around islands. On average, 1 354 artisanal boats fish all year round on 260 fishing sites over a cumulative shelf area of 5 394 km^2 (Table 2.1). About 40 demersal species are caught and the whole catch is landed at 85 artisanal fishing ports to be sold on local market.

2.2.2.2 Data source

The INDP database provides information about fishing boats, fishermen, fishing grounds' location, trip date and duration, species identification and catches, since 1996 until now. The database is supplied by a statistical sampling plan which combines a stratified three-stage sampling design for units of unequal sizes, as described in Medina (1995).

Abundance data are derived from Catches Per Unit Effort (CPUE) of the exploited demersal species collected from January 1996 to December 2002 (Medina *et al.* 2007). For the purpose of the present study, the exploited community was represented by the assemblage of the 18 most abundant species. Using only dominant species warrants the availability of data for all species under study, and avoids missing values, which enhances the robustness of statistical analyses. On the other hand, dominant species determine the main biological characteristics of demersal communities and the non-target assemblages appear to remain relatively unchanged, despite a long-term intensive fishing activity (Colvocoresses & Musick 1984; Greenstreet & Hall 1996; Jin & Tang 1996).

Tableau 2.1 Surface cumulative du plateau des îles du Cap-Vert par niveau de profondeur, estimé à partir de Bravo de Laguna (1985). Pour cette recherche, la surface cumulative du plateau jusqu'à l'isobathe de 200 m est considérée l'aire de distribution maximale pour les principaux poissons démersaux.

Table 2.1 Cumulative shelf surface by depth limit for Cape Verde islands, estimated from Bravo de Laguna (1985). For this research, the cumulative shelf surface down to the isobath of 200 m is considered to be the maximal distribution range for main demersal fishes.

	Cumulative shelf area (km^2) by depth limit		
	100 m	200 m	500 m
Santo Antão (SA)	187	270	377
São Vicente (SV)	248	379	585
Santa Luzia. Raso and Branco (LZ-IR-IB)	240	367	566
São Nicolau (SN)	199	304	470
Sal (SL)	223	287	460
Boavista (BV)	1 779	2 518	3 150
Maio (MO)	474	732	1 074
Santiago (ST)	179	289	490
Fogo (FG)	64	107	221
Brava (BR)	26	48	73
Secos islets (IG)	42	93	183
Total	3661	5394	7650

Each landing site was visited six times a month, and all active boats were sampled at each visit providing data on time at sea (in hours), fishing location and catch per fishing trip (in kilograms). Knowing the distance between landing ports and fishing sites as well as the average boat speed, time at sea was corrected to provide an estimate of the effective fishing time. For each sampled fishing site (Table 2.2), monthly average CPUE for each of the 18 species was estimated boat-by-boat as (Medina *et al.* 2007):

$$CPUE = \frac{\sum_{i=1}^{n} \frac{C_i}{f_i}}{n} \quad (1)$$

where C and f are respectively the catch (kg) and the fishing effort (h) of boat i, determined for each visit, and n is the total number of observations for the fishing site during the month. CPUE was further expressed in kg per 24 hours ($kg.d^{-1}$). Because of the characteristics of this small-scale fishery, we do not expect variation in fishing power between boats; therefore, no standardization of CPUE was necessary. As suggested by Lyons (1981) and Legendre & Legendre (1998), we used biomass of catches rather than number of individuals because catch samples contained individuals of different lengths and at different stages of maturity.

Winters & Wheeler (1985) advise for some precaution when using CPUE data as abundance index without prior information on population spatial distribution. However we considered island scale as a discrete unit of space and, since the dynamics of artisanal fishery is quite consistent all year round over seven years.

Tableau 2.2 Nombre de zones de pêche échantillonnées au Cap-Vert pendant la période d'étude. Les chiffres entre parenthèses représentent le nombre total de sites de pêche signalés dans la base de données de pêche de l'INDP.

Table 2.2 Number of fishing sites sampled in Cape Verde archipelago during the study period. Numbers between brackets represent the total fishing sites reported on the INDP fishery database.

	1996	1997	1998	1999	2000	2001	2002
SA (32)	17	17	13	18	18	18	14
SV-LZ-IR-IB (46)	34	26	18	24	24	22	24
SN (18)	14	16	15	14	12	16	15
SL (15)	14	15	13	15	14	14	15
BV-MO (33)	17	18	18	17	16	15	14
ST (85)	40	49	48	50	55	58	48
FG (22)	22	19	14	14	22	20	13
BR-IG (13)	6	6	5	6	6	7	11
Total (260)	164	166	144	158	167	170	154

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We assume that the spatial distribution of CPUEs reflects the spatial distribution of exploited demersal species and is representative of changes in the area occupied by demersal fish communities. So, for the purpose of this work, such a methodological procedure seems adequate according to the nature of data available and the particularities of fishery and ecosystem under study.

2.2.2.3 Geostatistical aggregation curves

According to Petitgas (1998), CPUE data can be seen as the density histogram tail of the spatial dispersion of the fish population. Therefore we considered monthly CPUEs over a definite period as discrete samples of that density histogram and each fishing site as a class density of that histogram for the entire island. Thus, each value of CPUE (c) represents sample abundance in each portion of the fishing site's surface T (c_n). Given that the various fishing zones within a fishing site are exploited in a sequential way during the year and the same pattern of exploitation is repeated from one year or season to another, it is then possible to estimate the abundance Q (c_n) on a fishing ground using the formulae proposed by Petitgas (1998):

$$Q(c_n) = \sum_{i=1}^{n} \frac{n_i}{N} \bar{c}_i \qquad (2)$$

Where $\bar{c}_i$ is the average CPUE over the time period considered, and n is the number of months in the time period. To compare the abundance between years, we set n = 12.

To compare seasons, we set n = 7 for the warm season, and n = 5 for the cold one. N is the total number of observations over the entire island. The total abundance Q (c_A) over the island becomes:

$$Q(c_A) = \sum Q(c_n) = \sum_{i=1}^{N} \frac{n_i}{N} \bar{c}_i \qquad (3)$$

The proportion P (c_n) of the abundance of each fishing site related to island's abundance is:

$$P(c_n) = \frac{Q(c_n)}{Q(c_A)} \times 100 \qquad (4)$$

The proportion T (c_n) of the surface of a fishing site related to the total fishing area A of the island is expressed as:

$$T(c_n) = \sum_{i=1}^{n} \frac{n_i}{N} \times 100 \qquad (5)$$

Q is expressed in kg per month and varies between zero and the maximum abundance per fishing site (Q_{max}). P and T are expressed in % and vary between zero and unity. For each island, Q (T) is a cumulative function of Q (c) on an increasing proportion of T(c) for the insular shelf area. Thus, P (T) is a cumulative function that relates the proportion of abundance P (c) to any portion T (c).

The concavity of Q (T) and P (T) curves is a dispersion parameter that characterises the spatial distribution of abundance and so represents a space selectivity index (or a concentration index) Ssp that can be derived from the P (T) curves by solving the following integration

$$Ssp = 2\int_0^1 P(T)dT - 1 \qquad (6)$$

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Ssp represent the geometrical area between the diagonal and P (T) curve. From the ecological point of view, in a dynamic process of spatial distribution, a higher Ssp means a higher ability of habitat selection, *i.e.* a higher concentration of individuals on the most favourable habitats.

2.2.2.4 Theoretical expectations and statistical inference

The variety of spatial dynamics observed in marine fish can be illustrated by four key models (Petitgas 1998; Shepherd & Litvak 2004) which describe patterns of population distribution based on how local density changes with respect to total abundance. The more recent model, indicated hereafter as D1 was proposed by Petitgas (1998) and describes spatial dynamics under the influence of the local environment. It corresponds to a differential density model in which an increase in population abundance is associated with an increase of fish density only in one or several specific subzones, but not elsewhere. The area of fish distribution does not change and local fish density is not related to total abundance, but to local environment. This is illustrated by an increase in space selectivity in the P (T) curves when abundance increases. In another model (D2), proposed by Houghton (1987) and Hilborn & Walters (1992) has the consistent spatial pattern and is refered to as proportional density model, the density varies proportionally to abundance in all distribution areas. In these spatial dynamics, local fish density changes at the same rate as population abundance and so, there are no significant changes in space selectivity between periods presenting different abundance levels. These spatial dynamics have been reported by Myers & Stokes (1989) for gadoids in the North Sea and by Petitgas (1997) for

Lemon Sole eggs distribution on the spawning ground in the Bay of Biscay. A third model (D3) illustrates an increase in abundance which is not associated with an increase in fish density. The maximum density remains constant. In such a case, space selectivity in the P (T) curves will decrease as abundance increases. This scenario was reported by Iles & Sinclair (1982) for the spatial distribution of herring larvae on spawning grounds. It can also be understood as a particular expression of the equilibrium theory of island biogeography assuming that the number of individuals within a *taxon* increases linearly with the area of an island, *i.e.* population density remains constant with increasing area (Connor *et al.* 2000). This is typical of a relative homogeneous environment where, with the increase in abundance, the populations tend to occupy increasingly larger surfaces. A fourth model (D4) represents a spatial dynamics reported by MacCall (1990) as the "basin model". At low abundance, only the best habitats should be occupied. As abundance increases, density also increases, and due to competition, fish should begin to occupy poorer habitats as profit rates in the best habitats decrease. Ecological niches expand to include suboptimal habitats. As density increases P (T) curves show decreasing space selectivity.

Spatial dynamics described by the first two models are density-independent with no significant correlation between abundance and distribution area. They are well discriminated by different space selectivity indices in P (T) curves. The last two models illustrate density-dependent processes where a distributional area is positively correlated with total abundance. Those two dynamics are almost similar but can be distinguished on

the Q (T) curves. Conversely to the model (D4), the Q (T) curves derived from (D3) coincide at the origin, showing that the maximum density on the habitat is constant.

In order to determine which dynamics are present in the Cape Verde system, a first step was to estimate SSp from the integration of the equation (6) for each period (year or season) and each island. Calculation routines were developed under EXCEL software using Simpson method. In a second step, the SSp obtained for two different periods were statistically discriminated using a bootstrap technique, by simulating a null hypothesis corresponding to dynamics D2. Two sets of original data Q and T from two different periods are pooled and randomly resampled n times, with replacement, to generate a random series of n Q and n T. This resampling was done k times to generate k series of Q and T. Then by using the equations previously described, k P (T) curves are derived and their corresponding Ssp are computed to provide a statistical distribution curve of Ssp through which it is possible to take a statistical decision. If the two Ssp values of original sets of P (T), for each period individually, are inside the confidence level, the null hypothesis can be preserved. If at least, one of the Ssp values is outside, the null hypothesis can be rejected and the spatial dynamics departs significantly from D2. In the present research this bootstrap test was carried out with n = 20 (Ssp computed with a set of 20 values of P and T) and k = 10^3 and a statistical decision was taken for $\alpha = 0.05$. The value of k was high enough to attain the convergence of results.

In order to investigate annual patterns on spatial dynamics at assemblage level, our research were conducted at each island or island groups, between two consecutive years. A first step was to compare two years of different abundance levels. Two consecutive years were selected presenting contrasting CPUEs and a sufficient number of data to allow a

robust model. Therefore, the period 1998/1999 was chosen for SA island; 1996/ 1997 was retained for the island groups of SV-LZ-IR-IB; 1997/ 1998 for ST, FG and BR-IG island groups, and 2001/ 2002 for SN, SL and BV-MO island groups. In a second step, for each spatial dynamics formerly identified, we investigated seasonal patterns by comparing the two seasons in the same years (cold season - from December to April; warm season – from May to November) on two selected islands, as well for low and for high abundances. Finally, the four most abundant species were selected (*Cephalopholis taeniops* - 457, *Pseudupeneus prayensis* - 322, *Seriola dumerili* - 699 and *Scarus hoefleri* - 402) to study spatial dynamics over two consecutive years at the species level on the previously selected islands representing each identified spatial dynamics. At that level, seasonal patterns were not studied due to low abundance values which prevented robust statistical analyses.

2.3 Results

2.3.1 Spatial dynamics at assemblage level - annual patterns

A proportional density model (D2) is observed at SA, SN, SL, ST and FG islands, as the null hypothesis of identical SSp cannot be rejected (Table 2.3). This is graphically illustrated by the spatial dynamic at SA Island (Figure 2.2 A). Q (T) curve for 1998 shows a lower Q_{max} than for 1999. However, the P (T) curves are well superposed and not statistically different (Table 2.3) because both values of Ssp (0.271 and 0.275) are inside de confidence interval in the bootstrap test. Such a graphical configuration suggests that local fish density changes at the same rate as population abundance. Conversely, three other island groups (SV-LZ-IR-IB, BV-MO and BR-IG) revealed a differential density model (D1) expressed by an increase in fish density associated with an increase of abundance.

Tableau 2.3 Variation d'abondance (Q_{max}) et indice de sélectivité de l'espace (Ssp) des poissons démersaux des plateaux insulaires du Cap-Vert. (Q_{max}) et (Ssp) sont calculés entre deux années d'abondance contrastée et l'hypothèse nulle (D2) est testée avec 1000 interactions à un niveau de signification de 0.05. Les valeurs de Ssp en gras se trouvent en dehors du niveau de confiance et donc permet de rejeter D2.

Table 2.3 Changes in abundance (Q_{max}) and space selectivity index (Ssp) of demersal fishes on the Cape Verde Island's insular shelf. Q_{max} and Ssp are computed between two years of contrasted abundance and the null hypothesis (D2) is tested by 1000 bootstraps at a significance level of 0.05. Bold values of Ssp are outside the confidence level and so allow the rejection of D2.

Island's Insular shelf	Years	Q_{max}	Ssp	Confidence level		Spatial dynamic
				Lower bound	Upper bound	
SA	1998	215.8	0.271	0.265	0.365	D2
	1999	315.4	0.275			
SV-LZ-IR-IB	1996	575.5	0.428	0.336	0.444	D1
	1997	472.4	**0.285**			
SN	2001	939	0.445	0.403	0.530	D2
	2002	1573	0.441			
SL	2001	1483.1	0.403	0.356	0.497	D2
	2002	996.4	0.393			
BV-MO	2001	2435.8	0.693	0.520	0.734	D1
	2002	1260.2	**0.498**			
ST	1997	1786.8	0.262	0.203	0.316	D2
	1998	1383.7	0.257			
FG	1997	610.7	0.459	0.376	0.508	D2
	1998	794.8	0.456			
BR-IG	1997	1224.9	0.317	0.262	0.357	D1
	1998	719.6	**0.201**			

Such analytical interpretation is confirmed by the rejection of the null hypothesis (Table 2.3). This is graphically illustrated by the spatial dynamic in SV-LZ-IR-IB (Figure 2.2 B). Q_{max} is higher for 1996 than for 1997, and P (T) curves present a higher Ssp in 1996. The Ssp of 1997 (0.285) departs far from the lower bound of the confidence interval (Table 2.3). This indicates that density increases locally at a higher rate than abundance.

2.3.2 Spatial dynamics at assemblage level - seasonal patterns

Considering that two different annual patterns were observed within the archipelago, two island groups representing each one a different dynamic were chosen to investigate the seasonal patterns as well for a year of high abundance as for that of low abundance: SV-LZ-IR-IB (years 1996 and 1997) and SA (years 1998 and 1999). Independently of the island or island group, Q_{max} is higher in the warm season than in the cold one. However, for SA island (Figure 2.3 A), P (T) curves of the two seasons are superposed and Ssp do not show statistical difference (Table 2.4). This trend is the same for the two years, independently of their abundance. Such a situation corresponds to the dynamic D2, as observed at the same island between years 1998 and 1999. At SV-LZ-IR-IB islands group (Figure 2.3 B), P (T) curves indicate always a higher Ssp for the warm season than for the cold one, and this is verified for the two years (Table 2.4). The P(T) curves are statistically well discriminated in both case by the Ssp of the cold season that departs far from the lower bound of the confidence interval. It means that the seasonal patterns of the spatial dynamic can also be described by D1, as previously observed by comparing the years 1996 and 1997.

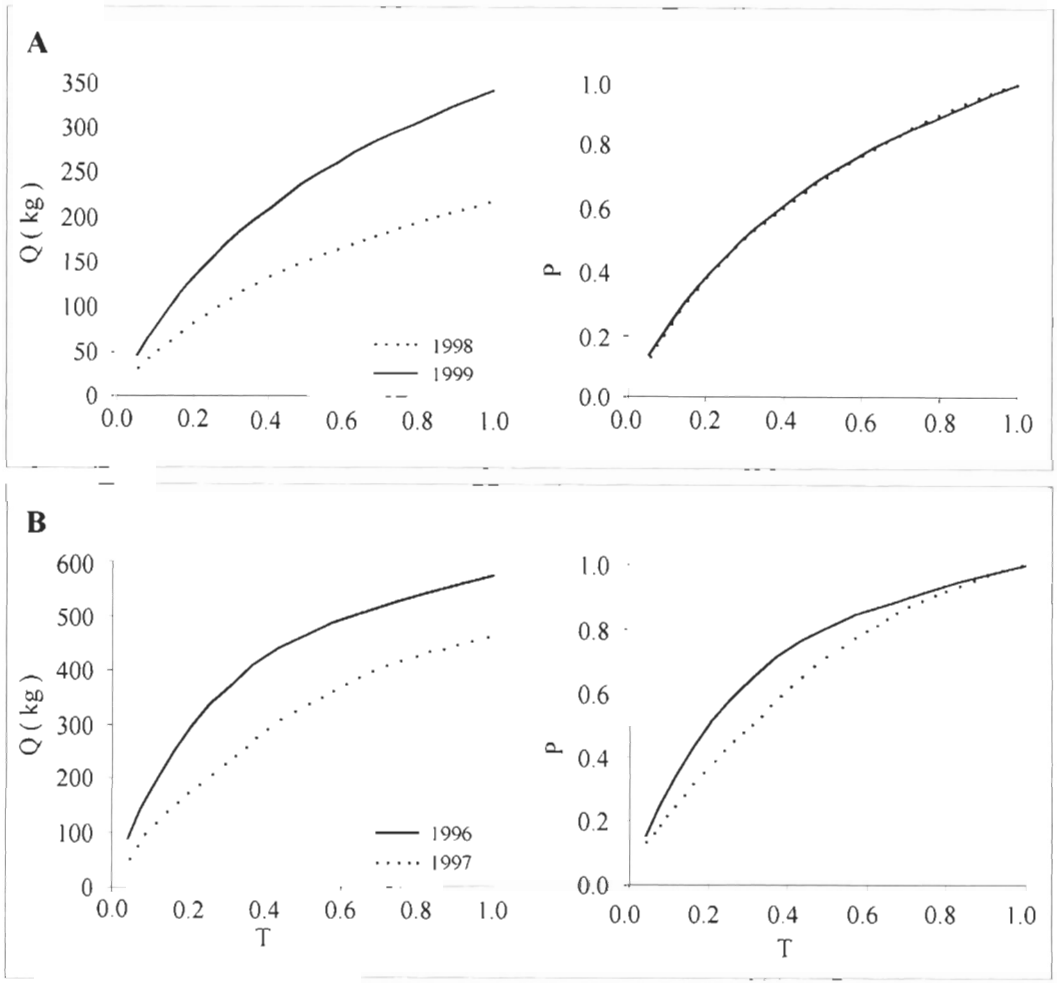

Figure 2.2

- Courbes d'agrégation géostatistique Q (T), à gauche, et P (T), à droite, calculées pour les assemblages d'espèces de l'île de Santo Antão (A) et du groupe d'îles São Vicente, Santa Luzia, îlots Raso et Branco (B), pour deux années de différents niveaux d'abondance. Cela illustre les deux dynamiques spatiales observées dans l'archipel du Cap-Vert: un modèle de densité proportionnelle D2 (A) et un modèle de densité différentielle D1 (B). Le premier scénario est commun aux îles de São Nicolau, Sal, Fogo et Santiago tandis que le second est commun aux groupes d'îles Boavista - Maio et Brava – îlots Grande.

- Geostatistical aggregation curves Q (T) on the left and P (T) on the right, computed for the species assemblages at Santo Antão island (A) islands group of São Vicente, Santa Luzia, islets Raso and Branco (B), for two years of different abundance levels. This illustrates the two spatial dynamics observed in Cape Verde archipelago: a proportional density model D2 (A), and a differential density model D1 (B). The first scenario is common to São Nicolau, Sal, Fogo and Santiago islands while the second one is common to the groups of Boavista - Maio and Brava – Islets Grande.

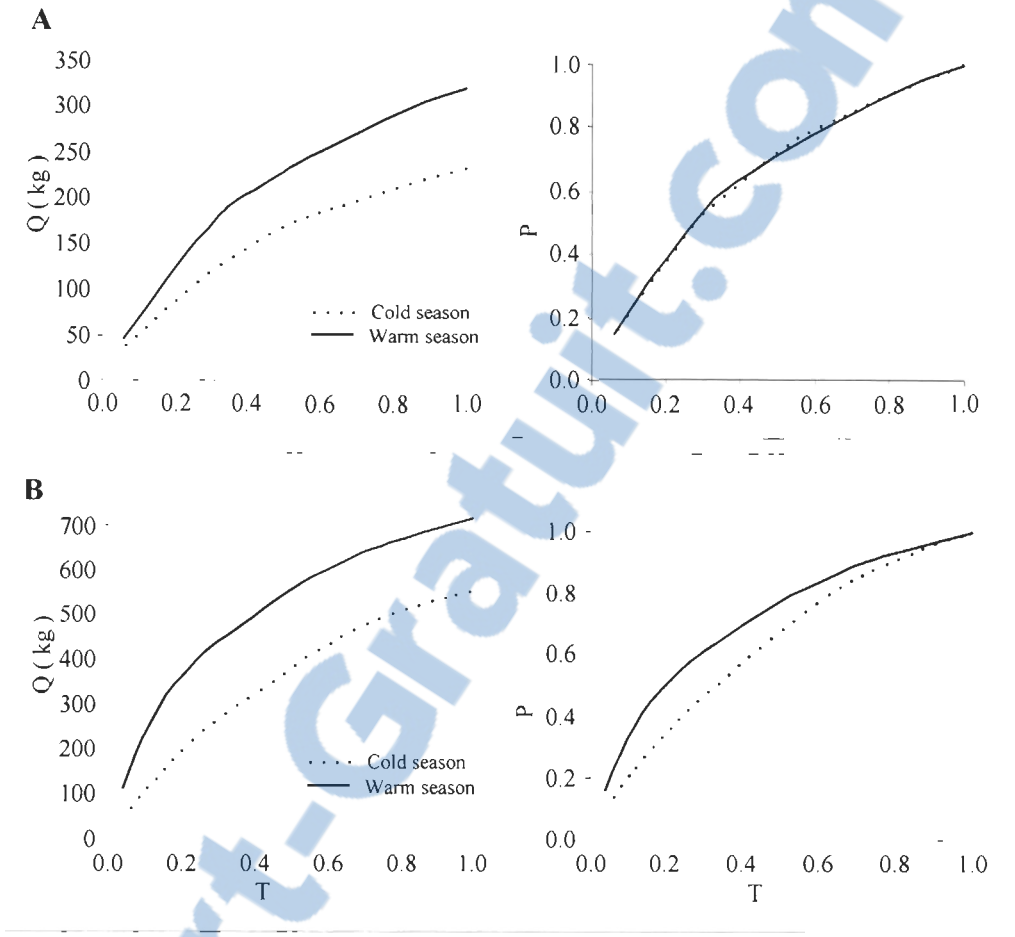

Figure 2.3

- Courbes d'agrégation géostatistique Q (T), à gauche, et P (T), à droite, calculées pour les assemblages d'espèces pour la saison chaude et la saison froide, pour l'année 1998 de faible abondance à l'île de Santo Antão (A) et 1996 de forte abondance au groupe d'îles de São Vicente, Santa Luzia, îlots Raso et Branco (B). Cela illustre le modèle de densité proportionnelle D2 (A) et le modèle de densité différentielle D1 (B). Le premier scénario est identique pour l'année 1999 de forte abondance à Santo Antão et le second pour l'année 1997 de faible abondance au groupe d'îles de São Vicente, Santa Luzia, îlots Raso et Branco.

- Geostatistical aggregation curves Q (T) on the left and P (T) on the right computed for the species assemblages for the warm season and cold season for the year 1998 of low abundance 1998 at Santo Antão Island (A) and year 1996 of high abundance at islands group of São Vicente, Santa Luzia, islets Raso and Branco (B). This illustrates the proportional density model D2 (A) and the differential density model D1 (B). The first scenario is identical for the year 1999 of high abundance at Santo Antão Island and the second one for the year 1997 of low abundance at islands group of São Vicente, Santa Luzia, islets Raso and Branco.

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Tableau 2.4 Variation d'abondance (Q_{max}) et indice de sélectivité de l'espace (Ssp) des poissons démersaux des plateaux insulaires de deux groupes d'îles de l'archipel du Cap-Vert. (Q_{max}) et (Ssp) sont calculés entre la saison chaude et froide de la même année et l'hypothèse nulle (D2) est testée avec 1000 interactions à un niveau de signification de 0.05. Les valeurs de Ssp en gras se trouvent en dehors du niveau de confiance et donc permet de rejeter D2.

Table 2.4 Changes in abundance (Q_{max}) and space selectivity index (Ssp) of demersal fishes on the insular shelf of two islands groups of Cape Verde archipelago. Q_{max} and Ssp are computed between warm and cold season in the same year and the null hypothesis (D2) is tested by 1000 bootstraps at a significance level of 0.05. Bold values of Ssp are outside the confidence level and so allow the rejection of D2.

Island's insular shelf	Years	Season	Q_{max}	Ssp	Confidence level		Spatial dynamic
					Lower bound	Upper bound	
SA	1998	Warm	319.9	0.286	0.269	0.361	D2
		Cold	232.7	0.294			
	1999	Warm	680.6	0.355	0.328	0.472	D2
		Cold	391.8	0.355			
SV-LZ-IR-IB	1996	Warm	715.8	0.410	0.280	0.426	D1
		Cold	490.3	**0.249**			
	1997	Warm	708.9	0.454	0.371	0.503	D1
		Cold	409.9	**0.354**			

2.3.3 Spatial dynamics at a species' level

The annual patterns on the spatial dynamic of the four selected species were studied at SA island and at SV-LZ-IR-IB island group for the same years as for the study done at assemblage level *i.e.* 1998/1999 and 1996/1997, respectively. Despite differences in abundance (Q_{max}), the four species demonstrate the same pattern of spatial dynamics, independently of the island considered. P (T) curves show no statistical difference in Ssp (Table 2.5) with all values inside the bound of the confidence interval in the bootstrap test, and therefore the hypothesis of dynamics D2 cannot be rejected. This is illustrated graphically by the spatial dynamics of *C. taeniops* (Figure 2.4). It suggests that, at species level, the spatial dynamic is characterized by D2, *i.e.* a change in species density is expected to be proportional to the change in its abundance. It's interesting to note that, despite the same pattern in spatial dynamics, all Ssp values are higher at SV-LZ-IR-IB than SA for all species.

2.4 Discussion

Spatial dynamics as the relationships between local density and population abundance has been studied in marine ecology by several methodological approaches. The present work used commercial CPUEs to derive indices of space selectivity by the means of geostatistical techniques to study the dynamics on the occupation of space at assemblage level as well as at single species level, for marine demersal fishes, in an archipelago system.

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Tableau 2.5 Variation d'abondance (Q_{max}) et indice de sélectivité de l'espace (Ssp) de quatre principaux poissons démersaux des plateaux insulaires de deux groupes d'îles de l'archipel du Cap-Vert. (Q_{max}) et (Ssp) sont calculés entre deux années d'abondance contrastée pour *Cephalopholis taeniops* (457), *Seriola dumerili* (699), *Pseudupeneus prayensis* (322) et *Scarus hoefleri* (402). L'hypothèse nulle (D2) est testée avec 1000 interactions à un niveau de signification de 0.05.

Table 2.5 Changes in abundance (Q_{max}) and space selectivity index (Ssp) of the four main demersal fishes on the insular shelf of two islands groups of Cape Verde archipelago. Q_{max} and Ssp are computed between years of contrasted abundance for *Cephalopholis taeniops* (457), *Seriola dumerili* (699), *Pseudupeneus prayensis* (322) and Scarus *hoefleri* (402). The null hypothesis (D2) is tested by 1000 bootstraps at a significance level of 0.05.

Island's insular shelf	Species	Years	Q_{max}	Ssp	Confidence level		Spatial dynamic
					Lower bound	Upper bound	
SA	457	1998	399.2	0.363	0.292	0.402	D2
		1999	516.3	0.365			
	699	1998	275.7	0.338	0.320	0.419	D2
		1999	399.1	0.371			
	322	1998	288.9	0.269	0.214	0.295	D2
		1999	487.5	0.271			
	402	1998	191.8	0.298	0.266	0.390	D2
		1999	282.0	0.290			
SV-LZ-IR-IB	457	1996	551.3	0.533	0.429	0.622	D2
		1997	338.7	0.540			
	699	1996	648.6	0.644	0.614	0.757	D2
		1997	279.4	0.676			
	322	1996	644.4	0.516	0.500	0.576	D2
		1997	381.4	0.563			
	402	1996	617.1	0.592	0.506	0.638	D2
		1997	334.3	0.575			

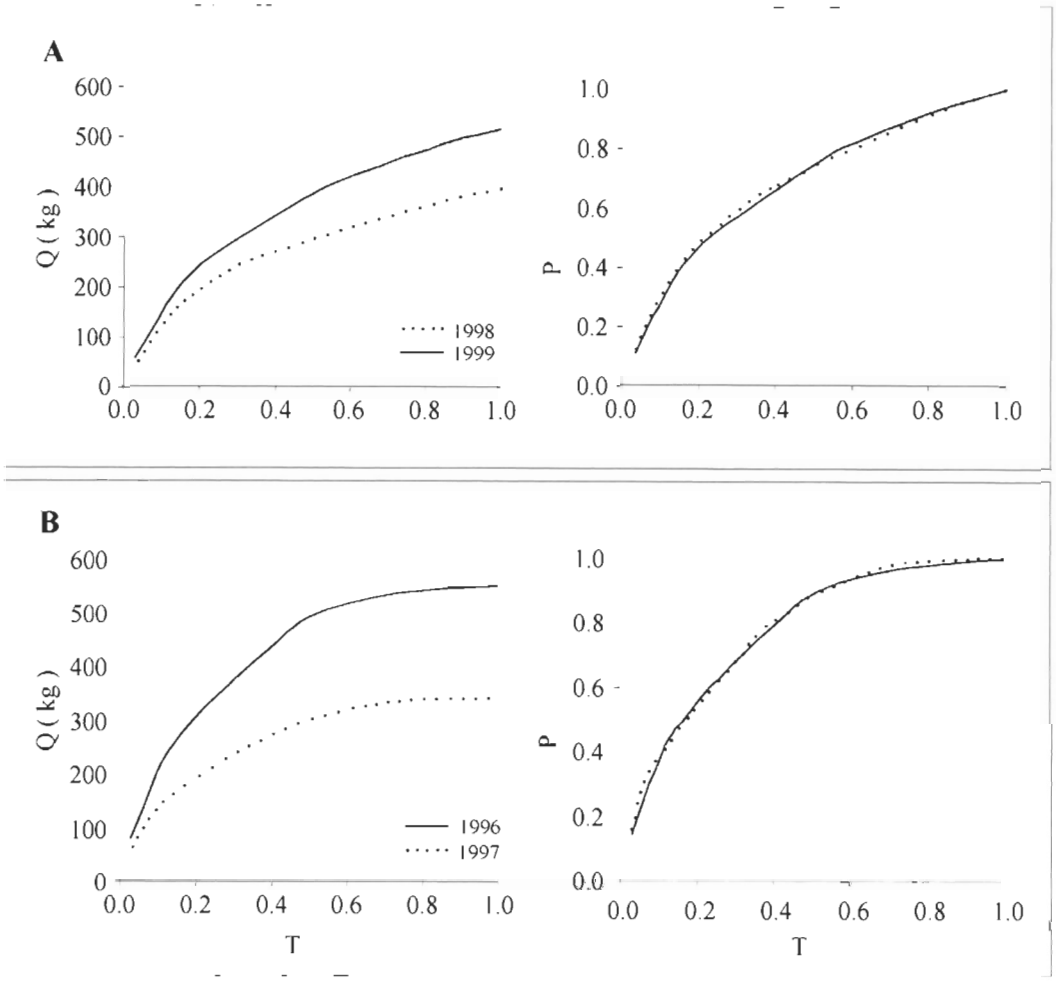

Figure 2.4

- Courbes Q (T), à gauche, et P (T), à droite, calculées pour l'espèce *Cephalopholis taeniops* à l'île de Santo Antão pour les années 1998 et 1999 (A) et au groupe d'îles de São Vicente, Santa Luzia, îlots Raso et Branco pour les années 1996 et 1997. Cela illustre le modèle de dynamique spatiale à densité proportionnelle D2, commune pour les quatre espèces étudiées.

- Curves Q (T) on the left and P (T) on the right computed for the species *Cephalopholis taeniops* at Santo Antão island for years 1998 and 1999 (A), and at islands group of São Vicente, Santa Luzia, islets Raso and Branco for years 1996 and 1997. This illustrates the spatial dynamics model of proportional density D2, common for the four species studied.

General criticisms have been formulated concerning the robustness of results obtained from the use of CPUEs as unbiased abundance indices without prior information on population spatial distribution (Winters & Wheeler 1985). However the relevance of using fisheries data for ecological purposes in such a scientific context has recently been discussed by Medina *et al.* (2007) with reference to a large number of fisheries and ecological researches (Ketchen 1964; Chadwick & O'Boyle 1990; Petitgas 1998; Begg & Waldman 1999; Salthaug & Godø 2001) and proved to be quite appropriate.

The results show the presence of two different patterns of spatial dynamics. A differential density model (D1) better describes spatial dynamics at assemblage level in islands presenting a relatively wide shelf, such as São Vicente, Santa Luzia, islets Raso and Branco, Boavista, Maio, Brava and Secos islets. Those islands are in the same insular shelf until the isobath of 200 m. A proportional density dynamics (D2) is found in islands with a narrow shelf, *i.e.* Santo Antão, São Nicolau, Sal, Santiago and Fogo islands, which are isolated from the other islands by depths greater than 500 m. According to the strong bathymetric heterogeneity in the archipelago, these differences in dynamics seem to be related to space availability. On one hand, differential density model is typical of more heterogeneous environments, related, among others factors, with larger varieties of ecological niches. Species are allowed to move freely over a relatively large and diversified area and to concentrate on the most favourable habitats, which is translated by a higher space selectivity index when abundance increases. On the other hand, proportional density model seems to be typical of less heterogeneous environments restricted by the surface of insular shelf. Hence species are almost constrained to maximize their ecological niche. As

abundance increases, species must occupy the available space, without regards to the suitability of the habitat and space selectivity index remains more or less constant.

Those results were obtained at assemblage level, represented by 18 of the most important demersal fish species from the entire community. Most of studies on spatial dynamics has been carried on at species level, either in a single-species context, for Atlantic Cod (*Gadus morhua*) in the Gulf of St. Lawrence (Swain & Wade 1993; Swain & Sinclair 1994; Atkinson *et al.* 1997) and American Plaice (*Hippoglossoides platessoides*) in the same region (Swain & Morin, 1996), or in the context of a mixed-species fisheries on the Georges Bank, in Northwest Atlantic (Murawski & Finn 1998). Focusing on the dynamics of the single species is supported by the metapopulation theory that has provided important perceptions on how the spatial mixture of local population permits the regional persistence of species, local extinctions and colonisations (Loreau *et al.* 2003). However, considering different organization levels for the understanding of processes and ecological phenomena lead us to investigate for each spatial dynamics described at assemblage level, how does behave single species in the occupation of their ecological niche. Results obtained at this level, for four of the most abundant species, reveal the existence of a proportional density dynamics model (D2), independently of the dynamics observed at the assemblage level. *A priori*, these results can be confounding, *i.e.* that two areas with two different dynamics at an assemblage level, present only one regular dynamics at the single species level. We suggest that, in a context where space availability is a critical factor on population distribution, as abundance increases, species tend individually to maximise their ecological niche. Consequently, an increase in population abundance is associated with an increase in

density in all points of the distributional area and so fish density changes at the same rate as population abundance. This spatial dynamics is the one that prevails in geographic distribution of demersal fish in Cape Verde Archipelago and the degree of its expression is mainly constrained at assemblage level by environmental factors that affect their ecological niche. This result suggests that spatial dynamics of marine populations is much more complex than provided by theoretical models. For a better understanding of this ecological phenomenon, we suggest to consider the probable scenario where, as long as space is available, the same species can, according to environmental conditions, progress from one dynamics to another for maximisation of its ecological niche. As stated by Petitgas (1998), spatial dynamics supporting the basin model (MacCall 1990) is a mixed one that can be obtained by combining proportional and constant density models.

As discussed before, the main spatial dynamics of demersal fish in Cape Verde Archipelago – differential or proportional density models – are constrained by space availability. Despite considerations of Winters et Wheeler (1985), who assume density-dependent habitat selection as a general feature of marine and freshwater fish populations, and other studies that support it for some species (Swain & Sinclair 1994; Atkinson *et al.* 1997; Salthaug & Aanes 2003; Swain & Benoit 2006), our results do not allow to validate it in a archipelago system such as Cape Verde. In such an ecosystem, the population abundance and distribution are strongly constrained by the insular shelf tightness and an ideal free distribution of fish is not likely to occur. Our results point in the same direction as suggested by Atkinson *et al.* (1997), who assumed that demersal populations are unlikely

to exhibit strong relationships between area occupied and overall abundance level, density being more limited by physical habitat than by social behaviours.

In the ecosystem under study, demersal communities are composed of spatially discrete populations distributed among several separate islands or island's group and obviously, spatial scale becomes crucial for a proper interpretation of different dynamics. Comparing our results that illustrate density-independent habitat selection, with some others showing density-dependent habitat selection, we observe a clear difference in spatial scale. On one hand, we worked with distribution ranges restricted by the surface of insular shelf, varying in the order of a few tens to a few hundreds km^2. On the other hand, in previous studies, the range of distribution area of the main demersal species showing density-dependent habitat selection was in the order of several thousands of km^2 (Winters & Wheeler 1985; Swain & Wade 1993; Swain & Sinclair, 1994; Salthaug & Aanes, 2003; Casini *et al.* 2005; Swain & Benoît 2006). Such comparisons lead us to believe that fish spatial dynamics is a scale-dependent process. At the scale over which most marine fish populations are distributed, it's unlikely that individuals would be adequately informed much beyond their immediate perceptual range. Even if they could get precise information about optimal suitability over the population's distribution range, the energetic costs of travelling to the optimal habitat may outweigh any benefit (Shepherd & Litvak 2004). Given the nature of physical environment in which marine fishes live, both abundance and area of distribution may co-vary with other factors not parameterized by the ideal free distribution and so a more reasonable model may consider both density-dependent and density-independent effects as suggested by Cushing (1972) for marine fish during the

period of larval drift. More recently, similar considerations have been highlighted by other researches on spatial dynamics (Anderson & Gregory 2000; Fromentin *et al.* 2001; Shepherd & Litvak 2004). In a tropical and oceanic system like Cape Verde that has, until now, received little scientific attention in marine ecology, it is strongly recommended that marine research effort should be directed according to the importance of spatial and temporal scale at different life organisation levels, combining as often as possible, commercial fisheries and surveys data (Fox & Starr 1996; Petitgas *et al.* 2003; Verdoit *et al.* 2003).

Another important finding of our research is that communities and single-demersal species tends to present basically the same density-independent pattern on the occupation of space and such a dynamics stays invariant all year round without seasonal changes. In classical ecology, species are considered to be the basic units of niche ecological theory, competition and succession, each local population representing a genetic pool more or less scattered according to energy cost effectiveness (Legendre & Legendre, 1998). Doing so, they are structured in community. In a context where all local systems reflect the imprint of large-scale processes (Loreau *et al.* 2003) the combination of these observations allow to suggest, as did Magurran (2005), that, for Cape Verde Archipelago, local communities at a islands scale are embedded in a metacommunity structure as a regional collection of communities at the archipelago scale. Implicitly this suggestion joined assumptions of the theory of island biogeography (MacArthur & Wilson 1967) applied to whole biota, fauna and community as well as to single-species.

For the archipelago system under study there is no information neither on spatial flows of energy and materials, nor on organisms across ecosystem boundaries. Future research on this matter would be very important for placing this metacommunity concept in the context of functional ecology, which becomes very important in the designing of appropriate conservation and management strategies. As stated by Loreau *et al.* (2003), explicit considerations of spatial interconnections among systems has the potential to provide novel fundamental insights on the dynamics and functioning of ecosystems from local to global scales. In an international context of integrated planning and management of marine resources, these considerations of theoretical and conceptual nature, lead Cape Verde archipelago to be understood as a meta-ecosystem in the large biogeographic region of Macaronesia, with other archipelago as Azores, Madeira and Canary islands. This integrated approach finds its interest in a global effort for a better understanding of regional ecosystems, normally affected by oceanographical phenomena acting on hundreds, even thousands kilometres such as upwelling system, large oceanic currents or transoceanic migrations of several fish species.

According to results on spatial dynamics, special precautions seem to be necessary, particularly in the regions where spatial dynamics are characterized by a differential variation of the density since the exaggerated concentration of the artisanal fishing fleets on particular resources agglomeration could generate important perturbations of the ecosystem by local overfishing (Maury & Gascuel 2001).

This study is the first one in spatial dynamics of marine species on the region. Further researches are still needed at different spatial and temporal scales (*i.e.* fishing

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grounds and months). However such a research orientation will require methodological precautions on the subtleness related to a proper assimilation of various niche dimensions (Holt 1987; Murawski & Finn 1988) in order to provide a better understanding of the overall spatial dynamics of marines resources in this archipelago. At this stage, the conclusions of this work, lead to a promising adjustment of the research and management efforts in the follow-up of demersal fisheries, by following some key species instead of the overall metacommunity.

Systems of oceanic archipelagos present several physical and geographical common particularities marked by space availability as a critical factor on the abundance and distribution of demersal fish populations. In such a context, it would be interesting to test how density-independent habitat selection is a common spatial dynamics for demersal species in archipelago system, at an island's scale.

CHAPITRE 3

HABITAT FRAGMENTATION AND BODY SHAPE VARIATION OF *Cephalopholis taeniops* (VALENCIENNES, 1828) IN AN ARCHIPELAGO SYSTEM (CAPE VERDE, EASTERN ATLANTIC OCEAN)

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Résumé

Parmi les barrières génétiques et écologiques, la distance et la bathymétrie jouent un rôle important dans la fragmentation des écosystèmes d'archipels et récifs coralliens. L'archipel du Cap-Vert est un système océanique tropical fortement fragmenté et dispersé, où ces barrières, avec des facteurs hydrodynamiques induisent divers degrés d'isolement entre les îles. La présente recherche vise à vérifier si les changements de forme du corps chez *Cephalopholis taeniops* varie entre les îles et comment elles peuvent être affectées par fragmentation naturelle de l'écosystème. Une approche morphométrique géométrique typique, complétée par des analyses statistiques multivariées a été employée pour analyser les variations de forme du corps. Bien qu'il existe un effet allométrique significatif (11.5 % de variation totale de la forme du corps), des différences liées au sexe et à l'ontogénie ne sont pas significatives. Une MANOVA suivie d'une CVA ont démontré que les variations inter-îles dans la forme du corps étaient plus fortes que intra-îles et que chaque île présente un modèle allométrique particulier. La forme moyenne du corps dans toutes les îles a été bien discriminée dans des modèles CVA. La comparaison de l'ontogénie des variations de forme entre les îles, deux à deux, a indiqué différents degrés de similitudes. Les îles du nord (Santo Antão, São Vicente et Santa Luzia) présentent une direction de changement ontogénique similaire avec Boavista. Toutes les autres comparaisons appareillées indiquent différents modèles ontogéniques. Quand on compare la direction de variation de forme inter-populations, les individus de Fogo, l'île plus au sud, semblent subir une trajectoire indépendante. Comme il était attendu, l'isolement physique par la distance géographique et la profondeur était corrélée positivement avec la divergence morphologique entre populations des différentes îles, corroborant ainsi l'hypothèse selon laquelle la fragmentation d'habitat dans l'archipel du Cap-Vert peut être interprétée en termes de structure des populations marines.

Mots clés : Fragmentation d'écosystème, système d'archipel, *Cephalopholis taeniops*, géométrie morphométrique, analyse multivariée, structure de population.

Abstract

Among genetic and ecological barriers, geographic distance and depth are considered to play major roles in ecosystem fragmentation of coral reefs and archipelagos. The Cape Verde Archipelago is a tropical oceanic system that is highly fragmented and dispersed. Along with hydrodynamic factors, these physical characteristics act as barriers that induce various degrees of isolation among islands. This isolation may induce morphological variations in populations of the serranid fish *Cephalopholis taeniops*. This study attempts to verify if the body shape in this species varies among islands and sought to determine if this variation was the result of ecosystem fragmentation. A typical geometric morphometric approach complemented with statistical multivariate analysis was used to analyze body shape variations. While a significant allometric effect exists (11.5% of total body shape variation), differences in body shape associated with sex and ontogeny were not significant. MANOVA followed by CVA showed that inter-island body shape variation was greater than that found in intra-island comparisons, and that each island presents a particular allometric pattern. Average body shape for all islands was well discriminated with CVA models. Pairwise comparisons of the ontogeny of body shape change between islands revealed different degrees of similarity. Northern islands (Santo Antão, São Vicente and Santa Luzia) along with Boavista Island showed a similar direction in shape ontogeny while all other paired comparisons indicated different ontogenetic patterns. Particularly, when comparing directions of inter-population shape changes, individuals from Fogo Island, the southernmost locality, depart far from the orthogonal relation, suggesting that they are undergoing independent body shape trajectories. As expected, physical isolation by geographic distance and depth were positively correlated with morphological divergence among populations from different islands. This finding supports the hypothesis that habitat fragmentation in the Cape Verde Archipelago can be interpreted in terms of marine population structure.

Key words: Ecosystem fragmentation, archipelago system, *Cephalopholis taeniops*, geometric morphometrics, multivariate analysis, population structure.

3.1 Introduction

Ecosystem fragmentation and population structure are assumed by ecologists to be crucial issues in biodiversity studies, resource management and the implementation of conservation measures. The pursuit of such scientific knowledge includes challenges related to a better understanding of geographic population structure, which generally results from spatial distribution patterns associated to historic or current barriers between local communities.

Previous studies have focussed upon the role that natural barriers play in driving genetic isolation and structuring populations in marine and terrestrial ecosystems. Among such barriers, geographic distance (De Wolf *et al.*, 1998, 2000; Planes & Fauvelot, 2002; Duda & Rolán, 2005), depth (Medina *et al.*, 2007), environmental patchiness and gradients (Bailey, 1997) are considered to play major roles in ecosystem fragmentation of coral reefs and archipelagos. This process favours speciation mechanisms by integrating major selection forces such as migration, extinction, random differentiation and adaptation, and thus generates inter- and intra-specific variations leading to diversification. Geographical isolation and variations in environmental conditions both play roles in population mixing (movement of gametes, eggs, larvae and organisms) and structure. Marine species may respond to these processes by divergent selection that can lead to phenotypic differences through either genetic differentiation or phenotypic plasticity (Schluter, 2000, 2001; Grether, 2005). Thus, species are able to produce more than one alternative form of morphology, physiological state, behaviour, or different degrees of expression of a given developmental process (Swain & Foote, 1999). Polymorphic signals and other phenotypic

traits may depend on environmental inputs or may result from gene–environment interactions (Swain & Foote, 1999; Klingenberg, 2003). Regardless of their cause, phenotypic traits have been useful in identifying populations units or sub-units since phenotypic plasticity in fishes can be adaptive (Webb, 1984; Stearns, 1989; Via *et al.*, 1995). Therefore, the analysis of body shape variations in fishes can provide useful information on marine population structure in relation to geographic range, connectivity or environmental variability. This scientific question becomes even more challenging in archipelagos, which are often characterized by a rich endemic marine biodiversity because of their relative isolation from continental landmasses. Archipelagos may have unique ecosystems with clearly established spatial limits. The relative physical isolation of many archipelagos has been proposed to drive genetic isolation and population structure, where dispersal ability is often constrained by distance and where gene flow most likely occurs between neighbouring populations.

The Cape Verde Archipelago is a tropical oceanic system that is highly fragmented and dispersed, with distance and depth along with other physical factors inducing various degrees of isolation between islands. Despite evidences in the structuring of inter-island demersal fish populations (Medina *et al.*, 2007), no study has thus far examined marine fish population structure in such a tropical oceanic system. The present study provides the first attempt to analyze habitat fragmentation in relation to the population structure of demersal fish within the Cape Verde Archipelago. Specifically, it provides an analysis of the

geographical variation of body shape among specimens of the African Hind, Cephalopholis taeniops (Valenciennes, 1828) (Serranidae: Epinephelinae), within the archipelago.

Shape analysis is useful for investigating a variety of biological processes, such as ontogenetic development, adaptation to local environmental factors or long-term evolutionary diversification (Zelditch *et al.*, 2004). By analyzing body shape variation in fishes, inferences can be made with respect to functional roles, responses to selective pressures, growth processes and morphogenesis. Shape variation may be due to divergent selective regimes or to local differentiation based upon genetic or ecophenotypic mechanisms (Klingenberg *et al.*, 2003). Individual body shapes in relation to habitat have been linked to various behaviours, such as feeding mechanisms (Carpenter, 1996; Walker, 1996; Trapani, 2003; Clabaut, 2005), mating processes (Klingenberg *et al.*, 2003; Neves & Monteiro, 2003; Hankison *et al.*, 2006) and locomotion performance (Webb, 1984, 2002; Webb & Fairchild, 2001).The present study aims at verifying whether the body shape of C. taeniops differs among islands. In the prevailing physical and biological conditions of habitat fragmentation, environmentally or genetically induced changes in body shape are expected to improve an individual's performance in a particular habitat. So, differences in habitats might create selective pressure, resulting in morphological divergence between conspecific populations (Langerhans *et al.*, 2003). Thus, one could hypothesize that demersal fish populations of an archipelago ecosystem are structured by island or island groups according to their degree of physical isolation and environment variability.

In addition, this study provides an analysis of how habitat fragmentation (*i.e.*, physical isolation between islands) may affect body shape divergence. Geographic distances and depths vary considerably among islands of the Cape Verde Archipelago, and the physical environment is largely under the influence of dominant winds and ocean currents. The insular shelf slope is also highly variable (Bravo de Laguna, 1985). Hence, one could hypothesize that a greater physical isolation would lead to correspondingly greater morphological divergences among populations if such isolation constrains connectivity among islands.

3.2 Material and Methods

3.2.1 Study area

The Cape Verde Archipelago is one of the four oceanic archipelagos belonging to the large biogeographic region of Macaronesia, which also includes Madeira, the Azores and the Canary Islands in the eastern Atlantic Ocean (Fig. 3.1). This archipelago is made up of ten volcanic islands and some islets. Seamounts (*i.e.*, Noroeste, Nova Holanda, Bancona and João Valente) also come close to the sea surface. A group of islands, locally known as "Barlavento" (Santo Antão, São Vicente, Santa Luzia, São Nicolau, Sal and Boavista islands; Raso and Branco islets), are located windward of the northeasterly trade winds. Another group, named "Sotavento" (Maio, Santiago, Fogo and Brava islands; Grande, de Cima and Luis Carneiro islets), are leeward of those winds. The geographical position of the islands (their major axis of orientation) relative to the dominant winds and ocean currents varies greatly, from quite parallel (Sal Island) to perpendicular (São Nicolau Island) or tilted (Santo Antão and Santiago islands).

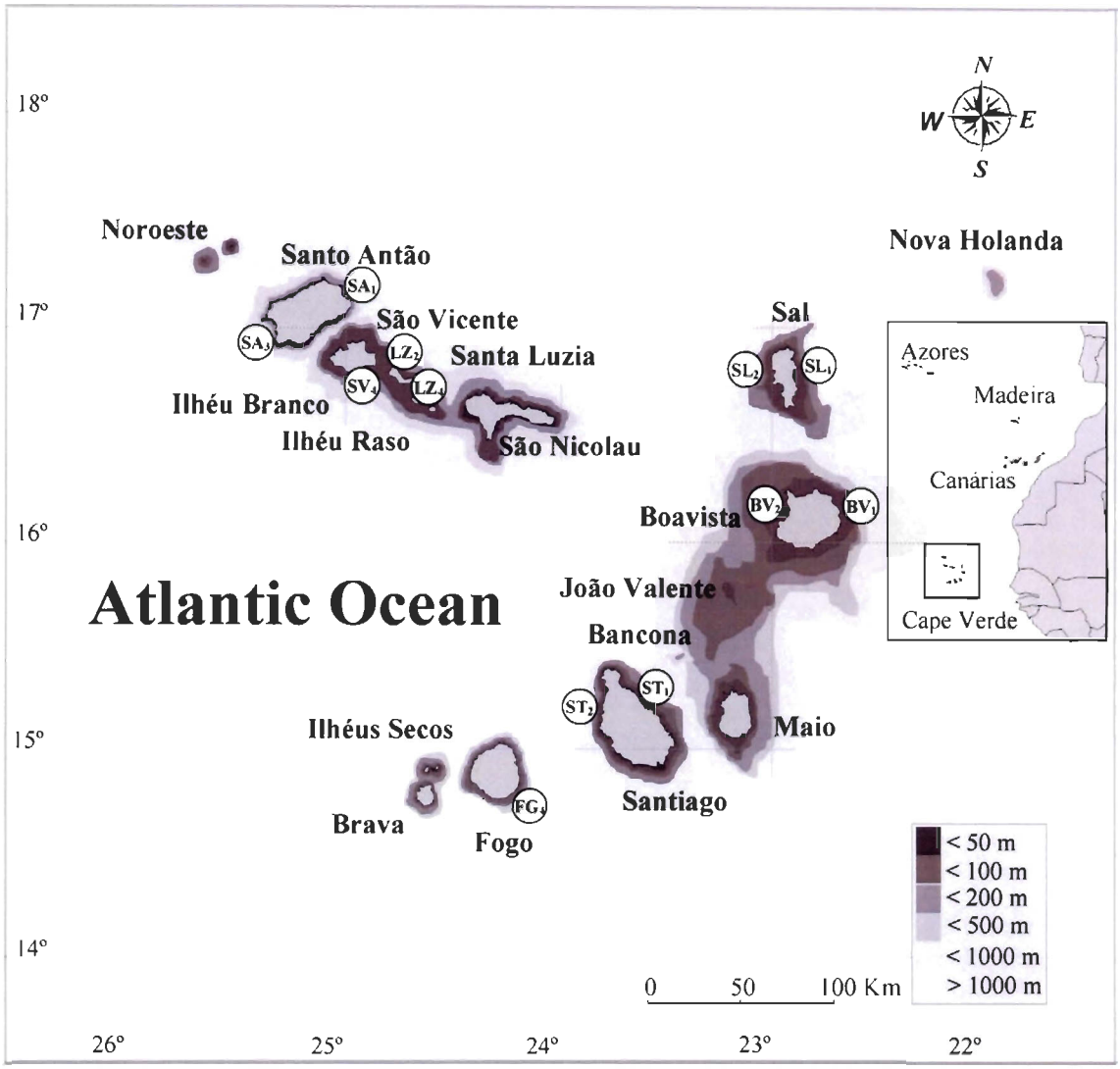

Figure 3.1

- *Cephalopholis taeniops*. Carte de l'archipel du Cap-Vert. Les sites d'échantillonnage sont indiqués dans les cercles avec les abréviations des îles (voir texte), suivis par un chiffre-indice indiquant la position géographique (1: nord-est; 2: nord-ouest; 3: sud-ouest; 4: sud-est). La carte insérée représente la localisation de l'archipel du Cap-Vert dans la région biogéographique de la Macaronésie.

- *Cephalopholis taeniops*. Map of the Cape Verde Archipelago. Sampling sites are shown in circles with the island's abbreviation (see text) followed by a subscript number indicating the geographical position (1: northeastern; 2: northwestern; 3: southwestern; 4: southeastern). Insert map shows the location of the Cape Verde Archipelago within the Macaronesia biogeographic region.

This geomorphologic characteristic, when associated with the overall form of the islands (*i.e.,* fairly round: Boavista, Fogo and Brava; oblong: Santiago; rectangle: Sal, Maio, Santo Antão; rhombus: São Vicente) and their coastal topography can induce different degrees of isolation between surrounding habitats. Furthermore, the volcanic nature of the archipelago is responsible for the great variability in the sea bottom composition, from mostly sandy (Boavista and Maio) to predominantly rocky (Santo Antão, São Nicolau, Santiago, Fogo and Brava) or sandy-rocky (São Vicente, Santa Luzia and Sal); the sea bottom includes coral reef structures and seamounts.

3.2.2 Species selection

Cephalopholis taeniops (Serranidae: Epinephelinae) is a pelagic spawning, protogynous hermaphrodite (Siau, 1994) with a low ratio of males within a given population. This species is distributed in the eastern Atlantic Ocean, from the western Sahara to Angola, including the Cape Verde, São Tomé and Principe islands, where it inhabits sandy and rocky bottoms. Although this species appears to be an adequate subject for this type of research because of its high abundance and broad distribution, it presents particular difficulties related to its reproductive behaviour and ontogenetic development. Members of the genus *Cephalopholis* are characterized by protogynous hermaphroditism, with individuals of at least some species functioning as both sexes, either simultaneously or sequentially (Siau, 1994; Nakai & Sano, 2002; Liu & Sadovy, 2004). When changing from a functional female to a functional male throughout its lifecycle, an individual can follow different developmental pathways, either by monandric or diandric processes. For the

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monandric form, all males are derived exclusively from functional females through sex change (*i.e.,* secondary male); for the diandric form, some males differentiate directly from juveniles through sexual differentiation (*i.e.,* primary male). Because of these processes, the adaptive significance of ontogenetic and sexual patterns can be either functional or ontogenetic, and the analysis of body shape differences becomes both interesting and particularly challenging.

3.2.3 Data collection and samples

Four quadrants were defined according to geographical positions for each island (1: northeastern; 2: northwestern; 3: southwestern; 4: southeastern) for seven of the islands (Santo Antão, São Vicente, Santa Luzia, Sal, Boavista, Santiago and Fogo). When wether conditions were favourable, samples were collected on sites located within two different quadrants off each island, except for Sao Vicente and Fogo, where fish came from a single site (Fig. 3.1). A total of 574 *C. taeniops* specimens were collected in August 2003 and June 2004 (Table 3.1). Specimens were captured by artisanal fishermen using hand lines. Once landed, fish were transported to the laboratory in a tank containing a mixture of cold water and ice. Sampling locations were noted and precautions were taken to prevent body deformation caused by the fast decompression of the swim bladder during capture.

In order to analyze fish morphology, 18 homologous landmarks defining the body outline were selected (Fig. 3.2-A). To capture landmarks, the approach described by Valentin *et al.* (2002) was used.

Tableau 3.1 *Cephalopholis taeniops*. Taille des échantillons selon différentes localisations, état ontogénique et sexe. Les chiffes en indice qui suivent les abréviations des site d'échantillonnage indiquent la position géographique par rapport à l'île (1 – nord-est; 2 – nord-ouest; 3 – sud-ouest; 4 – sud-est)

Table 3.1 *Cephalopholis taeniops*. Sample sizes according to different locations, ontogenetic stages and sex. Subscript numbers following the abbreviations of sampling sites indicate geographical positions relative to the islands (1 – northeastern; 2 – northwestern; 3 – southwestern; 4 – southeastern).

Island	Sampling site	Sex and ontogenetic stage				Total
		Immature	Female	Bi-Sex	Male	
Santo Antão (SA)	SA_1	-	54	-	-	54
	SA_3	-	26	-	14	40
São Vicente (SV)	SV_4	2	45	5	3	55
Santa Luzia (LZ)	LZ_2	-	40	2	19	61
	LZ_4	-	28	2	20	50
Sal (SL)	SL_1	-	32	-	-	32
	SL_2	3	38	-	6	47
Boavista (BV)	BV_1	-	36	4	10	50
	BV_2	-	46	1	4	51
Santiago (ST)	ST_1	27	22	-	1	50
	ST_2	33	19	-	-	52
Fogo (FG)	FG_4	-	26	-	6	32
TOTAL		65	412	14	83	574

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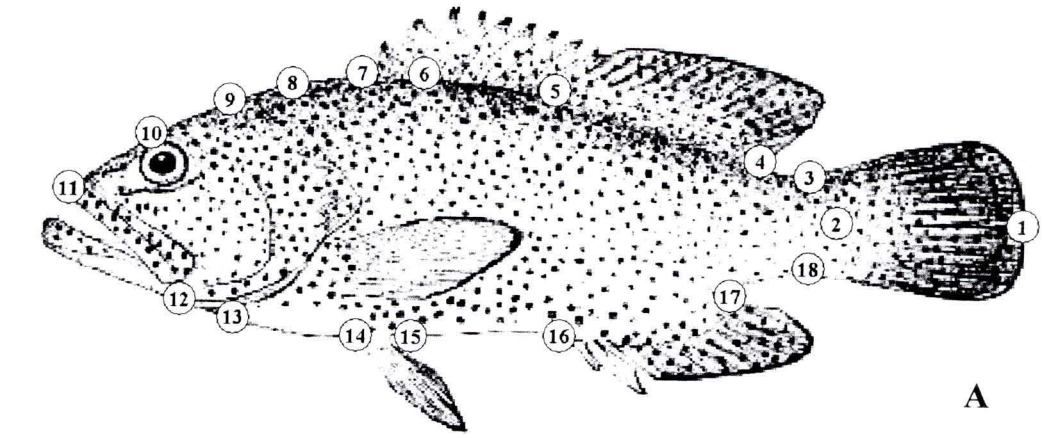
Figure 3.2 (Page suivante)

- *Cephalopholis taeniops*. Points de repère utilisés dans cette étude. (A) spécimen typique de *C. taeniops* et la configuration générale des repères. 1 - extrémité postérieure de la nageoire caudale; 2 - extrémité postérieure de la ligne latérale; 3 – base dorsale de la nageoire caudale; 4 – base postérieure de la nageoire dorsale; 5 – base postérieure du dernier rayon dur de la nageoire dorsale; 6 - insertion du 4^{e} rayon dur de la nageoire dorsale; 7 – base antérieure de la nageoire dorsale; 8 – partie supérieure de l'occipitale (nuque); 9 - extrémité postérieure du maxillaire avant; 10 - point inter-orbital; 11 – crête antérieure de la bouche; 12 extrémité postérieure de la mâchoire inférieure; 13 – base ventrale de l'opercule; 14 - insertion antérieure de la nageoire pelvienne; 15 - insertion postérieure de la nageoire pelvienne; 16 - premier rayon dur de la nageoire anale; 17 - insertion postérieure de la nageoire anale; 18 - base ventrale de la nageoire caudale. (B) Dispersion des résidus de la superposition généralisée des moindres carrés pour chaque point de repère par rapport à la configuration de référence pour 412 spécimens femelles.

- *Cephalopholis taeniops*. Landmarks used in this study. (a) Typical specimen of *C. taeniops* and overall landmark placements. 1: posterior end of the caudal fin; 2: posterior end of the lateral line; 3: dorsal base of the caudal fin; 4: posterior base of the dorsal fin; 5: posterior base of the last hard ray on the dorsal fin; 6: insertion of the 4th hard ray on the dorsal fin; 7: anterior base of the dorsal fin; 8: top of the supra-occipital (nape); 9: posterior end of the pre-maxilla; 10: inter-orbital point; 11: anterior apex of the mouth; 12: posterior end of the lower jaw; 13: ventral base of the operculum; 14: anterior insertion of the pelvic fin; 15: posterior insertion of the pelvic fin; 16: first hard fin ray; 1: posterior insertion of the anal fin; 18: ventral base of the caudal fin. (b) Scatter of residuals of the generalized least-square superimposition for each landmark relative to the reference configuration for 412 female specimens.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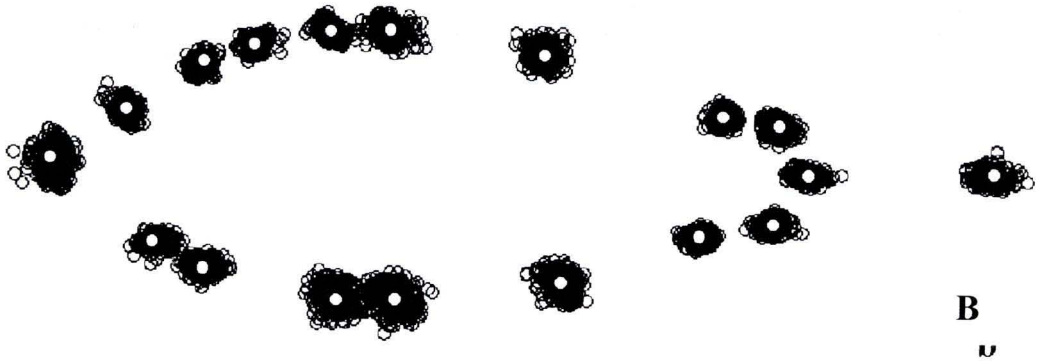
B

Each specimen was placed on its left side in its most natural position on a styrofoam board covered with a piece of waxed paper. The position of each landmark was determined by punching a hole in the paper with a needle perpendicular to the board. In order to minimize sampling-related error, this procedure was repeated three times by the same person for each specimen. Each waxed paper sheet was then digitized with a MicroScribe G2 digitizing system. A mean value of the three measurements, obtained by procrustes fitting (Bookstein, 1991), was used to provide a raw data file with 574 specimens described by 18 variables in *x, y* coordinates (Fig. 3.2-B). A fitting test carried out on 40 randomly re-sampled specimens showed that the sampling error was not significant (r^2 = 0.99). Thus, this approach is more appropriate for a large number of specimens because it avoids various potential sources of sampling error when capturing landmarks compared to other alternatives, such as by photographing, scanning, scaling and digitizing specimen data.

Specimens were classified according to ontogenetic stage and sex by histological inspection with a stereo magnifying binocular microscope (Nikon SMZ1000). Two developmental stages were assigned: immature, when it was not possible to identify fully differentiated gonads, and mature, when it was possible to distinguish between differentiating males (gonads containing spermatogenic tissue and/or sperm) and differentiating females (gonads showing different growth stages of oocytes). Some specimens were classified as bisexual or sexually transitional individuals (*i.e.,* containing degenerating vitellogenic or later-stage oocytes and spermatogenic tissue). Of the 574 specimens examined, 65 were considered immature, with standard lengths *(L_S)* ranging

from 109 to 173 mm, 412 were classified as females (L_S 150–330 mm), 83 were considered males (L_S 203–375 mm) and 14 were bisexual (L_S 233–320).

3.2.4 Geometric morphometric methods

Geometric morphometric methods (Bookstein, 1991; Dryden & Mardia, 1998; Rohlf, 1999; Adams *et al.*, 2004; Zelditch *et al.*, 2004) have proven useful for studying fish body shape variation within populations (Loy *et al.*, 2000; Neves & Monteiro, 2003; Trapani, 2003), among populations (Klingenberg *et al.*, 2003) and between species (Cavalcanti *et al.*, 1999; Lagerhans *et al.*, 2003; Hankison *et al.*, 2006). The strength of these methods is that the analysis can account explicitly for the spatial heterogeneity associated with anatomy and the ontogenetic origins of biological structures (Klingenberg, 2003). When associated with image processing techniques (Cadrin & Friedland, 1999), these methods have been proposed as useful tools for the identification of fish stocks.

In this study, a typical geometric morphometric approach was used to remove differences among specimens because of scaling, rotation and translation (Bookstein, 1991; Rohlf & Marcus, 1993; Dryden & Mardia, 1998; Zelditch *et al.*, 2004). Unlike traditional morphometric measurements, geometric morphometric techniques retain information on spatial covariation among landmarks and the position of each one relative to all others (Rohlf & Marcus, 1993; Rohlf, 1999). The first step was a generalized least-squares orthogonal procrustes superimposition (GLS) that separates shape from size and eliminates variations in the position and orientation of specimens during landmark capture. Specimens were first scaled to a centroid size (C_S: the square root of the sum of squared distances of a

set of landmarks from their centre of gravity). The scaled configurations were superimposed to produce a common centroid, then rotated and translated to the optimal fit, thus minimizing the squared distances between each landmark while the relative distances to each other remained constant. After that, shapes were projected to a linear tangent space to Kendall's shape space (Rohlf, 1999), allowing the use of linear multivariate statistical methods (Dryden & Mardia, 1998; Zelditch *et al.*, 2004).

Based on a generalized procrustes reference configuration, the thin-plate spline deformation model (Rohlf & Slice, 1990; Bookstein, 1991) was used as a linear transformation to depict the main relative shape changes among specimens. This procedure allowed the use of a conventional statistical test, because partial warps and uniform component scores have the same number of variables per specimen as degrees of freedom and so no information was lost during the linear transformation (Zelditch *et al.*, 2004; Nolte & Sheets, 2005).

All statistical and morphometric analyses were performed with the Integrated Morphometric Packages – IMP software (Sheets, 2004) in its different components (CoordGen6, CVAGen6o, Manovaboard6, Regress6k, Standard6, TwoGroup6h and VecCompare6).

3.2.5 Allometry, ontogeny and sex assessment

Geometric morphometric methods typically remove the geometric scale effect but not the shape variations associated with growth and ontogenetic stage (Trapani, 2003). Moreover, as described previously, sex change is a complex physiological and developmental process that can be associated with morphological variation. These are

important sources of shape variation in fishes (Loy *et al.*, 1996, 1998; Reis *et al.*, 1998; Trapani, 2003) and may lead to misinterpretations related to geographical population structure. For the purpose of this study, allometry, ontogenetic stage (*O*, two levels: immature and mature) and sex (*S*, three levels: male, female and bisexual) were previously assessed by three independent series of multivariate analysis of variance (MANOVA) followed by a multivariate analysis of covariance (MANCOVA) with centroid size (C_S) as the covariate. The first multivariate analysis allowed for the assessment of allometric effects. In all multivariate analyses, partial warps plus uniform components (n = 30+2) were used as dependent variables.

The effect of ontogenetic stage was studied using data from the two sampling sites at Santiago Island (ST_1: n = 50; ST_2: n = 52), which is the only island where immature and mature specimens were collected at both sampling sites (Table 3.1). First, a two-way MANOVA was performed with site *(L)* and ontogenetic stage *(O)* as the independent factors. A MANCOVA was then performed with the same factors to control for the size effect.

An analysis of body shape variation associated with sex *(S)* was carried out with samples from Santa Luzia Island (LZ_2: n = 61; LZ_4: n = 50); this site had the most balanced number of the main sexual groups (Table 3.1). The same statistical procedure mentioned above was used: a two-way MANOVA on shape variables with site and sex as the two independent factors followed by a MANCOVA with the same factors.

To assess patterns of body shape allometry associated with island and sampling site, a two-way MANOVA among islands and between sites was performed on data from females only (n=341). Data from São Vicente and Fogo were excluded because these

islands only had one sampling site. This procedure avoided any potential confounding effects associated with sex and (or) ontogenetic stage (Klingenberg, 1996). Using the same data set, a MANCOVA was then performed to control for the size effect. Depending on the type of relationship between body shape variables, centroid size (C_S) and classification factors, four main models were defined: a common slope model based only on C_S; two single models (factor 1 x C_S and factor 2 x C_S) and a model using all differing slopes (factor 1 x factor 2 x C_S). Each model was then compared by a permutation test with the common slope model in terms of the statistically significant variance explained (Sheets, 2004).

In the absence of allometry, geometric morphometrics provides a size variable that is uncorrelated with shape variables (Bookstein, 1996). Because of allometric growth, however, different groups may reach the same developmental stage at different sizes or ages, and so comparisons made at a comparable stage may require the use of different body sizes (Zelditch *et al.*, 2004). Nevertheless, it is also desirable to investigate shape differences in developmental terms by comparing groups at developmentally comparable stages. For this purpose, the results of the allometry, ontogeny and sex effects on body shape variations were subsequently integrated in the analysis of the overall body shape variation. Prior to the Canonical Variate Analysis (CVA), data were standardized to the mean centroid size (IMP software – Standard6).

3.2.6 Population structure

To test the hypothesis that samples from all islands and sampling sites did not differ in body shape, shape variables (partial warps plus uniform components) were used as dependent variables in a two-way MANOVA (Sheets, 2004). In fact the partial procrustes

distance can be used as a measure of the summed square variance (SS) instead of Lambda. With such a procedure, statistics should be more powerful and avoid the difficulties in calculating the correct degrees of freedom and the number of landmarks relative to sample size. To assess a factor effect (sampling site or island), an *F*-statistic is usually computed as the ratio between the variance explained by the factor and the unexplained variance. Extending this principle to shape variables, a generalized form of Goodall's *F*-test allows for the computation of an *F*-statistic with a squared partial procrustes distance. A permutation test was subsequently performed by computing the *F*-value for the observed data and then generating a distribution of *F*-values for permutated versions of all factors. During permutation steps, specimens are assigned randomly (without replacement) to a group, so that the permuted groups have the same numbers of specimens as in the original data. When the observed *F*-score is higher than 95% of the permuted data, there is a significant dependence of shape on the factor. In this study, island (five levels) and site (two levels) were used as independent factors and the statistical significance of the variance they explained was tested in 10^3 permutations. This analysis was carried out with pooled data (n = 487); data from São Vicente and Fogo islands were excluded because these localities had only one sampling site per island.

To investigate which dimension optimally discriminated average body shape both among islands as well as within islands, *i.e.,* between sampling sites from the same island, a series of canonical variate analyses (CVA) was performed using the IMP software (CVAGen6o). This multivariate analysis determines the set of axes that best discriminates among predefined groups (islands or sampling sites) by determining the linear

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combinations of the original variables that display the greatest variance between groups relative to the variance within groups (Zelditch *et al.*, 2004). A distance-based approach was then used to determine which island or site each specimen belonged to, based upon the scores of the canonical variates. The predicted group membership of each specimen was determined by assigning each one to the group whose mean was closest to the specimen. A jack-knife estimation of the assignment accuracy was run based on the bootstrap methods (Nolte & Sheets, 2005) and one of the following classifications was assigned: correct significant, correct non-significant, false significant and false non-significant. Tests were performed using 10^3 bootstraps.

Three CVA models based on a procrustes shape coordinates of standardized data were used to discriminate among islands. First, a CVA (model I) was run with specimens aligned relative to an archipelago reference configuration. Second, another CVA (model II) was run with the same data set, but each specimen was previously aligned relative to the island of origin (seven groups). Finally, a third CVA (model III) was run with specimens aligned according to the sampling site (10 groups). In model III data from São Vicente and Fogo were again excluded because each locality had only one sampling site. With this approach, which accentuates the variance between groups, it was possible to evaluate and compare the different levels of geographic body shape variability in the archipelago (intra-island, inter-island). Body shape variations were then described by using the thin-plate spline deformation model (Rohlf & Slice, 1990; Bookstein, 1991).

Finally, the developmental rate and ontogenetic change in shape for all islands were evaluated by comparing multivariate regression equations (Trapani, 2003; Zelditch *et al.*,

2003, 2004). The angle between two growth vectors is a measure of their similarity in direction and the cosine is a correlation that can be used as a metric of similarity. Using the IMP software (VecCompare6), the angles within and between islands were calculated and examined in pairwise comparisons with $3.6x10^3$ bootstraps (this number of bootstraps was set according to the convergence of results). The greater variability found within rather than between samples indicates that growth vectors of individuals overlap to some degree and therefore indicates non-significant differences in the direction of shape change. Typically, 90^o represents orthogonal morphological vectors and might indicate species divergence in terms of evolutionary trajectories. Thus, by testing whether angles between populations are significantly smaller than 90^o, it is possible to determine trends in the evolution of species' body shape and population divergence. Moreover, two shapes might not differ in their directions but in the length of their growth vector and so in how much change they undergo. Hence, for each island, the rate of change in body shape relative to size was estimated (IMP software - Regress6) by separate univariate regressions of the partial procrustes distance between each specimen and the smallest one in the data set against the centroid size. The regression slope represents the rate of response of shape to growth. The thin-plate spline deformation model allowed to visualize and describe the main allometric changes observed.

3.2.7 Role of habitat fragmentation

Geographic distances and average depths between pairs of islands were obtained from Medina *et al.* (2007). Distances varied from 6 km between Brava Island and the

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Grande islet to 270 km between Santo Antão and Maio. Depths varied from 55 m between Brava Island and the Grande islet to 3990 m between São Vicente and Fogo. Average geographic distance and depth were organized into two distinct matrices, respectively referred to as *G* and *B*. For statistical analyses, data were normalized to prevent scale measure effects.

Finally, using the IMP software (TwoGroup6h), average body shape from different islands was compared and a squared matrix of partial procrustes distance *(D)* was computed between islands in pairwise comparisons. Further, two other morphological matrices were computed between islands: the magnitude of shape change by centroid unit (D_1) and the direction of shape change (D_2). A preliminary series of Mantel tests was used to compute linear and first-order partial correlations between the three squared symmetrical matrices of dissimilarities (*D*: partial procrustes distance; *G*: average geographic distance; *B*: average bathymetry). Tests showed a weak and barely significant linear correlation ($r_{DxG} = 0.305$, $P = 0.045$; $r_{DxB} = 0.407$, $P = 0.040$), but partial correlations were not significant ($r_{PxG|B} = 0.071$, $P = 0.366$; $r_{PxB|G} = 0.482$, $P = 0.069$). Hence, to integrate the dual influence of geographical distance and depth, we computed a physical isolation factor $I_{GB} = G \times B$ (Medina *et al.*, 2007), with values varying from 0.33 km^2 between Brava Island and the Secos islets to 846 km^2 between Sal and Brava islands. The effect of physical isolation on overall body shape variability was investigated by a Mantel test between *D* and I_{GB}. After that, the nature of the I_{GB} effect was assessed by two more Mantel tests, first between D_1

and I_{GB}, and then between D_2 and I_{GB}. All correlation tests were performed by an exhaustive number of randomized permutations ($5x10^5$) with an α error level of 0.05.

3.3 Results

3.3.1 Allometry, ontogeny and sex assessment

The effects of sex (MANOVA: $F_{32, 3488} = 3.681$; $P = 0.001$) and ontogenetic stage (MANOVA: $F_{32, 3200} = 2.561$; $P = 0.006$) were significant. The shape variations associated with sex and ontogenetic stage, though significant, contributed only for 3.3% and 2.5% of the total variance, respectively. When size was held constant (*i.e.*, removing the effect of size on shape) in a MANCOVA with ontogenetic stage and sex, the effect of these two factors was still significant (Table 3.2, upper and middle panels). However, the permutation test comparing the variance explained by the four models showed non-significant P values for all combinations of factors. This suggests that only the common slope model (C_S) had statistically significant explanatory power (Table 3.3, upper and middle panels). Differences in body shape associated with sex ($P = 0.140$) and ontogenetic stage ($P = 0.180$) as single or combined factors at the same site ($P = 0.860$ and $P = 0.380$, respectively for sex and ontogenetic) were not significant. When the site effect was also controlled ($P = 0.900$ and $P = 0.994$, respectively for sex and ontogenetic) differences was still not significant. This implies that size had a significant effect (allometric effect), with C_S explaining 11.5% of the total body shape variation ($P < 0.005$).

When the effects of sex and ontogenetic stage were controlled, intra-island (MANOVA: $F_{160, 10592} = 6.695$; $P < 0.0005$) and inter-island (MANOVA: $F_{128, 10592} = 30.572$; $P < 0.0005$) shape variation were both significant.

Tableau 3.2 *Cephalopholis taeniops*. Résultats d'une série de trois MANCOVA avec les déformations partielles plus la composante uniforme comme variables dépendantes, la taille du centroïde comme covariable et site d'échantillonnage (*L*) contrôlé. Les facteurs indépendants ont été sexe (*S*: panneau supérieur), état ontogénique (*O*: panneau central) et îles (*I*: panneau inférieur). Les valeurs de P ont été obtenues avec 10^3 interactions.

Table 3.2 *Cephalopholis taeniops*. Results of a series of three MANCOVAs with partial warps and uniform components as the dependent variables, centroid size as the covariate, and sampling sites (*L*) controlled. Independent factors were sex (*S*: upper panel), ontogenetic stage (*O*: middle panel) and island (*I*: lower panel). *P* values were derived from 10^3 permutations.

	SS	F	df	P
L	0.0036	3.660	32, 3488	<0.001
S	0.0034	3.410	32, 3488	<0.001
L x *S*	0.0011	1.075	32, 3488	0.430
Error	0.1083	-	-	-
L	0.0098	8.020	32, 3200	<0.001
O	0.0035	2.865	32, 3200	<0.001
L x *O*	0.0007	0.576	32, 3200	0.800
Error	0.1224	-	-	-
I	0.1428	34.091	128, 10624	<0.001
L	0.0084	8.053	32, 10624	<0.001
I x *L*	0.0205	4.895	128, 10624	<0.001
Error	0.3476	-	-	-

Tableau 3.3 *Cephalopholis taeniops*. Résultats des tests de permutations de comparaison des pentes de quatre modèles différents de MANCOVA, basé sur la variance statistiquement significative expliquée (SS) par chaque source de variation de forme – site (*L*) et sexe (*S*) dans le panneau supérieure; site (*L*) et état ontogénique (*O*) dans le panneau central ; site (*L*) et île (*I*) dans le panneau inférieur. Chaque modèle a été comparé avec le modèle de pente commune (*Cs*). Des faibles valeurs de *P* (en gras) indiquent que le modèle correspondant présente un meilleure pouvoir explicatif que *Cs* et donc il explique plus de variance statistiquement significative. Les valeurs de *P* ont été obtenues avec 10^3 interactions.

Table 3.3 *Cephalopholis taeniops*. Results of permutation tests of slope comparisons between four different MANCOVA models based on the statistically significant variance explained (SS) by each source of shape variation – site (*L*) and sex (*S*) in the upper panel; site (*L*) and ontogenetic stage (*O*) in the middle panel; site (*L*) and island (*I*) in the lower panel. Each model was compared with the common slope model (C_S). Low *P* (in bold) indicates that the corresponding model has a better explanatory power than C_S. *P* values were derived from 10^3 permutations.

Model	Total SS	Model SS	Error	P
C_S	0.1214	0.0131	0.1082	
L x C_S	0.1214	0.0106	0.1108	0.900
S x C_S	0.1214	0.0129	0.1085	0.140
L x S x C_S	0.1214	0.0201	0.1012	0.860
C_S	0.1410	0.0187	0.1222	
L x C_S	0.1410	0.0158	0.1252	0.980
O x C_S	0.1410	0.0157	0.1253	0.180
L x O x C_S	0.1410	0.0314	0.1096	0.380
C_S	0.5598	0.1996	0.3602	
I x C_S	0.5598	0.1832	0.3766	**0.005**
L x C_S	0.5598	0.0308	0.5291	0.660
I x L x C_S	0.5598	0.2301	0.3297	**0.013**

When the size effect (MANCOVA with centroid size treated as a covariate) was removed, the model based on site variation had no significant explanatory power (P = 0.660) compared to the common slope model based only on the centroid size (Table 3.3, lower panel). Both the model based on all differing slopes and that based on the slopes of separate islands were statistically significant (P = 0.013; P = 0.005, respectively) compared to the common slope model. However, comparing single interaction models (L x C_S and I x C_S) with the model for all differing slopes (L x I x C_S), in terms of the significant variance explained, allowed to reject the former in favour of the separate-island slope model.

Inter-island body shape variations were greater than intra-island variations, and islands presented different allometric patterns. This developmental process is illustrated by a significant correlation between the partial procrustes distance and the centroid size (Fig. 3.3-A). All islands showed different shape change dynamics with size (different regression slopes), from a low rate at Santiago Island to a high rate at São Vicente Island (respectively 14.69 and 26.06 procrustes units. Except for Santiago, allometric patterns seem not well differentiated during early life stages. From a centroid size of 1.001 (approximately 230 mm in total length), differences in the shape change dynamics became more evident. Despite these differences, it was possible to depict the major ontogenetic change in body shape associated with allometry (Fig. 3.3- B). The overall change is expressed by an anterior and upward inflation of the head (landmarks 9 to 13), a posterior displacement of the ventral fin (landmarks 14 and 15) and a backward movement of the hard part of the dorsal fin (landmarks 6 to 8).

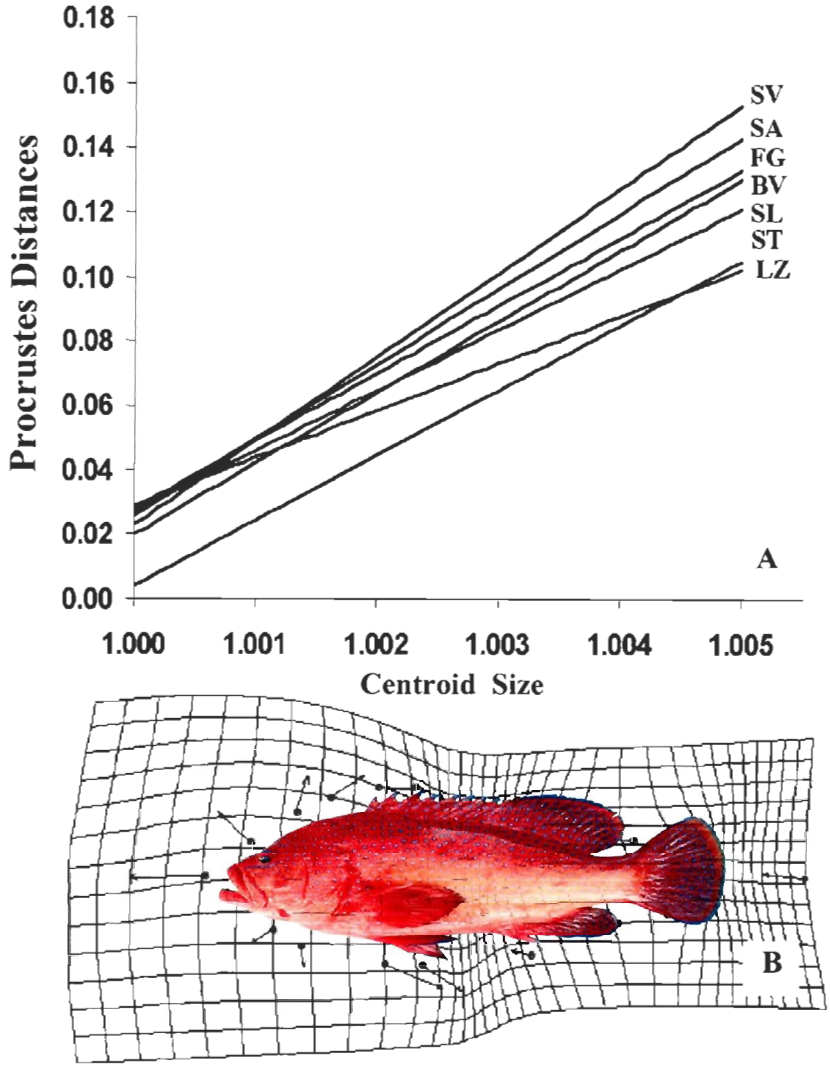

Figure 3.3

- *Cephalopholis taeniops*. Régression univariée des distances procrustes partielles en fonction de la taille du centroïde: (A) les différentes pentes de régression indiquent différentes dynamiques dans les variations de la forme avec la taille. (B) Le modèle de déformation des plaques minces montre les principales variations allométriques observées au cours du processus de croissance de l'espèce (voir texte). Les abréviations des îles se trouvent au Tableau 3.1

- *Cephalopholis taeniops*. Univariate regressions of partial procrustes distances against centroid size: (A) different regression slopes indicate different dynamics of shape change with size. (B) the thin-plate spline deformation model shows the main allometric changes observed during the growth process of *C. taeniops* (see text). Island abbreviations are given in Table 3.1.

These deformations are associated with an anterior displacement of the pelvic fin (landmarks 16 and 17) and the soft part of the dorsal fin (landmarks 4 and 5). The caudal peduncle tends to grow longer by a posterior displacement of landmarks 3 and 18.

3.3.2 Population structure

Body shape differences among islands and between sites of a single island are highly significant (Table 3.4). Despite the statistical significance of the site effect, the corresponding variance (0.8%) was not significant compared to the variance (24.8%) associated with islands. Such a statistical difference is associated with the significant interaction between islands and sites and suggests different local patterns in body shape variation among islands. Site effects are highly significant for Santo Antão, Sal and Santiago (all $P < 0.001$), explaining respectively 16.7%, 12.3% and 10.0% of the variation; site effects for Santa Luzia ($P = 0.194$) and Boavista ($P = 0.518$), explaining only 2.0% and 1.0% of the variation, were not significant. These results indicate that the body shape variation in inter-island comparisons was greater than that for intra-island comparisons.

The average body shape of all islands was well discriminated in CVA by five significant axes (*Wilk's lambda* = 0.0068, 0.0631, 0.2126, 0.3939, 0.6633; all $P < 2.2205 \times 10^{-16}$). Despite various degrees of data scatter, overlapped by the 95% of equal-frequency ellipses, Figure 3.4 (CVA model I) depicts the discrimination between islands by a graphical representation of the first three axes. The first separates a group formed by Santo Antão, São Vicente and Boavista, with a large overlap among them, from Santiago and Santa Luzia (Fig. 3.4-A). These latter two islands are quite well separated by the second axis.

Tableau 3.4 *Cephalopholis taeniops*. Résultat d'une MANOVA sur les déformations partielles plus la composante uniforme comme variables dépendantes, avec le site d'échantillonnage (L) et l'île (I) comme facteurs indépendants. Les valeurs de P ont été obtenues avec 10^3 interactions.

Table 3.4 *Cephalopholis taeniops*. Results of a MANOVA with partial warps and uniform components as the dependent variables and sampling site (*L*) and island (*I*) as the independent factors. *P* values were derived from 10^3 permutations.

	SS	F	*df*	*P*
L	0.0068	5.953	32, 15456	<0.001
I	0.2009	43.773	128, 15456	<0.001
L x *I*	0.0487	10.621	128, 15456	<0.001
Error	0.5541	-	-	-

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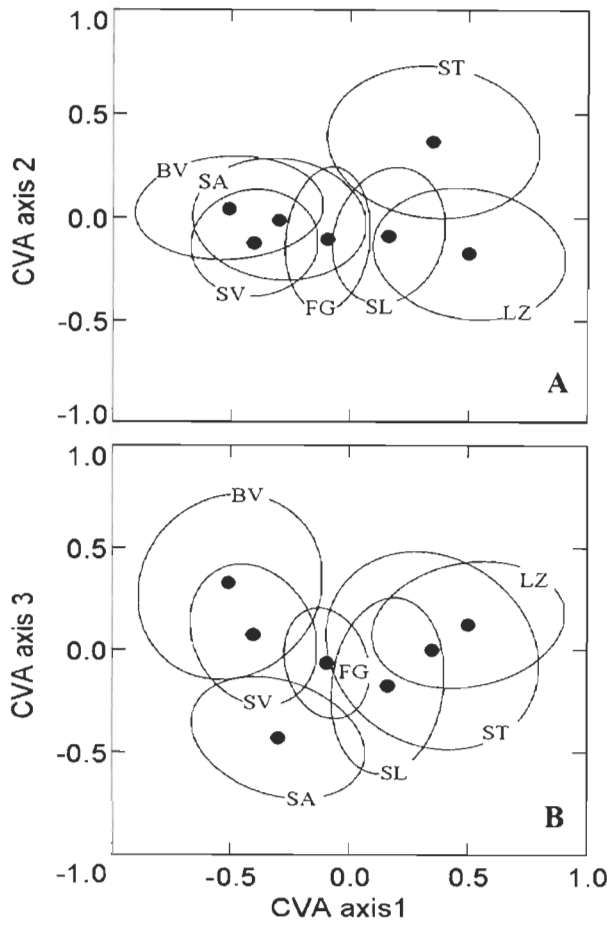

Figure 3.4

- *Cephaopholis taeniops*. Analyse canonique multivariée (CVA modèle I) de la variation de forme du corps de *C. taeniops*. Les spécimens sont alignés par rapport à une configuration de référence pour l'archipel. Parmi les 32 axes canoniques, les cinq premiers ont révélé un pouvoir discriminant statistiquement significatif. Les graphiques montrent la dispersion des données pour l'ensemble des échantillons de tous les sites. (A) L'axe 1 discrimine un groupe d'îles formées par Santo Antão, São Vicente, Boavista et un autre formé par Santiago et Santa Luzia. Au centre, les îles de Sal et Fogo chevauchent celles Santa Luzia et Santiago qui sont bien discriminés par l'axe 2. (B) L'axe 3 discrimine bien São Vicente (chevauchée avec Boavista) et Santo Antão. Au centre, l'île de Fogo est assez bien discriminée aussi bien qu'individus des autres îles, à travers différentes combinaisons des axes 1 a 5. Les abréviations des îles se trouvent au Tableau 3.1

- *Cephalopholis taeniops*. Canonical Variate Analysis (CVA – model I) of body shape variations among *C. taeniops*. Specimens are aligned relative to a reference configuration for the archipelago. Of the 32 CV axes, the discriminating powers of the first five were statistically significant. Plots show scatter data for samples pooled from all locations. (A) Axis 1 discriminates between a group of islands formed by SA, SV, BV and another one formed by ST and LZ. At the centre, SL and FG overlap ST and LZ, which are well discriminated by CVA-axis 2. (B) Axis 3 clearly discriminates between SV (overlapped with BV) and SA. At the centre, FG is quite well differentiated, as are individuals from all islands with different combinations of axes 1 to 5. Island abbreviations are given in Table I.

Despite an important overlap at the centre of the graph, it is possible to extract Sal with moderate overlap. With a slight overlap, the third axis (Fig. 3.4-B) separates São Vicente and Boavista from Santo Antão. A combination of the second and third axes identified Fogo at the centre of the graph. All of these discriminations become clearer when considering the full set of combinations between the five axes, which results in the correct and significant assignment of 77.5% of the specimens to islands. The overlap is shown by the significant incorrect assignment of 22.3% of the specimens. About 0.2% of specimens were assigned as being non-significant.

The discrimination power of the CVA improved when specimens had been previously aligned relative to the island of origin (CVA model II, Fig. 3.5-A) rather than to the sampling site (CVA model III, Fig. 3.5-B). In model II, all islands were completely discriminated by the first two axes (Wilk's lambda = 0.0000; $P < 2.2205 \times 10^{-16}$). Individuals were correctly and significantly assigned to islands (99%) with only minor significant scatter overlap. The first axis discriminated all islands excepting São Vicente and Boavista (Fig. 3.5-A). This discrimination was associated with a relative body depth expressed by an overall dorso-ventral inflation and an antero-posterior compression (Fig. 3.6-A). These two islands were well distinguished in the second axis, which showed an antero-ventral inflation of the head relative to a postero-ventral inflation of the trunk (Fig. 3.6-B). Santa Luzia and Boavista overlapped slightly on the first two axes but were separated completely by the third axis (Wilk's lambda = 0.0004; $P < 2.2205x10^{-16}$; not shown on the graph), which is associated with a pronounced ventral compression of the anterior and posterior parts of the body (Fig. 3.6-C).

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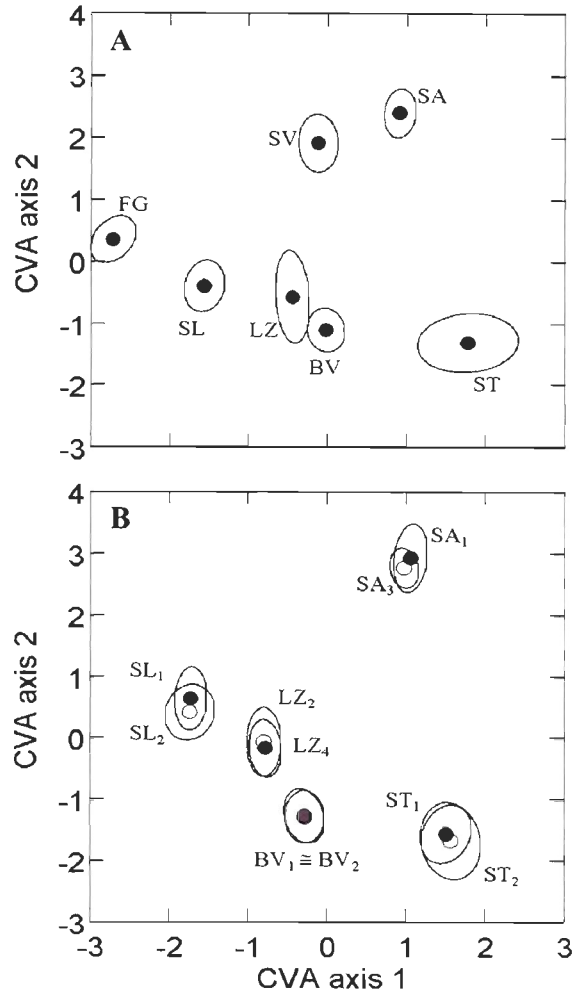


Figure 3.5

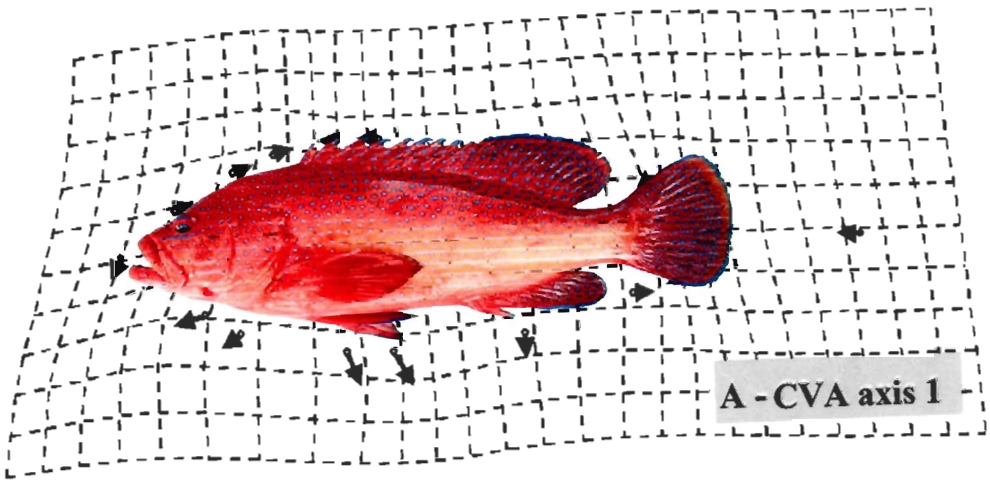
- *Cephalopholis taeniops*. Analyse canonique multivariée (CVA) de la variation de forme du corps de *C. taeniops*. (A) modèle CVA II: les spécimens sont d'abord alignés par rapport à la configuration de référence de l'île et ensuite par rapport à l'archipel. L'axe 1 fait la distinction entre Fogo, Sal, Santo Antão, Santiago, Boavista et Santa Luzia. L'axe 2 fait bien la distinction entre deux groupes: Santo Antão, São Vicente et Fogo, Sal, Santa Luzia, Boavista, Santiago. (B) modèle CVA III: les spécimens sont d'abord alignés par rapport à la configuration de référence du site et ensuite par rapport à l'archipel. Pour les deux modèles, à partir d'un nombre total de 32 axes canoniques, les cinq premiers ont révélé un pouvoir discriminant statistiquement significatif. Les îles ont été mieux discriminées entre elles que les sites pour la même île. Les abréviations des îles se trouvent au Tableau 3.1

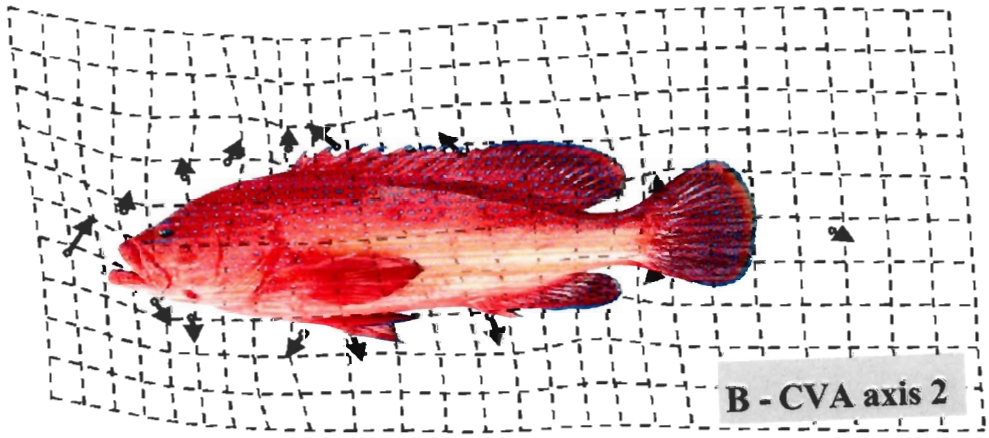
- *Cephalopholis taeniops*. Canonical Variate Analysis of body shape variation among *C. taeniops*. (a) CVA model II: specimens are first aligned relative to the island's reference configuration and then relative to the archipelago's reference. Axis 1 clearly discriminates between FG, SL, SA, ST, BV and LZ. Axis 2 axis clearly discriminates between two groups: SA, SV and FG, SL, LZ, BV, ST. (b) CVA model III: specimens are first aligned relative to the site's reference configuration and then relative to the archipelago's reference. For the two models, from a total of 32 CV axes, the first five revealed statistically significant discriminating power. Inter-island discriminations were better than intra-island discriminations. Island abbreviations are given in Table I.

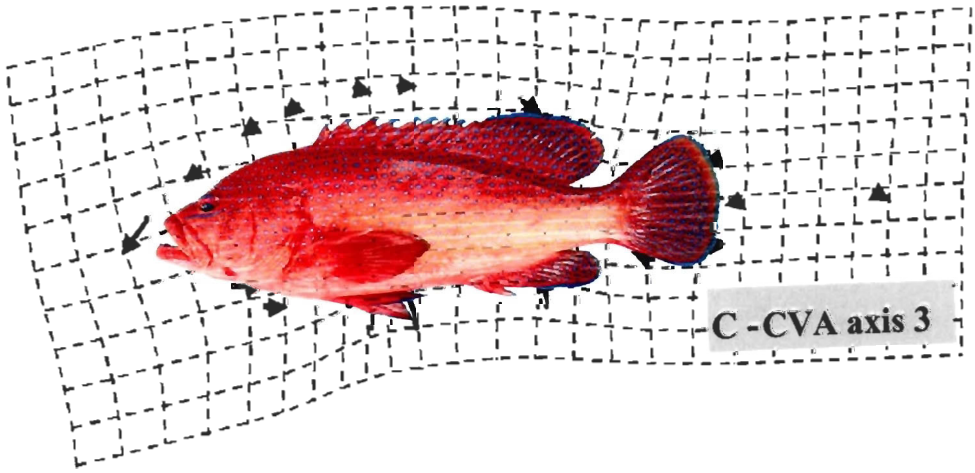
Figure 3.6 (page suivante)

- *Cephalopholis taeniops*. Grille des déformations des plaques minces montrant le déplacement des vecteurs induit par les axes du modèle CVA II. Les changements de forme peuvent être visualisés en tant que déplacement relatif des vecteurs pour chaque point de repère et sont exprimés en termes d'inflation ou compression des parties du corps. L'axe 1 montre une inflation dorso-ventrale générale et une compression antéro-postérieure, exprimant la hauteur relative du corps. L'axe 2 montre une inflation antéro-ventrale de la tête par rapport à une inflation postéro-ventrale du tronc. De plus, il suggère une compression antéro-postérieure des parties dorsales du corps. L'axe 3 montre une forte compression ventrale aussi bien des parties antérieures que des parties postérieures.

- *Cephalopholis taeniops*. Thin-plate spline grid of deformations showing displacement vectors implied by axes from CVA model II. The shape change can be visualized as the relative displacement of vectors for each landmark and are expressed in terms of inflation or compression of body parts. Axis 1 shows an overall dorso-ventral inflation and an antero-posterior compression, expressing relative body depth. Axis 2 shows an antero-ventral inflation of the head relative to a postero-ventral inflation of the trunk; this suggests an overall antero-posterior compression of dorsal parts of the body. Axis 3 shows a pronounced ventral compression for anterior parts as well as for posterior ones.


A - CVA axis 1


B - CVA axis 2


C - CVA axis 3

The CVA model III (Fig. 3.5-B) showed an overall lower discriminating power (74% correct site assignment and 25.3% incorrect site assignment). When the CVA's discriminating power was analyzed between two sites at the same island, it was statistically significant for Santo Antão (Wilk's lambda = 0.1630, $P = 4.2\text{x}10^{-15}$), Sal (Wilk's lambda = 0.0377; $P = 2.2\text{x}10^{-16}$) and Santiago (Wilk's lambda = 0.4217; $P = 5.6\text{x}10^{-5}$), and not significant for Santa Luzia and Boavista. The percentiles of correct and incorrect assignments to sites were 74.1% and 25.7%, respectively, for Santo Antão, 53.3% and 45.3% for Santa Luzia, 75.4% and 22.2% for Sal, 48.7% and 50.8% for Boavista, and 59.0% and 40.8% for Santiago. These results confirm that body shape variability between inter-island localities was greater than that for intra-island sites and clearly demonstrates that islands can be considered as independent population units for phenotypic purposes based on body shape variation.

Pairwise comparisons of the ontogeny of body shape change between islands revealed different degrees of similarity. For northern islands (Santo Antão, São Vicente and Santa Luzia), the angles within samples were significantly greater than those between samples, thus suggesting that they show similar direction in shape ontogeny (Table 3.5). In the same way, the Boavista Island results show a pattern identical to that of the group of northern islands. For all other paired comparisons, angles within samples were smaller than between samples, indicating different patterns in the direction of shape changes. The angles between all pairs of islands except Fogo were still significantly smaller than 90°. However, when comparing Fogo with all other islands, the inter-population angles depart far from the orthogonal relation, suggesting that individuals from that island are undergoing independent body shape trajectories.

Tableau 3.5 *Cephalopholis taeniops*. Matrice des vecteurs ontogéniques de *C. taeniops* intra-île (coin inférieurs et supérieurs de chaque cellule) et inter-îles (centre de chaque cellule) après superposition procruste des espèces par GLS. Les calculs ont été réalisés avec $3.6x10^3$ interactions.

Table 3.5 *Cephalopholis taeniops*. Matrix of ontogenetic vectors of *C. taeniops* within islands (lower-left and upper-right corners of each cell) and between islands (centre of each cell) after GLS procrustes superimposition of specimens. Calculations were performed by $3.6x10^3$ bootstraps. Island abbreviations are given in Table I.

	SA	SV	LZ	SL	BV	ST	FG
SA	0.0 **0.0** 0.0						
SV	67.4 **38.9** 57.9	0.0 **0.0** 0.0					
LZ	60.2 **61.3** 52.7	59.7 **40.3** 62.2	0.0 **0.0** 0.0				
SL	62.4 **88.9** 29.3	59.7 **69.6** 33.2	55.8 **70.6** 29.7	0.0 **0.0** 0.0			
BV	60.2 **67.2** 67.8	59.7 **55.9** 73.8	52.2 **54.9** 65.1	29.6 **79.9** 68.5	0.0 **0.0** 0.0		
ST	60.2 **66.7** 58.2	59.7 **72.4** 60.0	52.1 **62.5** 58.0	29.6 **62.3** 62.2	65.0 **76.1** 57.9	0.0 **0.0** 0.0	
FG	78.8 **94.6** 68.8	70.0 **108.3** 67.9	74.7 **111.9** 68.4	42.3 **110.0** 67.8	83.7 **107.3** 67.7	83.5 **105.4** 67.7	0.0 **0.0** 0.0

3.3.3 Role of habitat fragmentation

There is evidence that physical isolation plays a significant role in island differentiation based on body shape variation. The Mantel test showed a significant linear correlation ($r = 0.416$, $P = 0.025$) between the I_{GB} and D matrices. Thus, physical isolation based on the combined effect of geographic distance and depth appears to increase morphological divergence between islands. The influence of this physical isolation seems more related to the direction of shape change (D_1), expressed by a significant partial correlation with I_{GB} ($r_{D_1 x\, I_{GB}|D_2} = 0.543$; $P = 0.003$), rather than to the rate of shape change (D_2), with which the correlation is weak and not significant ($r_{D_2 x\, I_{GB}|D_1} = 0.113$; $P = 0.298$). These results show that the most isolated islands tend to undergo more independent ontogenetic direction on body shape variation, as does Fogo Island.

3.4 Discussion

3.4.1 Allometry, ontogeny and sex assessment

Despite the biological and physiological complexities in the reproduction of *Cephalopholis* spp. (Siau, 1994; Nakai & Sano, 2002; Liu & Sadovy, 2004), this study reveals that body shape does not vary significantly with sex, reproductive stage or ontogenetic stage. Even though no relationship between body shape changes and sexual adaptation was found, significant shape variation was found to be associated with growth, indicating an allometric pattern in the ontogeny of shape for this species. This pattern varies significantly among islands, not only in direction but also in the rate of shape change. Growth vectors of specimens from Fogo Island were very different from those of other

islands. Santo Antão and São Vicente had high rates of shape change relative to Santiago and Santa Luzia, while the remaining islands showed moderate levels of size-related shape changes. Thus, allometry seems to be inherent in this species, independent of sex but potentially influenced by environmental factors. These results allow hypothesizing that *C. taeniops* is a species predisposed to body shape change with growth, but the degree of expression of this trait is environmentally dependent.

Although allometric patterns vary among islands, the main deformations associated with size show that as individuals grow larger, the anterior part of the body lengthens and the mid-body region shortens, and there is a stretching of the caudal peduncle along the dorso-ventral axis. The pronounced head displacement observed in this study can be considered as static allometry and underlies developmental processes (Klingenberg, 1996). All other allometric changes can be associated with different ecological adaptations that occur according to a species' life history. On one hand, large body depth may have a greater defensive value than improved motor function (Webb & Fairchild, 2001) because aquatic predators tend to aim at the centre of mass of their fish prey, which is near the region of maximum depth (Webb, 1984). On the other hand, slender bodies have more ability to react to perturbations and correct disturbances when swimming (Webb, 2002).

3.4.2 Population structure

When other sources of body shape variation are controlled (*i.e.,* allometry, ontogeny and sex), body shape change is still revealed to be associated with geographical variations. Such variations are not only observed among islands but also between sites of the same

island. At Santo Antão, body shape reveals significant differences between the northeastern and southwestern parts of the island. Also, at Sal and Santiago islands, morphological differences are observed between the northeastern and northwestern sites. Those geographical variations are related to several factors, but the topographic features and geomorphological characteristics of those islands seem to play important roles in the heterogeneity of the environment. On one hand, they are islands with a very restricted insular shelf until 200 m in depth (Bravo de Laguna, 1985), which constrains population mixing; on the other hand, an island's main axis of orientation may act as a barrier between populations from two opposite sides. In contrast to these three islands, fish body shape from Santa Luzia and Boavista do not show significant divergences in local variations. Santa Luzia is a very small island with a large insular shelf that is shared at an average 77 m depth with São Vicente, the nearest island. Boavista is relatively large and round, with the shallowest and largest insular shelf of the archipelago. These geomorphological features seem to positively influence population mixing.

Despite these two levels of geographical variation, body shape variability among islands is usually greater than between sites, highlighting an effect of the ecosystem fragmentation and suggesting that each island can be considered as an independent unit for phenotypic purposes based on body shape. These are very promising results. In fact, patterns in morphometric variation can indicate intraspecific variations in life histories associated with population attributes (*e.g.*, growth, reproduction, fecundity, longevity and size structure). These are intimately related to population dynamics (*e.g.*, intrinsic rate of increase, carrying capacity, resilience) and determine how each stock responds to

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exploitation (Cadrin & Friedland, 1999). Very often, the location of fishing effort is non-random relative to a population's spatial distribution, being concentrated where the harvestable biomass is greatest or where target fishes are most accessible. Hence fishing mortality is selective with respect both to species and phenotypic variation within species (Law, 2000). Therefore, phenotypic stocks can be defined (Swain & Foote, 1999) for management and conservation purposes (Utter, 1981; Lowe et *al.*, 1998) despite the existence of genetic homogeneity. As a result, taking into account the natural ecosystem fragmentation in the archipelago, which tends to establish a population structure by island or island group, management and conservation approaches based on phenotypic stocks can be an effective and complementary tool to control selection generated by fishing.

The population units are well discriminated by CVA, and the thin plate spline deformation model based on the same shape variables allows one to depict shape changes mainly related to variations in body depth. A large body area is associated with a large maximum depth of the body and median fins. In contrast to a large area increasing drag, the large body depth should reduce slip and promote better performance in structurally complex habitats. Similar results were found in other fishes (Klingenberg *et al.*, 2003; Langerhans *et al.*, 2003; Neves & Monteiro, 2003) and suggest that such patterns of body shape variation in fishes are associated with the manoeuvrability of individuals, as stated by Webb & Fairchild (2001). This adaptation allows individuals to adjust their swimming behaviour and manoeuvres to foraging, predator–prey interactions, agonistic interactions or courtship. These are likely to be important in all aspects of fish biology and ecology,

particularly in a complex and very heterogeneous environment. In fact, in the Cape Verde Archipelago, the habitats of demersal species are diverse. The spatial heterogeneity associated with a diversified coastal zone and insular shelf (*i.e.,* space availability) surrounding islands is assumed to be at the origin of a huge number of ecological niches and habitats (Medina *et al.*, 2007). These factors can explain a substantial part of the phenotypic variability and the population structure revealed in this study of *C. taeniops*.

3.4.3 Role of habitat fragmentation

As expected, physical isolation by geographic distance and depth are positively correlated with morphological divergence among populations from different islands, thus corroborating the hypothesis that habitat fragmentation in the Cape Verde Archipelago can be interpreted in terms of the marine population structure. Similar results were found by Langerhans *et al.* (2003) in two neotropical fish species (*Bryconops caudomaculatus* and *Briotodoma wavrini*) in southwestern Venezuela. While their results showed the magnitude of morphological divergence increasing with spatial distance between habitats, the present results reveal the same trend—not in the rate of shape change, but in the direction of shape change. Growth trajectories tend to be more independent when islands are physically more isolated. However, the influence of isolation on morphological divergence among distinct habitats is not a common phenomenon for all ecosystems or for all species. Hankison *et al.* (2006) did not find any statistically significant effect of spatial isolation in the morphology of Mexican sailfin mollies (*Poecilia velifera* and *P. petensis*) among populations from different states in the Yucatán Peninsula. The results of the present research allow to

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identify two important forces that may drive population differentiation and divergence in a highly fragmented archipelago system: (1) The mixing of organisms between alternative environments depending on the degree of connectivity between populations. This can be constrained or enhanced by the degree of physical isolation and gene flow; (2) The environmental pressure that tends to induce adaptive variation. Aquatic environments can exhibit large spatial or temporal variability in both abiotic and biotic conditions (*i.e.,* resource composition and availability between the near-shore, littoral, off-shore and open-water zones). Thus, species tend to exhibit morphological variants according to prevailing environmental conditions. While the first force is expected to drive divergences in direction, the second ones are supposed to play important roles in the rate of morphological change. Hence, for *C. taeniops* on the insular shelf of the Cape Verde Archipelago, the present research suggests a differentiation among populations from different islands as a result of a balance between the heterogeneity of the environment and the role of physical isolation by distance and depth.

Although this study does not allow to speculate on speciation in the archipelago, intraspecific diversity is perceived as the raw material for evolution (Zelditch *et al.*, 2004). In addition, highly differentiated populations have more potential to generate new species and even more biological diversity (Magurran, 1998). Despite results were statistically significant, their biological consequence should be further examined. Similar results have been found recently for the genetic structure of gastropod populations (*Conus* sp.) in the eastern Cape Verde islands (Duda & Rolán, 2005). These authors found that species from Boavista and Maio islands are genetically more similar to each other than they are to

species from Sal Island. In fact, the migration of species between Boavista and Maio has apparently been more common than between Sal and Boavista. This phenomenon seems to be facilitated by a larger physical isolation (I_{GB}) between Sal and Boavista. Hence, aside from the importance of oceanographic influences on larval dispersal and their consequences for population connectivity (Werner *et al.,* 1997; Cowen, 2002), a long-term persistence of such physical isolation among the Cape Verde islands has been suggested to be at the origin of strong differentiation and even speciation processes, resulting in high marine biodiversity at the genetic, specific, taxonomic, ecological and functional levels (Medina *et al.*, 2007).

This study reveals very promising results, indicating a demersal population structure based on islands as independent units. However, any decisive conclusion of such a model requires extensive studies on other demersal species that are common to all islands and islets. Such studies should integrate genetic approaches aimed at a better understanding of genotypic and environment covariance in phenotypic expression. According to Swain & Foote (1999), both environmental and genetic differences between islands may affect phenotype. On one hand, environmental influences may reinforce genetic differences, which inflate phenotypic discrimination (*i.e.,* cogradient variation). On the other hand, environmental influences may counteract genetic differences, reducing or even eliminating phenotypic differences between islands (*i.e.,* counter-gradient variation).

Because there has been no other scientific research on the population structures of the Cape Verde islands with the aim of preventing the loss of genetic resources and

biodiversity related to fishing or for conservation and management purposes, populations from spatially distinct islands should be considered as discrete management units. Thus, as stated by Stephenson (1999), aside from the debate on the basic premise behind the modern concept of a stock (Booke, 1999; Swain & Foote, 1999), this is particularly important as part of a precautionary approach framework to fisheries management (FAO, 1995) and to topical discussions of the potential value of Marine Protected Areas.

The nature and the degree of population mixing among islands should be another fundamental question to be addressed in future studies. These studies should include modelling of the spatial and temporal patterns of hydrodynamic features affecting species dispersal and distribution.

CHAPITRE 4

MODELING THE OCEAN CIRCULATION AND THE ECOSYSTEM CONNECTIVITY WITHIN CAPE VERDE ARCHIPELAGO (EASTERN ATLANTIC OCEAN) BY MEANS OF EMPIRICAL ORTHOGONAL FUNCTIONS AND LAGRANGIAN STOCHASTIC MODELLING

Article en préparation pour publication

Résumé

Le Cap-Vert est un archipel de l'océan Atlantique nord-est sous l'influence des vents alizés du nord-est et des systèmes de circulation océaniques à grande échelle. Bien que l'on ait montré récemment que les populations démersales sont structurées par îles, aucune information n'est disponible sur les flux spatiaux d'énergie, de matière, ou d'organismes à travers les frontières des îles. Ainsi, la circulation océanique et le degré de mélange des populations demeurent inconnus. Dans ce travail, nous utilisons la vitesse du courant obtenue à partir des données du programme Mercator pour modéliser la circulation océanique dominante à l'aide d'analyses EOF. La connectivité entre les îles a été étudiée au moyen de simulations LSM. Nous proposons des indices de connectivité écologiques qui sont appliqués pour estimer la rétention locale, le taux d'importation/exportation entre les îles, les pertes des particules hors de l'archipel, la connectivité et l'interconnectivité hydrodynamiques. Ensuite, au moyen d'analyses statistiques multivariées et de corrélation nous étudions la connectivité de l'écosystème à différentes profondeurs et la relation entre la connectivité hydrodynamique, les traits phénotypiques, la distance géographique et la bathymétrie moyenne. Les résultats révèlent un régime général de circulation océanique selon un patron de variation correspondant à la variation saisonnière du climat, c.-à-d. une saison chaude de mai à novembre et une saison froide de décembre à avril. En surface, le patron spatial du bilan de transport de particules est différent d'une île à l'autre. Les îles de Santo Antão, Sal et Brava sont exposées aux courants dominants et subissent les plus importantes pertes. La rétention locale et l'importation sont les plus fortes sur le plateau insulaire de São Vicente, Santa Luzia, îlots Raso et Branco à longueur d'année. Ces résultats sont confirmés par la connectivité entre les îles montrant que l'île de Sal est fortement isolée des autres. Ce travail confirme que l'hydrodynamisme, lié à la bathymétrie moyenne et à la distance géographique joue un rôle principal dans la connectivité des écosystèmes d'archipels.

Mots clés : Mercator, Système d'archipel, distance géographique, bathymétrie, bilan larvaire, indices de connectivité écologique, circulation océanique, structure de populations

Abstract

Cape Verde is an archipelago in the Northeastern Atlantic Ocean under influence of dominant westerly trade winds and large-scale oceanic circulation system. Despite recent evidences of marine demersal populations structured by islands, no information is available neither on spatial flows of energy and materials, nor on organisms across islands boundaries. Thus, the ocean circulation and the degree of population mixing remain unknown. In this paper we use current velocity obtained from Mercator to model the main ocean circulation by means of EOF analysis and to investigate the implications of hydrodynamics in the ecological connectivity between islands by means of LSM. We propose ecological connectivity indices and apply them to estimate the local retention, the rate of import/export between islands, the loss of particles outside the archipelago and the hydrodynamic connectivity. Then by means of statistical multivariate and correlation analysis we study the ecosystem connectedness at depths and the relationship between hydrodynamic connectivity, phenotypical traits, geographic distance and average bathymetry. Results show a general ocean circulation regime with a seasonal pattern corresponding to the climate seasonal variation, *i.e.* a warm season from May to November and a cold season from December to April. At the surface, the spatial pattern of "larval" balance is different from one island to another. Santo Antão, Sal and Brava are exposed to dominant surface currents and experience the most important loss of particles. The local retention and the import are strongest all year round at the insular shelf of São Vicente, Santa Luzia, Raso and Branco islets. These results are confirmed by islands connectivity showing Sal strongly isolated from the others. This work confirms that hydrodynamics play a key role in the ecosystem connectivity in the archipelago and are related to geographic distance and average bathymetry between islands.

Key words: Archipelago system, geographic distance, bathymetry, ecosystem connectivity, larval balance, Mercator, ecological indices, ocean circulation

4.1 Introduction

Ocean circulation within archipelago systems is affected by many factors including islands size, presence or absence of insular shelf, the sharpness of the bottom slope, the speed and vertical structure of the local flow impinging on the islands, water column stratification, wind-induced effects and latitude related to Coriolis effects (Tomczak 1998; Bowman *et al.* 1996). The various mesoscale circulation patterns associated with larger scale flows and their direct interactions with coastline topography can interject a strong influence on the ocean circulation around island and create strong variability in the coastal flow within archipelagos (Cowen 2002). Islands and seamounts close to the surface can steer the flow and generate enough forces to produce the scission of oceanic eddies associated with transfer of energy, movement, salinity and temperature at a small dissipative scale (Chapman & Haidvogel 1992; Simmons & Nof 2000). These topographic figures function like frontier zones between oceanic basins. The vorticity balance, which is established after the contact of the water masses with these figures, induces particular circulation patterns and turbulent mixing processes around the islands and seamounts. The upward and downward movements of water masses produce respectively an increase and a reduction in the relative vorticity, resulting in the formation of cyclonic and anti-cyclonic eddies upstream and downstream respectively (Spall 2000). Observations in the North Atlantic Ocean at the Canary basin (Richardson & Tychensky 1998) and in the Caribbean (Cowen 2002) and in Pacific islands (Tomczak 1998) showed the role of islands and seamounts in swirling oceanic circulation. Two eddies are formed and co-rotate clockwise around the topographic figure until one is swept away with the imposed inflow, leaving the

other eddy trapped over the seamount. Other observations show that the dynamics of the anti-cyclonic structures remains always related to the topographic figure while the dynamics of the cyclonic structures can, according to current velocity, drift downstream (Kamenkovich 1986). Those circulation patterns around islands and seamounts are related to the inertial forces that result from the deformation of the flow field and are assumed to be an important process of dispersion and mixing (Robinson 1983) that can support eggs and larval retention around islands.

Archipelago systems are highly dynamic largely because of complex interactions among physical and biological processes operating on a variety of spatial and temporal scales. One of the major scale-dependent phenomena of crucial importance in marine ecology and oceanography is the larval dynamics associated with the transport of residual water mass in the ocean. Laboratory experiments, theoretical and field studies of flow around islands and seamounts (Tomczak 1998; Dong *et al.* 2007) have indicated the effect of flow disturbances producing eddying motions capable of upwelling nutrients above the thermocline. Contrary to periods of slower local flows, during periods of moderately high flow crossing islands, isopycnals are elevated in the lee of the island suggesting the existence of a trapped eddy. This influence of hydrodynamic processes is one of the key controlling factors affecting species distribution and marine ecosystem connectivity (Cowen *et al.* 2007). These factors influence recruitment directly by advection or retention and indirectly through general suitability of ecological niches *i.e.* temperature, food availability, predator/prey interactions (Agostini & Bakun 2002). Thus, knowledge of larval drift pathway and links between populations and sub-populations are important to develop

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successful management strategies for fisheries by taking into account the spatial and temporal variations of recruitment processes. It's unanimously accepted by researchers and managers that, understanding ecosystem connectivity at appropriate spatial and temporal scales is important to the long-term success of Marine Protected Areas because it reduces the risk of local extinction (Gawarkiewicz *et al.* 2007, Pineda *et al.* 2007). The understanding of ecosystem connectivity becomes a crucial issue in the development and implementation of the strategies and policies of sustainable exploitation of natural resources (Fogarty & Botsford 2007, Jones *et al.* 2007, Taylor *et al.* 1993). This issue is particularly challenging in archipelagos, which are characterized by a rich endemic marine biodiversity due to their isolation from continents. Archipelagos often represent unique ecosystems with clearly established spatial limits. Such a physical isolation has been proposed to drive genetic isolation and population structure where, species dispersal ability is very often constrained by distance and where gene flow most likely occurs between neighbouring populations.

As generally admitted in ecology, ecosystem connectivity is the degree to which the ecosystem facilitates or slows down movements among resources patches (Cowen *et al.* 2007, Taylor *et al.* 1993). This ecological concept assumes a functional relationship among habitat patches, owing to the spatial contagion of habitat and movement reactions of organisms to ecosystem structure (With *et al.* 1997). Connectivity has been measured as the dispersal success in simulation models either by counting the number of successful immigrants into all territories in an ecosystem (Schippers *et al.* 1996; Schumaker 1996; Tischendorf & Fahrig 2000) or by counting the number of links and the search time

between all pairs of territories (Doak *et al.* 1992), or by comparing movement frequencies among different observation points (Pither & Taylor 1998).

Cape Verde is an archipelago made up of ten volcanic islands, some islets and seamounts coming close to the sea surface. Islands are largely under the influence of dominant winds and large-scale oceanic circulation, located on the southeastern boundary of the North Atlantic's subtropical gyre and the northern limit of the equatorial counter-current. Both current systems present seasonal variations that affect the circulation of the surface layer down to 200 m depth (Stramma & Siedler 1988; Stramma & Schott 1999). There are recent evidences that marine demersal populations are structured by islands and islands group in that archipelago (Medina *et al.* 2007). There is an increasing scientific interest towards the understanding of the role of that region in the biogeography (Bolten *et al.* 1998), biodiversity and evolution of marine species in the Central Atlantic Ocean, acting probably as a refuge area during glacial periods (De Wolf *et al.* 2000). Despite scientific interest of that biogeographic region, no information are available neither on spatial flows of energy and materials, nor on organisms across islands boundaries and therefore the degree of population mixing among islands remains unknown. In addition, the ocean circulation between islands is still not well described and not well understood at appropriate spatial (island) and temporal (week, month, season and year) scales. Hence, it is important to model the spatial and temporal patterns of hydrodynamic features affecting species dispersal and distribution. By analysing to what extent hydrodynamic connectivity within that archipelago can regulate marine population structure, this study is the first attempt to establish some of the main ecological, biological and physical bases structuring demersal

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fish populations in the Cape Verde archipelago. We estimate the rate of dispersal, retention, import/export and loss of eggs and larvae in an insular ecosystem connectivity context.

In a first stage by means of Complex Empirical Orthogonal Functions (CEOF) analysis on velocity components provided by the Mercator operational ocean forecasting system (see http://www.mercator-ocean.fr/ for a complete description) the space and time variability of the dominant ocean circulation structure is characterized. In a second stage, Lagrangian Stochastic Modelling (LSM) of fluid particles using Mercator currents is applied to infer the influence of the dominant hydrodynamical features on the ecological connectivity between islands.

4.2 Material and Methods

4.2.1 Study area

The Cape Verde archipelago is one of the four oceanic archipelagos belonging to the large biogeographic region of Macaronesia, which also includes Madeira, Azores and Canary Islands in the eastern Atlantic Ocean. It is made up of 4 033 km^2 of land distributed among ten volcanic islands of different size and some islets (Figure 4.1). Four main seamounts (Noroeste, Nova Holanda, Bancona and João Valente) come close to the sea surface. Islands' insular shelf is steep until 200 m depth, but slope is less pronounced down to 1 000 m presenting different extension (Bravo de Laguna 1985). The islands' coastline morphology is much diversified and there is a large variety of geographic distances and depths in the archipelago, which explains ecological and phenotypical isolation between islands and islands groups (Medina *et al.* 2007; this thesis, Chapter 3).

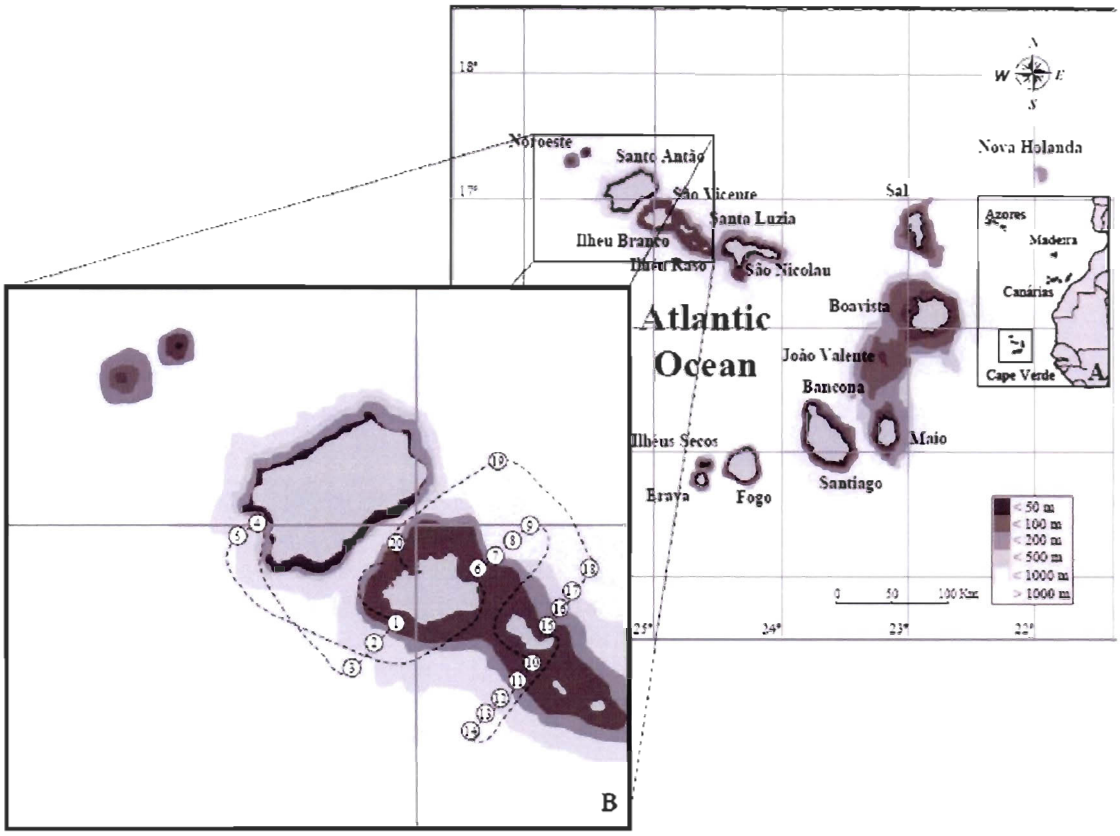

Figure 4.1

- Carte de l'archipel du Cap-Vert. La carte insérée carte représente la localisation de l'archipel du Cap-Vert dans la région biogéographique de la Macaronésie. La partie amplifiée représente les sites d'échantillonnage.

- Map of the Cape Verde archipelago. Insert map represents location of Cape Verde archipelago within Macaronesia biogeographic region. The amplified chart represents sampling sites.

The influence of dominant winds allows to describe two main group of islands based on the physical environment. One group, named locally "Barlavento" are located windward of the northeasterly trade winds (Santo Antão [SA], São Vicente [SV], Santa Luzia [LZ], Raso [IR], Branco Islet [IB], São Nicolau [SN], Sal [SL] and Boavista [BV]). Another group, named "Sotavento" is leeward of those winds (Maio [MO], Santiago [ST], Fogo [FG], Brava [BR], Islets Grande, de Cima and Luis Carneiro [IG]; the island abbreviations are used throughout the present document).

Two main seasons are recognized during the year: a warm one from May to November and a cold one from December to April. The warm season is divided in a dry period between May and July, under the influence of Harmattan wind and dust from the Sahara desert, and a wet period from August to September, which is influenced by northeasterly Trade Winds from the Azores anti-cyclone and by southwesterly Trade Winds from the Santa Helena anti-cyclone. When rains occur on land, they are torrential, irregular and concentrated in the wet period (90%) according to topography and altitude (De Brum Ferreira 1989). Sea-surface temperature follows the average air temperature, varying from 18°C to 27°C during the year.

An important aspect of the oceanography of the Cape Verde islands, well described by Lázaro *et al.* (2005), is the seasonal variation that affects the two main large-scale circulation systems, *i.e.* the Canary Current and the North Equatorial Counter-Current (Stramma & Siedler 1988; Stramma & Schott 1999). Due to these two circulation systems, water enters and leaves the archipelago *via* a number of passages between islands and

seamounts. This water flow is importantly influenced by local topography, generating so, a great variety of hydrodynamic conditions which vary year round.

4.2.2 Data source

4.2.2.1 Mercator forecasts

The Mercator operational ocean forecast products provided by the high-resolution system of the North Atlantic and Mediterranean PSY2V2 are used (Lellouche *et al.* 2007). PSY2V2 is based on the Ocean General Circulation Model code - OPA8.1 (Madec *et al.* 1998) with a 5 to 7 km of horizontal resolution ($1/15^{o}$) and 43 z-levels on the vertical, a resolution from 6 m at the surface to 300 m at the bottom (Drillet *et al.* 2005). A realistic bathymetry is used. Atmospheric forcing that drives the ocean circulation (wind stress, heat and water fluxes) are provided daily by the European Center for Medium range Weather Forecast. Assimilation of satelite altimetry (Sea Level Anomalies) *in-situ* data (temperature and salinity vertical profiles), and satelite Sea Surface Temperature is performed on a weekly basis, using SAM1V2, a multivariate scheme. SAM1V2 corrects models forecasts by means of a reduced-order optimal interpolation algorithm combined with a vertical multivariate Empirical Orthogonal Function (EOF) algotithm, which projects in a consistent statistical way the innovations (*i.e.* differences between all observations and model estimates) into the three dimension model state vector (De Mey & Benkiran 2002, Etienne & Benkiran 2007).

For the purpose of the present research, daily Mercator outputs of *T*, *S*, zonal *(u)* and meridional *(v)* velocities from years 2004 and 2005, covering the ocean domain ranging in the North Atlantic Ocean from 13-19°N, 20-28°W *i.e.* about 55 000 km^2 were considered.

4.2.2.2 Validation of Mercator forecasts

The Mercator operational forecasts have already been validated on several areas (*e.g.* Crosnier & Le Provost 2007; *e.g.* Lellouche *et al.* 2007) on the other hand the scientific questions which justified the present research refer to a much smaller spatial scales, *i.e.* island and archipelago. Thus, a preliminary assessment on the Mercator forecasts for the studyied area was performed using *in-situ* data gathered in 2004 from a research survey that was conducted in the northern part of the Cape Verde archipelago, from Santo Antão to São Nicolau islands (Figure 4.1) from May 31st to June 6st. CTD temperature and salinity profiles, and ADCP currents were compared to Mercator PSY2V2 outputs interpolated at the same location and time. The results on Figure 4.2 illustrated by an inshore (100 m) and an offshore (2 000 m) CTD cast show an overall good fit between the Mercator and observations. These results allow using Mercator data, on one hand, to model the spatial and temporal regimes on the ocean circulation between islands and, on the other hand, to study the hydrodynamic connectivity between the islands. The first modeling approach was realized by means of Complex Empirical Orthogonal Function (CEOF) analysis on horizontal velocity components and the second one by simulating Lagrangian stochastic dispersal of passive particles.

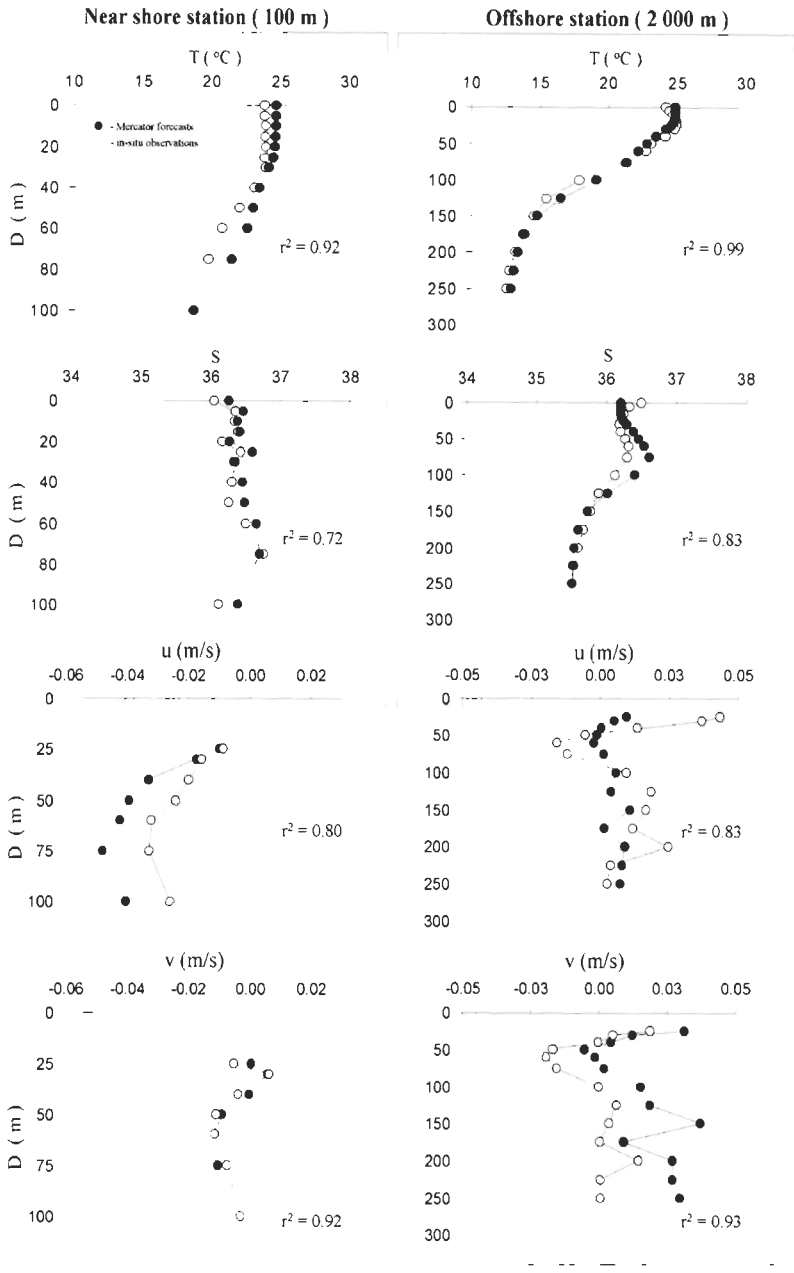

Figure 4.2

- Validation des prévisions Mercator PSY2V2 pour l'archipel du Cap-Vert. Seulement deux stations sont présentées pour illustrer la tendance entre des observations *in situ* indépendantes et les prévisions Mercator pour une station côtière et une profonde. Les variables température (T), salinité (S) et les composantes *u* et *v* du courant ont été examinées.

- Validation of Mercator PSY2V2 forecast for the Cape Verde archipelago. Only two stations are shown illustrating a trend between independent in-situ observation and Mercator data in an inshore and offshore station. Variables as temperature *(T)*, salinity *(S)* and currents velocity components *u* and *v* were considered.

4.2.3 Modeling the hydrodynamic patterns (CEOF analysis)

Empirical Orthogonal Functions (EOF) analysis (Lorenz 1956) has been extensively used as the most useful statistical technique in meteorology and oceanography to analyse multivariate data sets of large dimensions describing the space-time distribution of physical variables (Koutitonsky *et al.* 1990; Vézina *et al.* 1992; Kaihatu et *al.* 1998; Pedder & Gomis 1998; Storch & Zwiers 1999; Korres *et al.* 2000; Fernandes *et al.* 2005). The EOF analysis is a multivariate technique designed to derive the dominant variability patterns of eigenvectors in a covariance matrix. The successive eigenvectors are characterized by mutual orthogonality that allows an efficient representation of the initial fields by solving the dimensionality problem. Although conventional EOF analysis can be applied as well to a single space-time field as to a combination of fields, it extracts only stationary patterns in the sense that they are not evolving (Fernandes *et al.* 2005; Hannachi *et al.* 2007). We used then an alternative technique, CEOF, which use the same algorithm but in an augmented data field by adding a complex component to the data matrix. Following other works carried out on velocity fields (Kundu & Allen 1976; Horel 1984; Koutitonsky *et al.* 1990; Fernandes *et al.* 2005), our analysis takes a velocity matrix as $(u + iv)$ and use v as the complex part of the data matrix. Such methodological option helps detecting propagating features within the data and so is well adapted for pairs of scalar dynamics data.

In the present research we considered horizontal velocity components u and v as extracted from Mercator PSY2V2 for the extent of the study domain according to a grid model composed by 11 374 horizontal grid points (94 x 121 points are equivalent of 6^{o} x 8^{o} of latitude and longitude) and 10 depth levels (0 m, 10 m, 20 m, 30 m, 50 m, 75 m, 125 m,

175 m, 225 m, 275 m). From daily data of the two years (730 days) we computed an average year data matrix and did a weekly resampling according to a time step of seven days in order to obtain a set of 52 observations. Thus, the initial matrix dataset D consists of a three-dimensional field with p grid points for each l depth levels and n time steps realizations.

According to Korres *et al.* (2000), D is decomposed into its singular vectors allowing its representation as a sum of products of depth-invariant temporal modulation coefficients of three-dimensional CEOF patterns, where σ_i (i =1, …, r) are the singular values, r is the matrix rank, x runs all the grid points in the horizontal (x = 1, …, p), z runs the l level and t = 1, …, n. Thus, we can have

$$d(x,z,t) = \sum_{i=1}^{r'} e'_i(x,z)\sigma'_i a'_i(t) \qquad (1)$$

This decomposition involves an expansion of the initial four-dimensional fields into depth-invariant temporal coefficients and allows for a study of the spatial and the temporal behaviour of hydrodynamic patterns. We did this decomposition by using the algorithm proposed by Storch & Zwiers (1999). By projecting the initial dataset on the eigenvector basis, we obtain a representation of D in terms of CEOF (e_i) and their Amplitude Time Series (ATS) coefficients (a_i). The CEOF explain the spatial patterns and the ATS represent the corresponding temporal patterns. CEOF functions, or modes, are numbered in a descending eigenvalues order so that the first mode accounts for the largest amount of the total variance on the dataset. Hence, D can be efficiently represented by the first dominant

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functions allowing a significant reduction of the degrees of freedom and thus an economical representation. Then, the statistical significance of the modes could be assessed by an empirical – the rule of the thumb (North *et al.* 1982) and the overall efficiency of the method could be measure by estimating the L2-error norm on the reconstruction of D from the statistically significant EOF modes as,

$$error = \sqrt{\sum_{i}^{r} \left| (D - a_i e_i)^2 \right|} \qquad (2)$$

4.2.4 Modeling the ecosystem connectivity

4.2.4.1 Lagrangian Stochastic Model

In physical and biological oceanography, the individual-based approach of simulating LSM is gaining ground because, on one hand, it allows the inclusion of state modulated behaviour and, on the other hand, the output of individual trajectories often yields deeper insight into the dispersion, growth and mortality of marine species larvae than the global statistics at population-level. The LSM theory (Rodean 1996) assumes that, for oceanographic purposes, egg/larvae-water density differences are typically small, and the bias induced by this assumption is not significant (Brickman & Smith 2002). On average, species early life's stages behave as passive particle traveling in a particular ocean layer. In the present research, aiming at a better understanding of demersal population structure, LSM approach is used to investigate hydrodynamic connectivity between islands within Cape Verde archipelago.

Two-dimensional Lagrangian model. The oceanic domain of the model extends horizontally on the same grid used for the CEOF analysis. The same 10 depth layers were also considered. The modeling of particles tracking is driven by daily input of three-dimensional *u* and *v* provided by the Mercator PSY2V2 model. Such a time step in the input of data current is justified, *inter alia*, by the fact that in the study area, the influence of tides is weak and the winds vary on a much larger temporal scale. The current fields are interpolated linearly in time until a time step lower than the threshold established by the Courant-Friedrich-Lewy condition. The particles trajectories are then computed by means of the Runge-Kutta Fourth Order algorithm and PSY2V2 daily outputs. The current at a precise particle position is estimated by bilinear interpolation (Press *et al.* 1989) and the horizontal turbulent diffusion at a grid model scale is simulated by a random-walk process (Ribergaard *et al.* 2004; Engie & Klinger 2007) with a coefficient of 1 $m^2.s^{-1}$. Assuming a weak influence of tides and upwelling systems in the region and considering that the eggs and larvae floatability remains constant during the considered interval of time, the vertical velocity and diffusion are neglected in the trajectory computation. In an inhomogeneous turbulent environment, maintaining the well-mixed condition (WMC) is a key property of a robust LSM, *i.e.* the model is expected to maintain an initial distribution of particles uniform for all time steps (Brickman & Smith 2002). For the region under study, due to islands effect related to topographic features, the flow is baroclinic and the WMC could not be demonstrated. This theoretical-practical compromise was taken into account by performing particle tracking at different depths (0 m, 25 m, 50 m, 75 m, 100 m) that are expected to play an ecological role in the distribution and ontogenetic development of

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species early life's stages. Such a technical procedure allows estimating the sensitivity of transport to depth (Ribergaard *et al.* 2004).

Lagrangian simulations. We simulated dispersal from nine release sites distributed throughout the archipelago. Each site was composed of island or group of islands (SA, SV-LZ-IR-IB, SN, SL, BV, MO, ST, FG, BR-IG) according to their physical connection by the insular shelf down to 100 m depth. The simulation conditions were set according to methodological precautions in view of obtaining robust and convergent results by avoiding undersampling errors related to the number of particles, the number of trials the source and target areas (Brickman & Smith 2002). Starting on January 1, 2004, we performed weekly simulations by releasing 50 particles at each site and at the same time, corresponding to 23 400 particles for all the year (50 particles, 52 weeks, 9 sites). This procedure was repeated for the five depth levels considered. The model was initialized by a starting date and particles were tracked until one of the three scenarios took place: 1) the particles left the study domain, 2) the particle reached an island domain and 3) the model was stopped by the elapsing simulation time. Results were organized in a particle matrix containing, for each particle, information about its identification, starting/ ending date, starting/ ending location, and duration of dispersal. These matrices were then submitted to statistical analyses.

4.2.4.2 Hydrodynamic balance of particles exchange

In an attempt to quantify the hydrodynamic exchange within the archipelago, we estimated the local retention of particle in each island R, the rate of import/export between

two islands E and the loss of particles outside the ocean domain considered L. Let us consider n as the number of particles released at each island's domain. After a dispersal time d, a number of them will be back to the same island (n_r) and the others will either settle in another islands (n_e) or be definitely lost out of the ocean domain delimiting the archipelago (n_l). R, E and L are estimated as:

$$R = \sum_{i=1}^{m} \frac{n_i N}{\overline{t_i} T} \tag{3}$$

$$E = \sum_{i=1}^{m} \frac{n_e N}{\overline{t_e} T} \tag{4}$$

$$L = \sum_{i=1}^{m} \frac{n_l N}{\overline{t_l} T} \tag{5}$$

Where T is the sum of the drift periods of all particles and t_i is the average drift duration of particles for each of the three cases. Those three variables were computed monthly between each pairs of islands and the 'larval' hydrodynamic balance was studied in space and time.

4.2.4.3 Ecosystem connectivity

Connectivity is a feature of a whole ecosystem where the scale is a function of the habitat use and of the movement scales of organisms. In the present study we consider the connectivity driven by hydrodynamic at two levels: 1) the hydrodynamic connectivity gives information about the strength of exchange (import, export) of materials (gametes, eggs and

larvae) between islands considered two by two and 2) hydrodynamic interconnectivity gives information about the strength by which one island is connected to the whole archipelago through hydrodynamics processes. These two levels of ecosystem connectivity have different implications in the overall population structure and dynamic.

Hydrodynamic connectivity. In order to describe the hydrodynamic exchange between two islands (*1*) and (*2*), we consider that (n_1) is the number of particles released in (*1*) going to settle in (*2*) and (n_2) is the number of particles released in (*2*) going to settle in (*1*) after one release period (t). Before all computation, in order to assimilate the hydrodynamic aspect of the exchange processes, the number of particles (n) moving from one island to another must be weighed by their mean velocity *i.e.* by the duration of their drift between the releasing and the settling sites (t_i):

$$n'_i = \frac{n_i}{t_i} \tag{6}$$

We then computed the sum of the half difference in n during m releases as:

$$c = \sum_{t=1}^{m} \frac{n'_1 - n'_2}{2} \tag{7}$$

and a first approximation of the connectivity can be expressed as

$$C = 1 - \frac{|c|}{N'} \tag{8}$$

where N' denotes the total weighed number of particles exchanged during m releases. A problem arises with double-zeros in the data matrix, which introduce indetermination into the equation. However, double-zeros may have ecological or physical meanings. Thus, in order to avoid such a computation problem, we introduced a factor representing an infinitely small number I as:

$$I = \frac{1}{(2m)^m} \tag{9}$$

The hydrodynamic connectivity index C_h is finally computed as

$$C_h = \frac{|c|I}{N'I} \tag{10}$$

and varies from zero, for completely isolated islands to unity comfort completely connected islands.

Hydrodynamic inter-connectivity. Conversely to the connectivity index, the interconnectivity index is computed from the exclusive information from each island in relation to the information from other islands as a whole. In the hydrodynamic exchange process within the archipelago, r_i represents the number of particles retained by each island and R the number of particles coming from all islands. After weighing r by the mean duration of the drift, a hydrodynamic inter-connectivity IC_h for each island was computed as:

$$IC_h = 1 - \sum_{i=1}^{m} \left(\frac{r_i}{Rk} \right)^2 \tag{11}$$

where k is the number of islands which provided particles, and varies between 1 (only island's retention) and 9. The IC_h index varies from zero, for no connection, to unity (one island equally connected to all other islands)

4.2.5 Ecological applications of connectivity indices.

In order to analyze the spatial patterns of the hydrodynamic connectivity, C_h was computed between all pairs of islands at five depth levels (0 m, 30 m, 50 m, 75 m and 125 m) and results represented a squared matrix that was subsequently submitted to a Principal Component Analysis (PCA) based on the Pearson correlation coefficient. This analysis was complemented by an agglomerative hierarchical clustering (AHC) on the same matrix by using a single linkage method (Legendre & Legendre 1998). Subsequently, at the same depth levels, IC_h was computed monthly for all islands and the spatial and the temporal pattern in the average IC_h for the archipelago was analyzed. Since the ecological isolation between islands varies between the two seasons, being higher during the warm than during the cold season, the seasonal variation of the hydrodynamic interconnectivity was compared with the seasonality of the ecological isolation between islands for demersal assemblages as reported by Medina *et al.* (2007).

4.2.6 Geographical distance, bathymetry and ecosystem connectivity

The concept of ecosystem connectivity in an archipelago implies necessarily physical variables such as the geographical distance and bathymetry. Medina *et al.* (2007) showed how geographic distance and depth drive ecological variability and isolation of

demersal fish communities in an archipelago system. Based on data from those authors (see Chapter 1 of this thesis), we investigated the relationship between hydrodynamic connectivity at three depth levels (C_{h0}, C_{h50} and C_{h100}), the geographic distance *(d)* and the average bathymetry *(b)* to evaluate the relationship between such variables and the hydrodynamic connectivity. Islands were compared two by two and each pair of islands was then characterized by (1) the hydrodynamic connectivity C_h, (2) the geographical distance *(d)*, and (3) the average bathymetry *(b)* between those islands. For the entire system, those parameters are represented in three square matrices that were compared through a series of Mantel tests (Legendre & Legendre 1998), which provided total and partial correlations between those three matrices.

4.2.7 Ecosystem connectivity and phenotypical variation

The local environments around islands are very heterogeneous, related to geomorphological characteristic of the islands and their coastal topography, associated with different coral reefs structures and seamounts. As it has been demonstrated for *Cephalopholis taeniops* (Serranidae), a demersal fish of the insular shelf of Cape Verde islands, the heterogeneity, associated with geographical distance and depth, may induce phenotypical variation in the body shape (this thesis, Chapter 3). Hence, in an attempt to elucidate to what degree hydrodynamic connectivity affects phenotypic variations, we used a morphometric procrustes distance computed for the studied species and investigated the correlation with hydrodynamic connectivity at different depths. The phenotypical index (P_d) was computed at two levels of environmental variability within the archipelago: 1) –

by comparing all fish with the average of corresponding island (P_{di}); 2) by comparing them with the average of the archipelago (P_{da}).

In the present research, the 2D-LSM was made available by the Hydrodynamic Modelling Laboratory from the Université du Québec à Rimouski – Institut des Sciences de la Mer de Rimouski (François Saucier and Pierre Saint-Laurent, UQAR – ISMER). Appropriate Matlab software routines were used for all other modeling purposes and all statistical analysis was made with the XLSTAT-Pro v.7.5.3 software.

4.3 Results

4.3.1 Modeling ocean circulation

Spatial and temporal variations. From a total of 50 possible modes in the EOFs analysis *(n-2)* the first four reveal to be statistically significant (Figure 4.3-A). These reduced dimensions explain 78.4 % of the total variance related to the dynamics of the system. The first mode of EOF, accounting for 46.1% of the total variance, is the most explanatory on surface but becomes less important with depth until approximately 30 m (Figure 4.3-B). The second one explains 15.3 % of total variance and, contrary to the first one, reaches its maximum explanatory power at 30 m and is reduced thereafter, remaining however relatively important until approximately 150 m. The third and the fourth EOFs, explaining respectively 9.9 % and 7.1 % of the total variance have also explanatory power in an opposite trend related with depth, both reaching their maximum at approximately 20 m. The physical significance of these statistical patterns is described below.

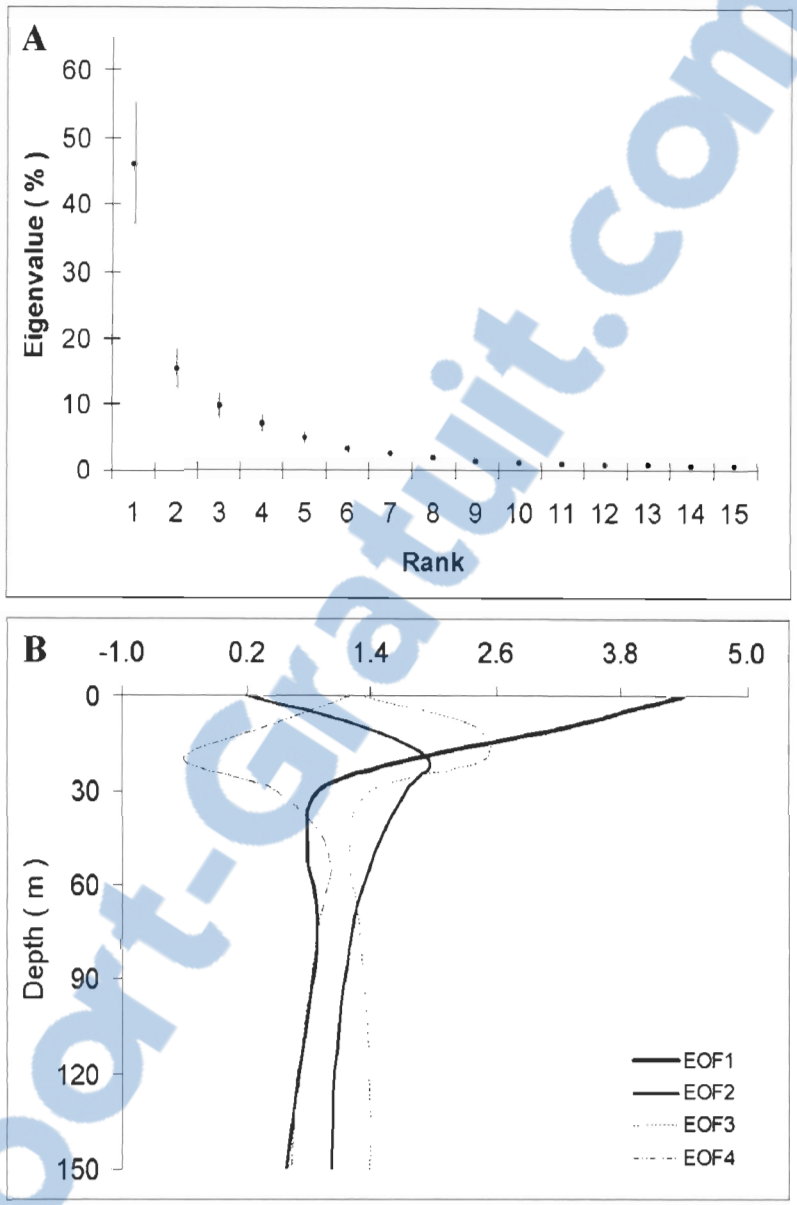

Figure 4.3

- Résultats de l'analyse en Fonctions Empiriques Orthogonales Complexes (CEOF) effectuée sur la matrice complexe (*u* + *iv*) proposée. A - Spectre de la matrice de covariance, en pourcentage, pour les 15 premières valeurs propres. Les barres verticales montrent l'intervalle de confiance à 95 % donné par méthode empirique (North *et al.* 1982) illustrant que seules les quatre premières CEOF ont une signification statistique. B - Variation de l'importance de chaque CEOF avec la profondeur, jusqu'à 150 m.

- Results of Complex Empirical Orthogonal Functions (CEOF) analysis carried on the complex matrix *(u + iv)*. A – Spectrum, in percentage, of the covariance matrix for the first 15 eigenvalues. Vertical bars show the 95 % of confidence interval given by the rule of thumb (North *et al.* 1982) illustrating that only the first four CEOF have a statistical significance. B – Variation of the importance of CEOF with depth up to 150 m.

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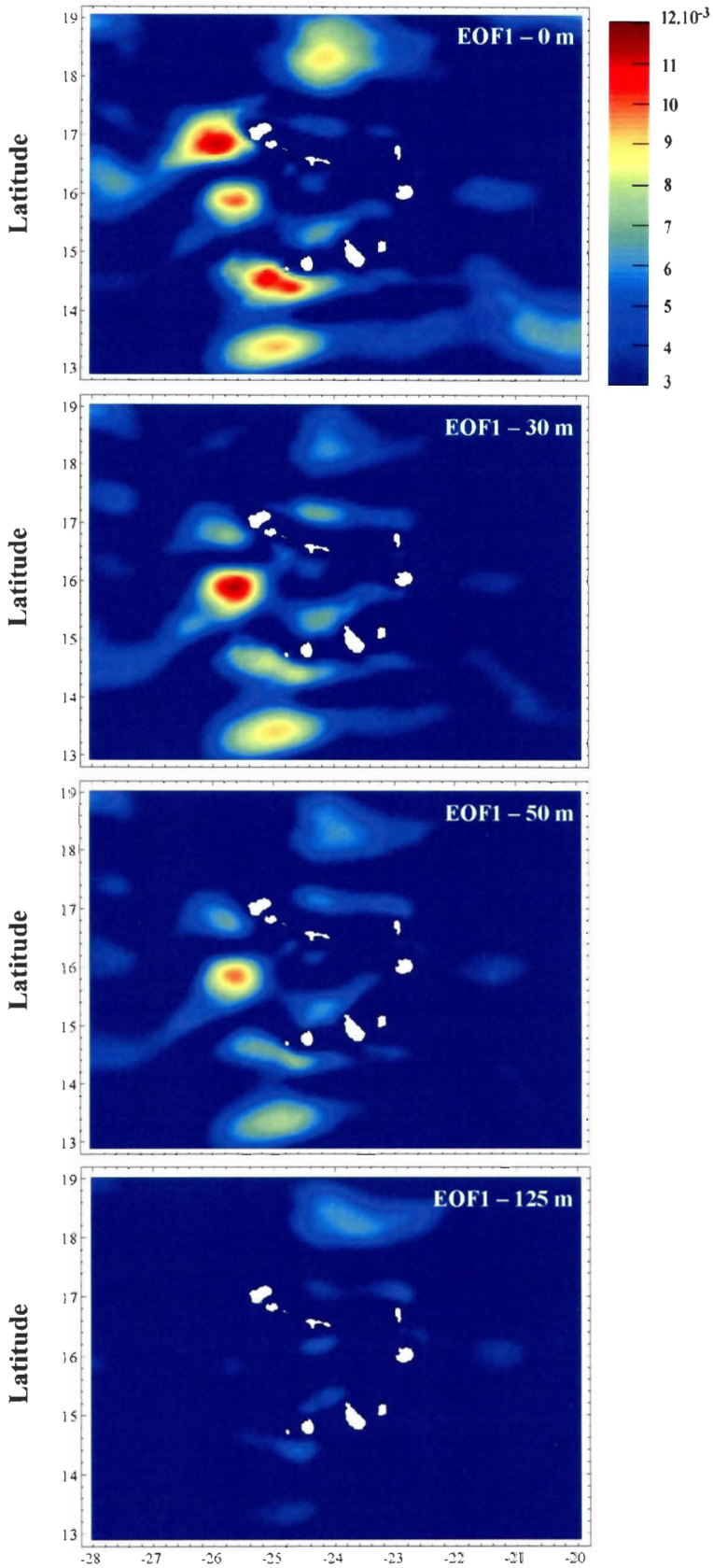
Figure 4.4 A-D (sur les quatre pages suivantes)

- Patrons spatiaux des quatre premières CEOF selon quatre niveaux de profondeur: en surface (A), à 30 m (B), à 50 m (C) et à 125 m (D). Nous observons différents patrons dans l'intensification des courants du côté des îles sous le vent et de tels phénomènes s'affaiblissent avec la profondeur jusqu'à 125 m.

- Spatial patterns of the first four EOF modes according to four depth levels: surface (A), 30 m (B), 50 m (C) and 125 m (D). We observe a different pattern on the intensification of currents in the leeward of the islands and such phenomena becomes weaker with the depth up to 125 m.



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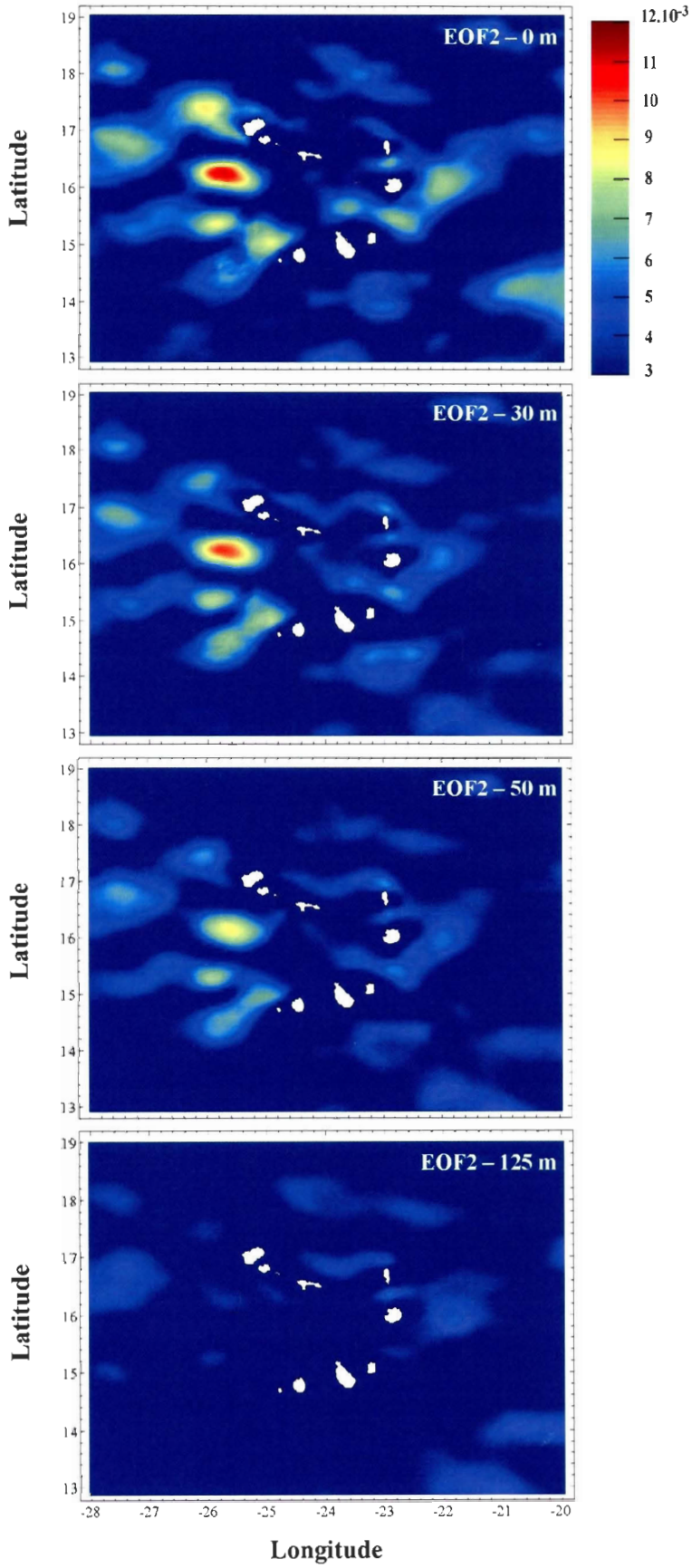
EOF2 – 0 m
EOF2 – 30 m
EOF2 – 50 m
EOF2 – 125 m
12.10-3
11
10
9
8
7
6
5
4
3
Latitude
Longitude
19
18
17
16
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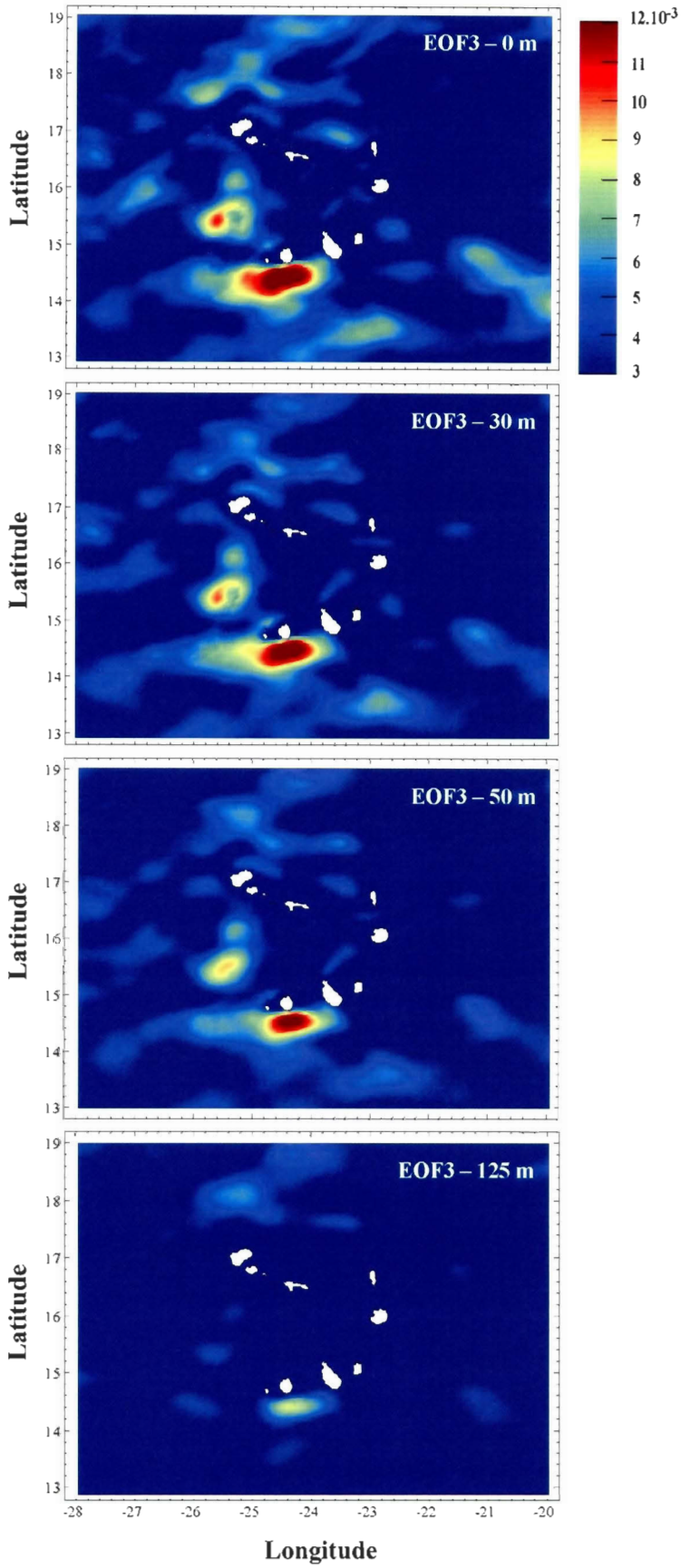
14
13
-28
-27
-26
-25
-24
-23
-22
-21
-20


EOF3 – 0 m
EOF3 – 30 m
EOF3 – 50 m
EOF3 – 125 m
12.10-3
11
10
9
8
7
6
5
4
3
Latitude
Longitude
19
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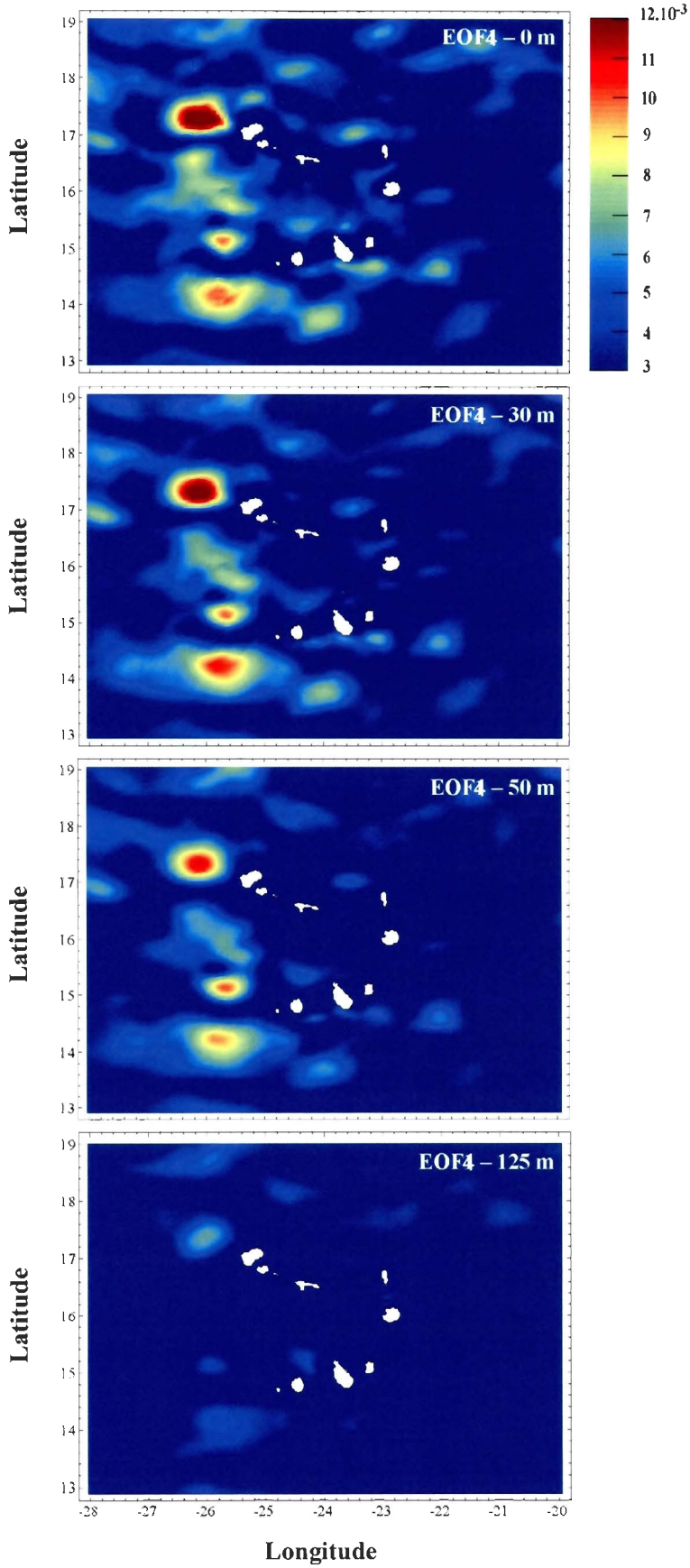
-24
-23
-22
-21
-20


EOF4 – 0 m
EOF4 – 30 m
EOF4 – 50 m
EOF4 – 125 m
12.10-3
11
10
9
8
7
6
5
4
3
Latitude
Longitude
19
18
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16
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14
13
-28
-27
-26
-25
-24
-23
-22
-21
-20

Spatial patterns. When analyzing the spatial patterns associated with each EOF (Figure 4.4, A-D), an intensification of currents downstream the islands is observed associated with eddies structures. Current intensity decreases with depth, becoming weak around 100 m. The EOF 1 extracts a first marked signal in the south-west of Santo Antão island, a second one in the south-west of the northern islands (approximately 15°/16° of latitude and 25°/26° of longitude), and a third signal in south-west of the Brava island (Figure 4.4-A). Two other less intense signals can be located, one completely on the north and other completely on the south of the archipelago. The intensity of such a spatial pattern decreases with depth and tends to disappear near 50 m. However, the second structure identified at the southwest of the northern islands increases considerably its intensity at 30 m and remains relatively intense down to 50 m. The second EOF seems to be much more related to the second structure, already identified and, once again, its intensity decreases with depth (Figure 4.4-B). The third EOF (Figure 4.4-C) also extracts a signal already identified in the South of Brava and remains very intense up to 50 m. The fourth EOF points out a very strong signal in the north-west of Santo Antão islands and in the south-west of Brava and Fogo islands, remaining intense down to 50 m. Among these swirling structures, the one located almost around 15°/16° of latitude and 25°/26° of longitude in the southwest of the northern islands seemed to be the more stable.

Temporal patterns. The temporal variation of the modes is analyzed through the ATS corresponding to each CEOF. The first four ATS describe the temporal patterns of the spatial variations highlighted by the corresponding EOFs (Figure 4.5).

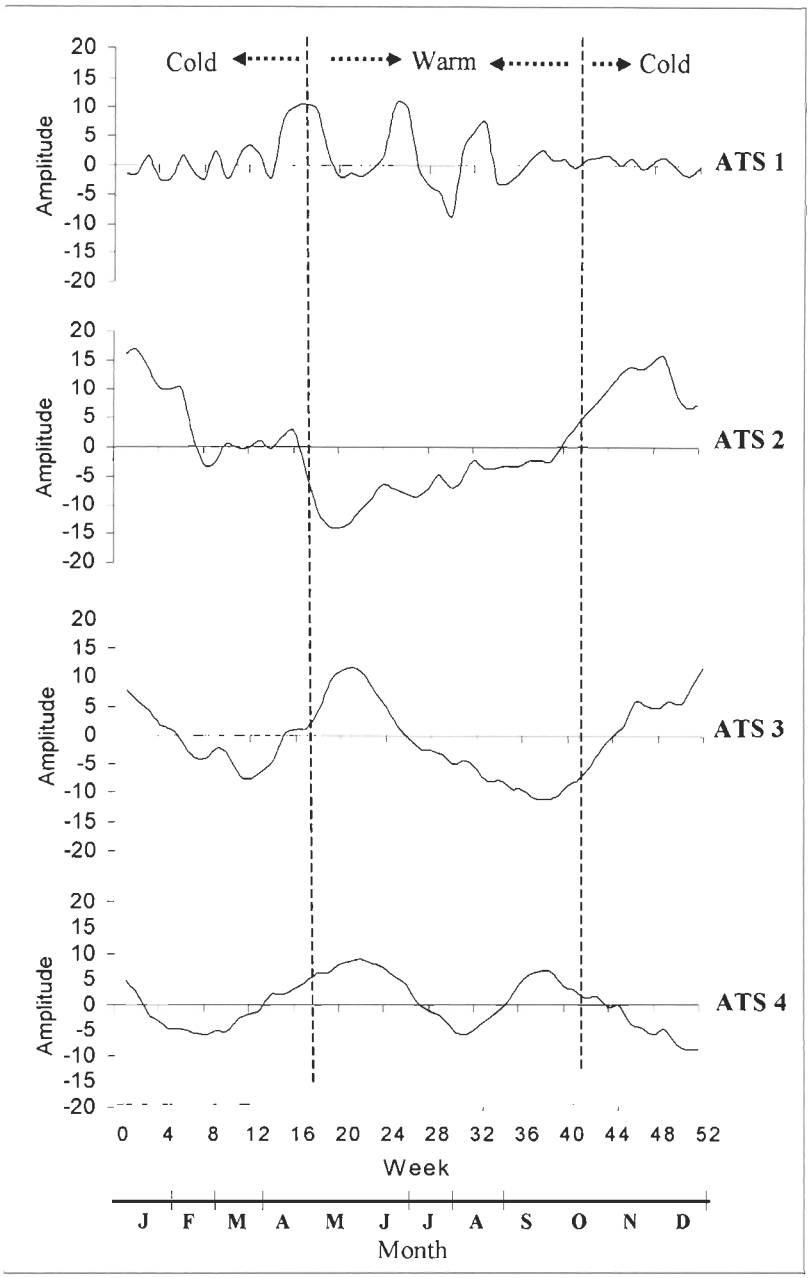


Figure 4.5

- Amplitude des Séries Temporelles (ATS) montrant les variations temporelles des patrons spatiaux des quatre premières CEOF pendant l'année.

- Amplitude time series showing the temporal patterns of the first four spatial EOF modes year round.

The first ATS illustrates processes of short time variations, primarily for two periods of different amplitudes: the period from mid-April to mid-September shows large variations of amplitudes and the remaining months show more regular and low amplitudes. The second ATS discriminates three main periods: the first one between October and February, characterized by positive wide amplitudes; the second one corresponds to a short period between March and April with very low amplitudes; a third one corresponds to the period from May to October with negative irregular amplitudes. The third and the fourth ATS tend to illustrate phenomena of long time variations and strong amplitudes, according to two cycles and two cycles and a half, between May and November and, between November and May, respectively. If the variations at the monthly scale are not considered, the four ATS, together, discriminate two major seasons: May to October and November to April. Assuming a temporal dephasing of approximately one month (four to five weeks), this seasonal pattern corresponds to the climate seasonal pattern in the archipelago, *i.e.* a warm season from May to November and a cold season from December to April.

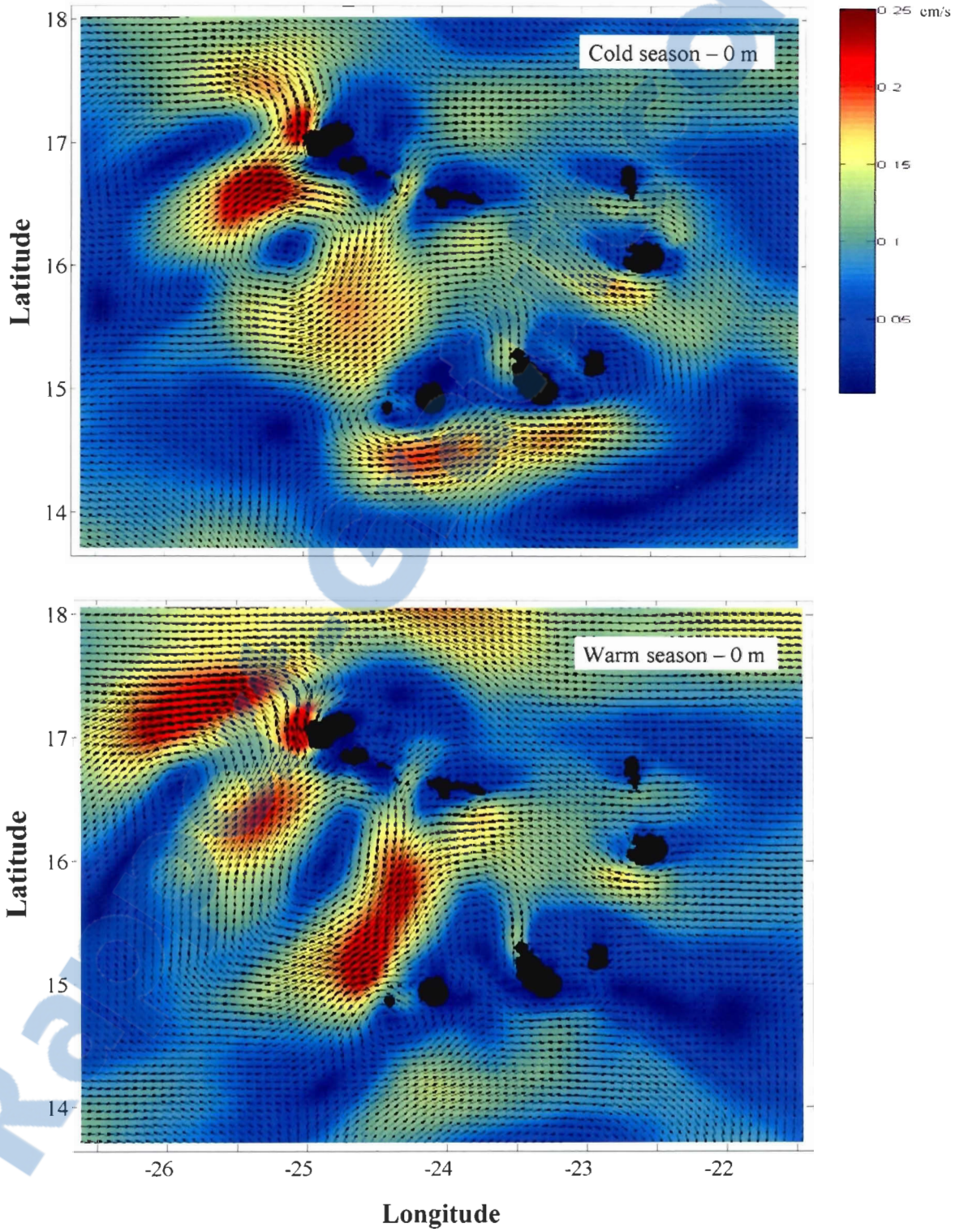
4.3.2 Ocean circulation patterns

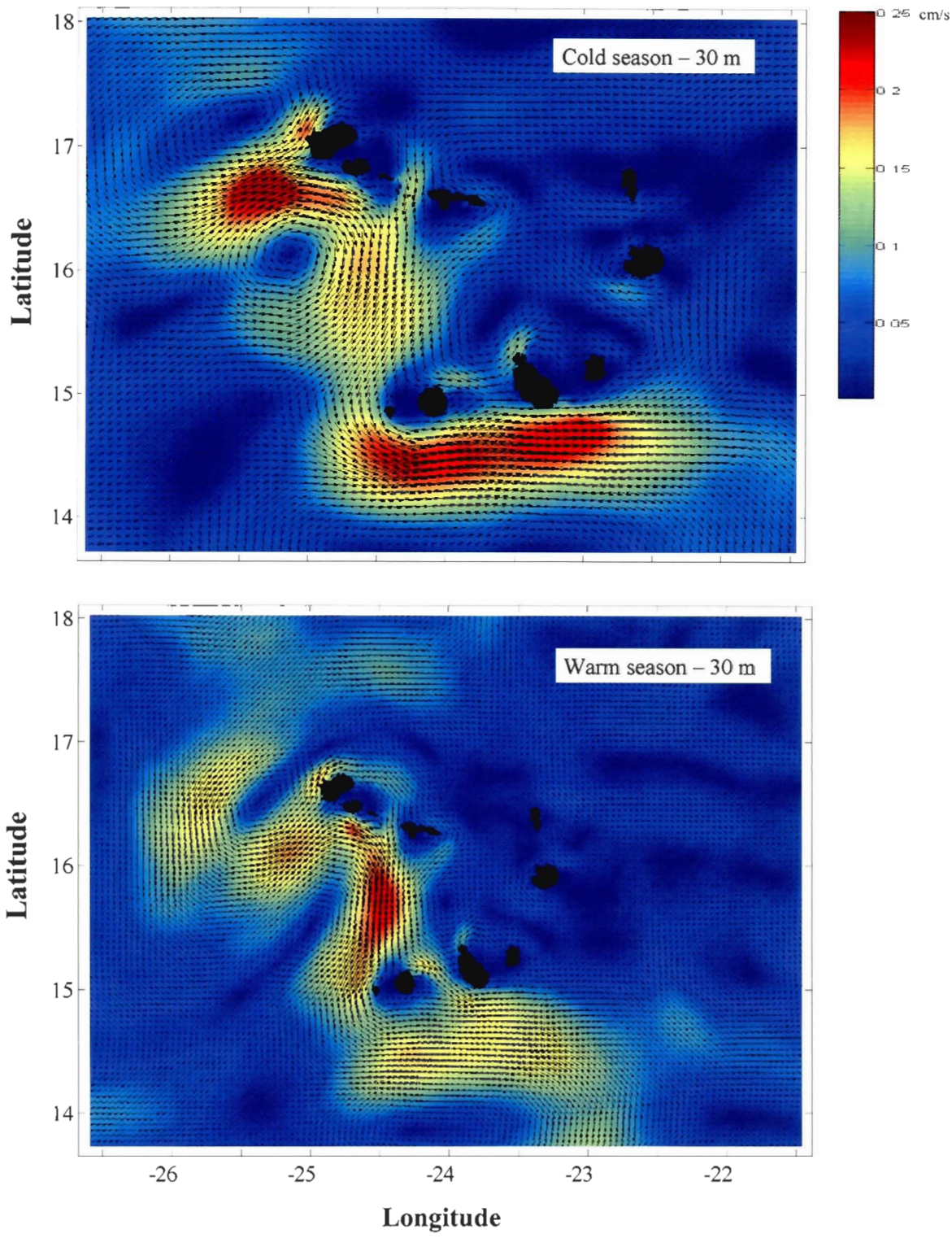
The spatial and temporal patterns identified by the CEOF analysis allow to compute seasonal-averaged currents at different depths (Figure 4.6 A-D). As shown above, the surface currents velocity is intensified downstream of the islands with the formation of eddy structures. On the northern part of the archipelago, this asymmetric small-scale circulation structures are stable during the cold season with the persistence of two eddies at south-west of Santo Antão islands.

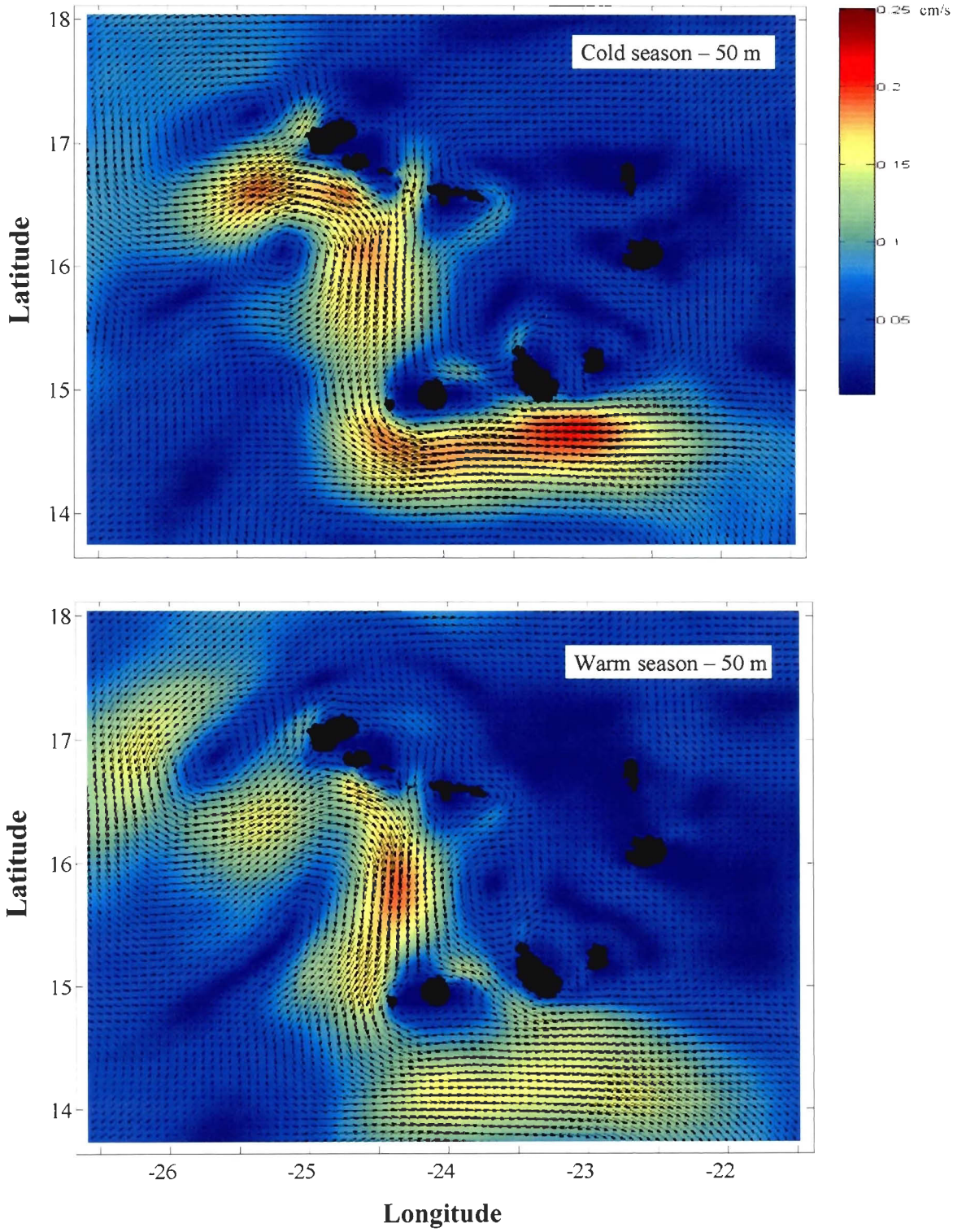
Figure 4.6 A-D (sur les quatre pages suivantes)

- Courants moyens calculés selon deux principales saisons: la saison froide, de novembre à avril et la saison chaude de mai à octobre telle qu'illustrée par l'analyse CEOF. Quatre niveaux de profondeur sont indiqués - surface (A), à 30 m (B), à 50 m (C) et de 125 m (D).

- Computed average currents according to two main seasons: Cold season from November to April and warm season from Mai to October as elucidated by CEOF analysis. Four depth levels are shown – surface (A), 30 m (B), 50 m (C) and 125 m (D).


Cold season – 0 m
Warm season – 0 m
Latitude
Longitude
18
17
16
15
14
-26
-25
-24
-23
-22
0.25 cm/s
0.2
0.15
0.1
0.05


Cold season – 30 m
Warm season – 30 m
Latitude
Longitude
18
17
16
15
14
-26
-25
-24
-23
-22
0.25 cm/s
0.2
0.15
0.1
0.05



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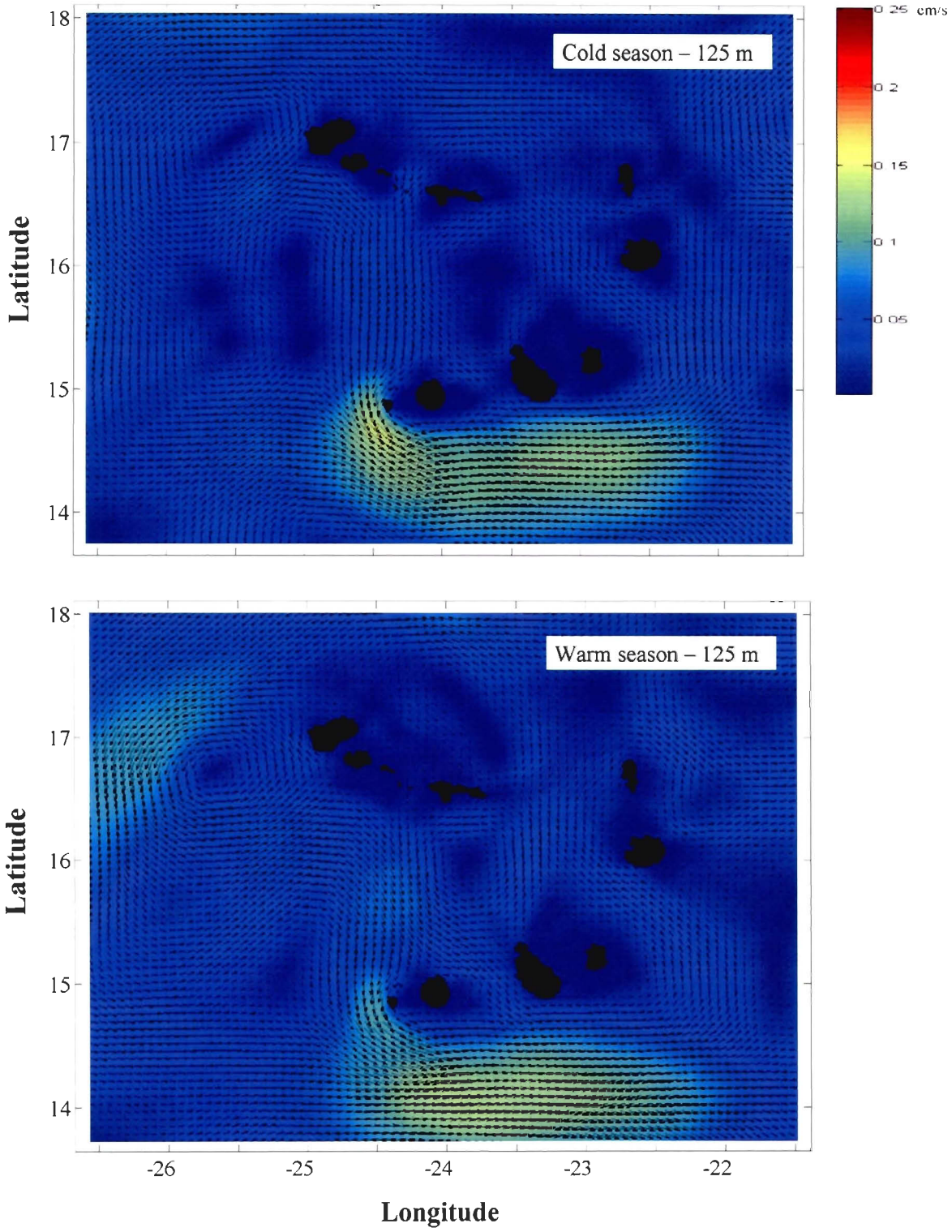
Cold season – 125 m
Warm season – 125 m
Latitude
Longitude
18
17
16
15
14
-26
-25
-24
-23
-22
0.25 cm/s
0.2
0.15
0.1
0.05

The first structure is an anticyclonic eddy towards the south of the island; it is more stable (from December to April) and has a diameter varying from 60 to 120 km and velocities around 15 to 40 $cm.s^{-1}$. The second one is a cyclonic eddy towards the north. It is less stable and reaches the north-western coast of the island, with velocities reaching 30 $cm.s^{-1}$ close to the coast. During the cold season, all islands are surrounded by zones of calms (Figure 4.6-A). Those zones of clams are more marked during January, surrounding groups of islands: all the northern islands, the southern islands (Fogo, Brava, Santiago and Maio), and the eastern islands (Boavista and Sal). The formation of eddies south of the archipelago is much more transitory and unstable. However, during certain months, cyclonic eddies are observed south of Brava Island, being able to surround the island completely. With the exception of the intensification of the west-east currents in the south of the archipelago, probably related to strong shears in the first 50 m (Figure 4.6-B and C), the currents velocity and the intensity of the eddies, as well as their seasonal variations, tend to decrease with depth down to 125 m, where hydrodynamics is more stable throughout the year (Figure 4.6-D).

Differences are noted at the surface between the cold and the warm season. Those differences can be related to the instability of the anticyclonic eddy south-west of Santo Antão. During the warm season, the eddy tends to degenerate in the direction of dominant currents (Figure 4.6-A), which generate strong shears mixing waters originating from the north of the archipelago with the waters from the south.

Figure 4.7 (sur la page suivante)

- Illustration des principaux courants à petite échelle, identifiés dans l'archipel du Cap-Vert au cours de l'année. 1) Courant au nord – passe au nord de l'archipel sans une forte influence sur la circulation entre les îles; 2) Courant à travers les îles – les courants de direction est-ouest traversent les îles et ont un impact majeur sur la circulation entre les îles; 3) Courant au sud - courant passant au sud de l'archipel sans effets majeurs sur la circulation entre les îles; 4) Une partie des eaux du courant au nord change de direction vers le sud; 5) et 6) Tourbillons asymétriques du nord-ouest, provenant de la circulation induite par les courants 2 et 4, après avoir traversé les îles; 7) Courant nord-sud – induit le transport d'une importante quantité d'eau du nord avec son origine dans les courants 2, 4, 5 et 6; 8) – Circulation cyclonique au sud - provient de courants 2 et 7. Il entoure complètement les îles au sud ; 9) circulation anticyclonique au sud - provient de la circulation des courants 7, 8 et 3. Ces courants à petite échelle à l'intérieur de l'archipel, se succèdent souvent dans une circulation tourbillonnaire asymétrique ou selon les directions est-ouest et nord-sud, produisant ainsi le mélange des eaux entre les îles. Cette circulation est induite par des interactions entre la saisonnalité du climat, la circulation océanique à grande échelle et des effets locaux à petite échelle de la géomorphologie des îles.

- Illustration of the main small-scale currents identified within the Cape Verde archipelago during the year. 1) North-current - passing on the North without strong effects on the circulation between islands; 2) Islands-cross current – the currents from east-west direction cross the islands and have a major impact on the circulation between islands; 3) South-current - passing on the South without strong effects on the circulation between islands; 4) Part of North-current that change direction towards the South; 5) and 6) – Northeastern asymmetric eddies circulation originating from currents 2 and 4 after penetrating the islands; 7) North-South currents – transport of significant amount of water from the North with his origin in currents 2, 4, 5 and 6; 8) – Cyclonic current originates from currents 2 and 7. It encloses southern islands completely. 9 Southern anticyclonic circulations originate from currents 7, 8 and 3. These small-scale currents within the archipelago often follow one another in asymmetrical rotational circulation, or in the East-West or North-South directions originating thus complete water mixing between the islands. This circulation patterns is driven by interactions between the climate seasonality, the large-scale oceanic circulation and the local small-scale effects of islands geomorphology.

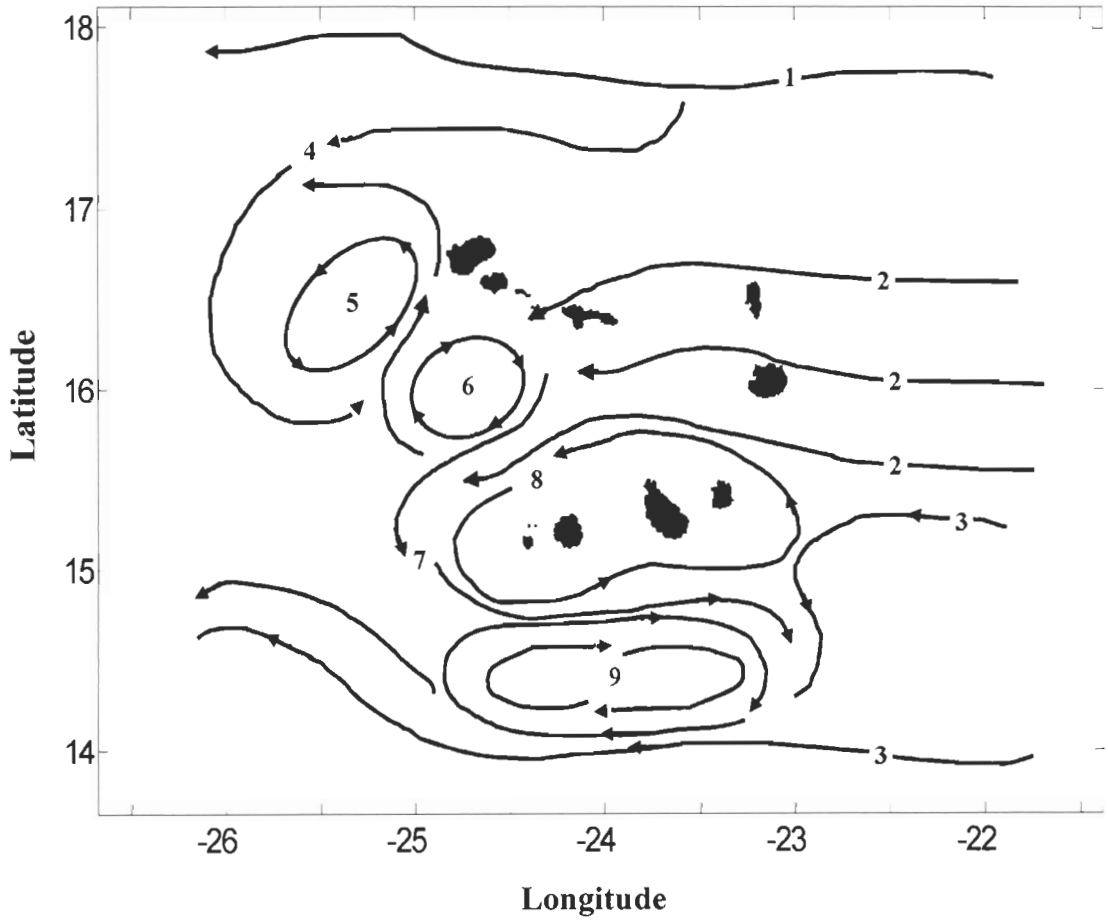

Figure 4.7

A general ocean circulation pattern can then be drawn within the Cape Verde islands over the two years (Figure 4.7). Water masses coming from the Canary Current reach the archipelago at relatively low speeds (10 to 15 $cm.s^{-1}$). These water masses are then divided into several branches. Two branches, one in the north (Northern-Current) and one in the south (Southern-Current) go around the islands without any significant influence on the circulation inside the archipelago. Other branches cross the archipelago, passing north of Sal Island, between São Vicente and São Nicolau, Sal and Boavista and between Boavista and Maio islands. While entering the islands system, water masses induce complex hydrodynamic effects related, *inter alia*, with topography, coastline morphology, islands geographical position, nature and extent of insular shelves. Their velocity also increases, generating cyclonic and anticyclonic swirling structures downstream. In the northern part of the archipelago, two eddy systems are created. A cyclonic eddy appears west/south-west of Santo Antão Island, more stable during the cold season, especially from December to January, and it tends to degenerate towards the Northern-Current. It does not seem to exist during the warm season. An anti-cyclonic eddy, which is very stable throughout the year, persists south of the island. It is however better established during the cold season, when it seems to play an important role in the water circulation inside the archipelago. This eddy is less stable during the warm season being stretched in a north-south direction. It becomes then very important in the exchanges between the northern and southern islands. When current velocity exceeds 40 $cm.s^{-1}$, the eddy is stretched towards south-west and is degenerating in the direction of dominant currents. That process, well observed from June to August, seems to represent a major contribution to the water flow out of the archipelago

system. Part of the water masses which penetrate the archipelago form a North-South Current. When reaching the southern islands (Maio, Santiago, Fogo and Brava), it creates a cyclonic movement which goes round these islands. It finally gets the direction of dominant water flow leaving the archipelago. During the warm season, another branch of that North-South Current forms an anticyclonic movement in the south of Brava, Fogo and Santiago islands, but this swirling structure is not stable and degenerates in the South-Current leaving the archipelago.

4.3.3 Lagrangian stochastic modeling

Particle trajectories. The LSM simulations identify five main types of particle trajectories of ecological importance (Figure 4.8). The first one is related to local retention after a relatively short dispersal period of 2 weeks and seems to be induced by coastal circulation processes, which are strongly influenced by the topography and the morphology of islands coastlines. The second one is also related to local retention but after a longer dispersal period of 3 to 4 months, during which the particles remain trapped in eddies, normally downstream of the islands. A third trajectory resembles the second one, *i.e.*, the particles remain trapped in eddies circulations during a certain time, but, due to the physical instability of eddies, they are finally ejected out of the system domain and thus lost for that system. Another kind of trajectory is related to direct loss by dominant currents leaving the system. Finally, some particle trajectories are related to islands connections either in one or in two directions. This kind of dynamic connection is related to import/ export processes of particles from one island to another, being retained in the system.

4.3.4 Hydrodynamic balance of particles exchange

The results illustrated in the former paragraph allow the estimation of a 'larval' balance in the archipelago system under study, by estimating the retention, the import/ export and the loss of particles out of the system. At the surface, the spatial pattern of the larval balance differs among islands (Figure 4.9-A). Santo Antão, Sal and Brava islands experience the most important loss of particles. Those islands are exposed to the dominant surface currents in the north (Sal and Santo Antão) and in the south (Brava). Loss is more important for Sal than for the others because a notable misbalance exists between retention processes (retention and import), which are very weak, and strong export processes (export and loss). Conversely, import and export processes are well balanced for Santo Antão and Brava. Santo Antão (SA box) experiences an important loss throughout the year, except for January and February. For Sal islands (SL box), losses are the most important between October and January. For Brava Island (BR box), the period of major losses can be identified between May and June. Boavista Island presents a high level of export all year round, February excepted. The local retention and the import processes are the strongest all year round at the insular shelf of São Vicente, Santa Luzia, Raso and Branco islets.

The 'larval' balance patterns are modified with depth and are completely different at 100 m (Figure 4.9-B). Losses of particles for the system and local retention are reduced, and import/export processes remain quite constant (CV box).

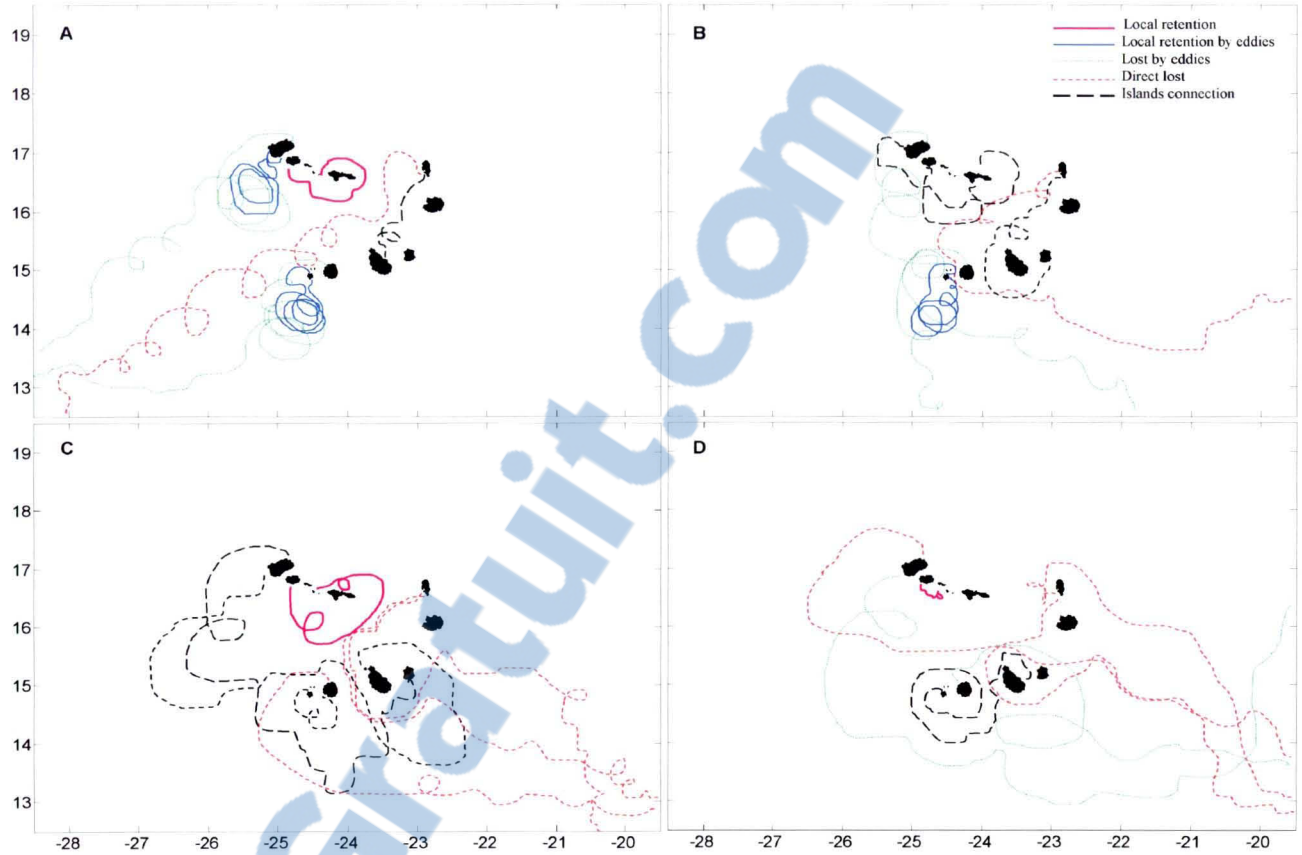

Figure 4.8

- Illustrations des principaux types de trajectoires de particules au cours des simulations de dérive lagrangienne. Cinq types ont été identifiés dans les quatre niveaux de profondeur (A – surface, B – 25 m, C – 50 m, D – 125 m): 1) rétention locale par des courants côtiers; 2) rétention locale par des tourbillons; 3) perte directe hors de la zone d'étude; 4) perte via des tourbillons et 5) connexion entre îles.

- Illustrations of the main types of particles trajectories during Lagrangian drift simulations. Five types were identified at the four depth levels (A – surface, B – 25 m, C – 50 m, D – 125 m) : 1) Local retention by coastal currents; 2) local retention by eddies; 3) direct lost from the study domain; 4) lost by eddies and 5) islands connection.

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Figure 4.9 A-B (sur les deux pages suivantes)

- Bilan "larvaire" dans l'archipel du Cap-Vert tel qu'estimé par des indices écologiques établis à partir des simulations LSM. Quatre indices sont établis: la rétention, l'importation, l'exportation et la perte à partir du système. L'encadré CV présente les configurations spatiales entre les îles et les encadrés d'îles (majuscules) montrent les patrons temporels. L'axe-*y* représente un nombre absolu de particules, pondéré par leur temps de dispersion. A – en surface; B – à 125 m.

- "Larval" balance in the Cape Verde archipelago as estimate by ecological indices computed from LSM simulations. Four indices are computed: retention, import, export and lost from the system. The CV box shows the spatial patterns among islands and the islands boxes (capital letters) show the temporal patterns. The y-axes represent an absolute number of particles weighted by their dispersal time. A – Surface; B – 125 m.

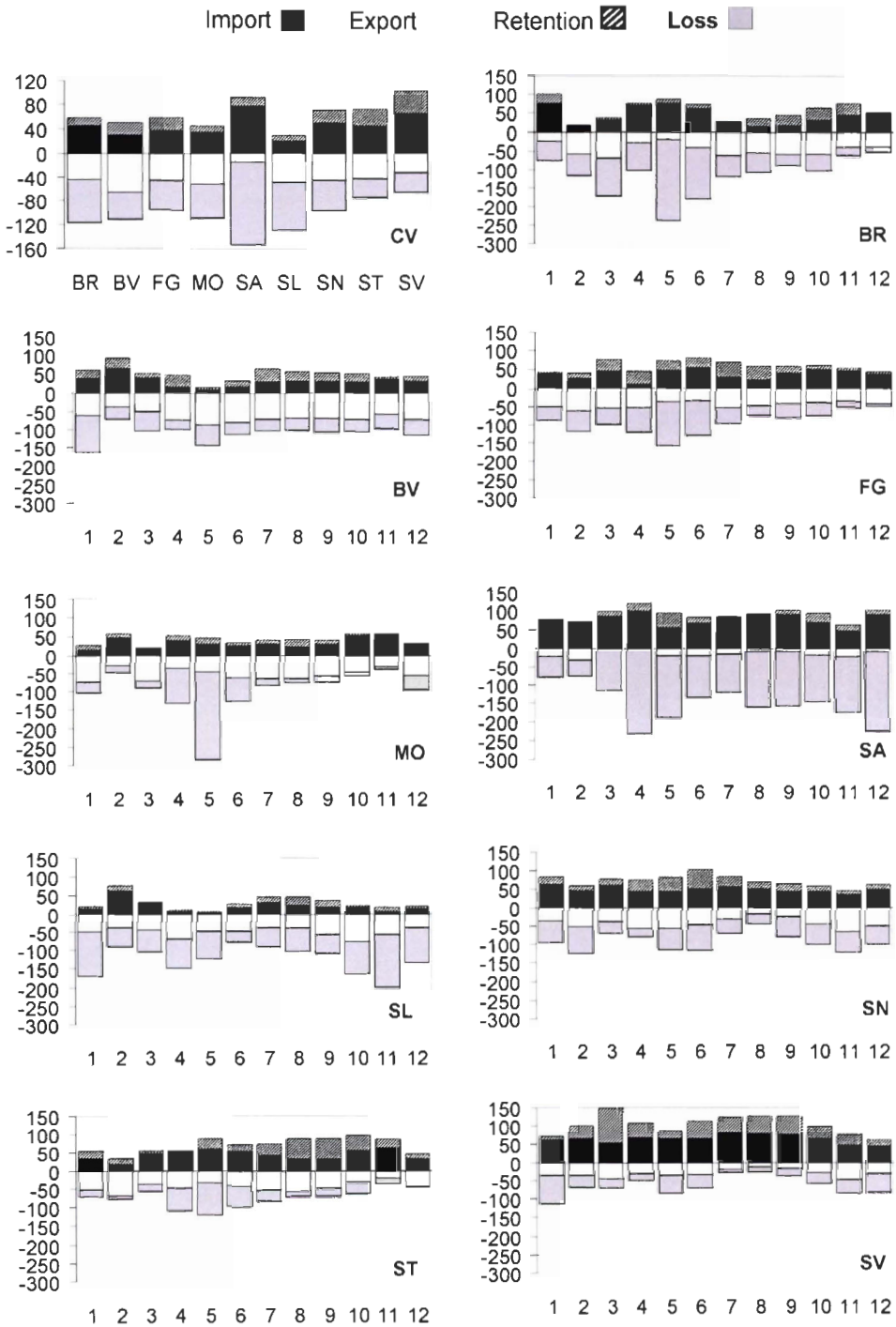

Figure 4.9-A (surface)

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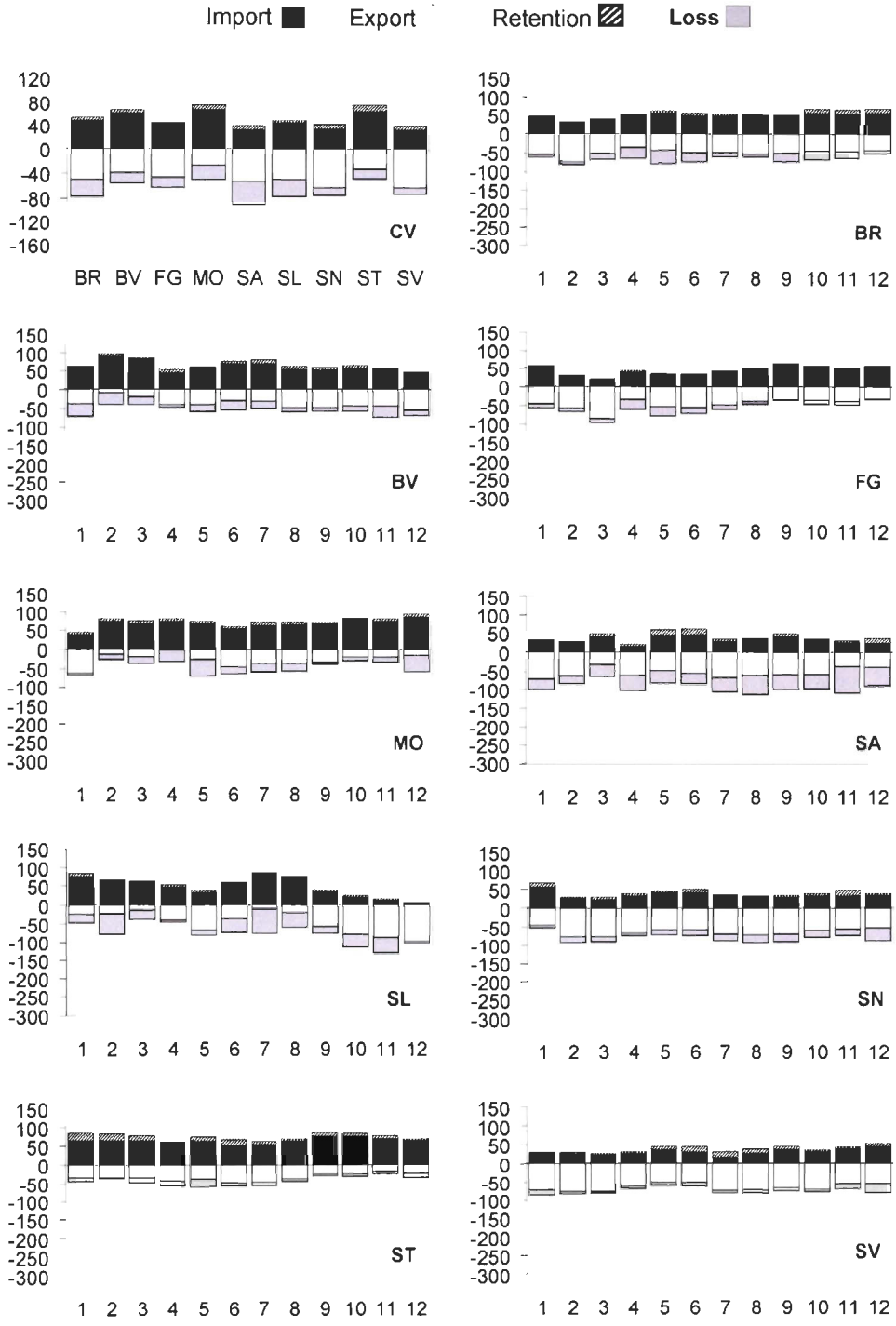

Figure 4.9-B (125 m)

Some islands such as Santo Antão and São Vicente are mainly net importers at the surface and become exporters in the deeper layers. Others (Sal, Boavista and Maio) are net exporters at the surface and become importers at deph. These results highlight the existence of deep dynamical processes which differ from those on the surface, due to counter-currents and coastal currents. Those deep processes are weak enough to prevent significant loss of particles out of the system, but strong enough to drive connectivity between the islands through import/export processes. The temporal variations are also more pronounced at the surface than at deph.

4.3.5 Ecosystem connectivity

Hydrodynamic connectivity. Results of the PCA and AHC on the matrix of C_h, illustrated by a Wroclaw diagram, show a complex spatial pattern where hydrodynamic processes, geographic distance and average depth interact (Figure 4.10). On surface (Figure 4.10-A), two main islands groups are discriminated on the first two axes, which extract 79.4 % of the total variance. The first one, formed by eastern (Boavista and Maio) and southern (Santiago, Fogo and Brava) islands are well connected at 48 % of similarity. Those islands are on the same pathway of dominant residual northeast-southwest currents, which could explain that high connectivity. Such an analysis is reinforced by a strong connectivity (> 55 %) between Maio, Santiago, Brava and Fogo islands. The second group is formed by the northern islands (Santo Antão, São Vicente, Santa Luzia, Raso and Branco islets). For this group, geographic distance and depth seem to be the major connectivity

factors. It is also interesting to note that, on surface, Sal island remains strongly isolated from the others, which corroborates the results showed by the "larval" balance.

At 30 m depth (Figure 4.10-B), the first two axes extract 81.1 % of the total variance. The northern islands become strongly connected (46 % and 79 %), and geographic distance and depth are the major connectivity factors. The same factors also explain the connectivity between Boavista and Maio in the east and between Santiago, Fogo and Brava in the southern part of the archipelago. The hydrodynamic processes appear to play a decreasing role when depth increases (Figure 4.10-C and D) up to 300 m. For those deep layers, the geographic distance and the average bathymetry become the dominant factors of connectivity.

Hydrodynamic interconnectivity. The spatial patterns of IC_h in the archipelago show that the Sal Island is weakly interconnected with an average annual IC_h value of 0.21, much lower than the average IC_h of the archipelago (0.41). The northern islands are the most strongly interconnected in the archipelago with values between 0.48 (Santo Antão and São Vicente) and 0.51 (São Nicolau), higher than the average, while the eastern islands are slightly inter-connected with values below the mean for the system. Among the southern islands, Fogo presents IC_h lower than the average of the archipelago, while Brava and Santiago present higher values, 0.44 and 0.47 respectively

The temporal pattern of average IC_h shows two main seasons (Figure 4.11-A). The first one, during colder months, between November and April, with higher IC_h than the average and, the second one, during warmer months, between May and October, inferior to the average.

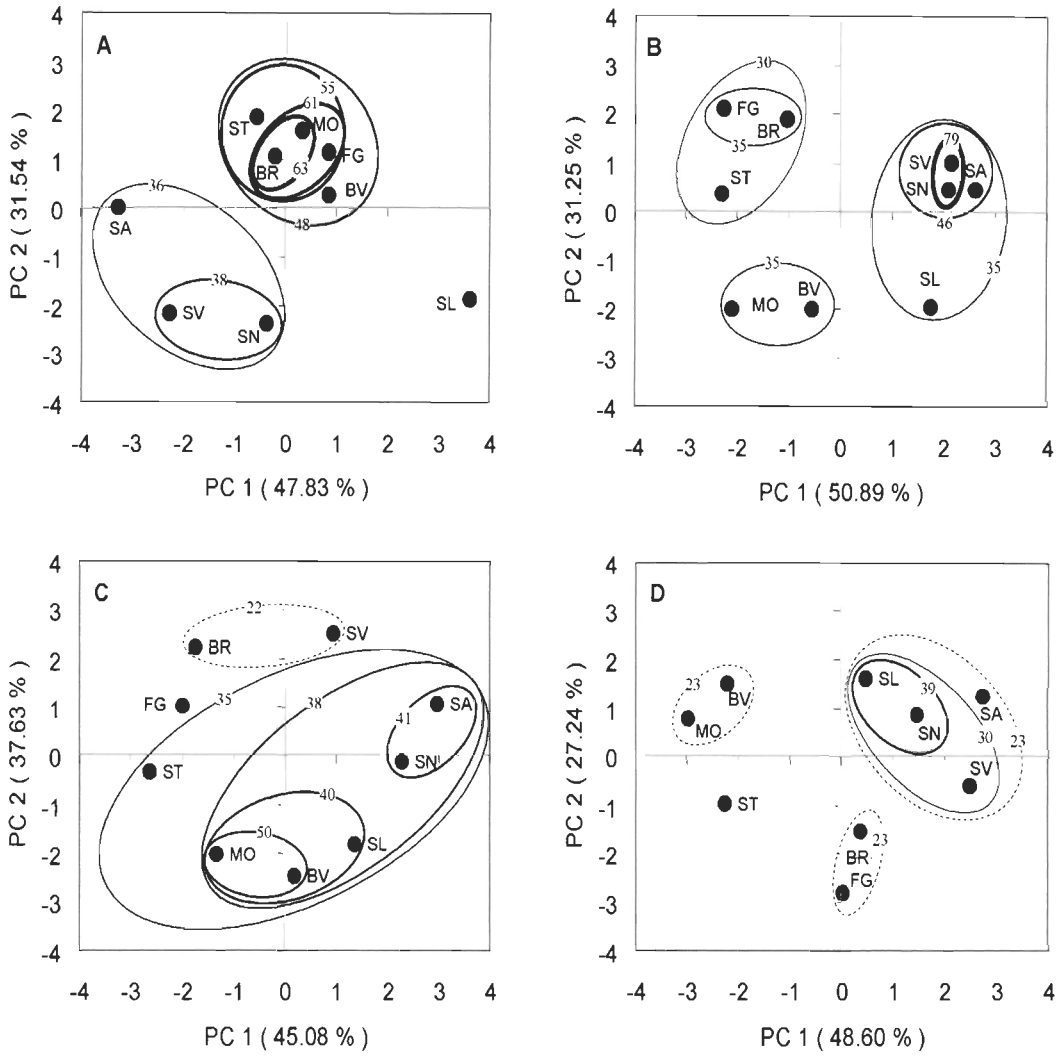

Figure 4.10

- Patrons spatiaux entre les îles du Cap-Vert tel que déterminés à partir d'une Analyse en Composantes Principales (ACP) et d'une Analyse Hiérarchique Ascendante (AHA) calculées avec une matrice de corrélation de Pearson basés sur la connectivité hydrodynamique entre les îles, deux à deux. A (surface); B (25 m); C (50 m); et D (125 m). La AHA est illustrée par un diagramme de Wroclaw où l'épaisseur des contours représente l'intensité de connexions. Les caractères majuscules dans le graphique représentent les îles.

- Spatial patterns among Cape Verde islands as determined from a Principal Component Analysis (PCA) and a Hierarchical Agglomerative Clustering (HAC) computed with a Pearson correlation matrix based on hydrodynamic connectivity between islands two by two. A (surface); B (25 m); C (50 m); and D (125 m). A Wroclaw diagram illustrates the HAC where the thickness of contour represents the intensity of connectness. Capital letters in the graph represent the islands.

This seasonality is clearer for the islands São Vicente, Santiago, Boavista and Brava (Figure 4.11-B). The effect of the seasons is statistically significant only at the surface (ANOVA, S: $F_{1, 99} = 6.142$, $p = 0.015$; I: $F_{8, 99} = 5.383$, $p < 0.000$).

4.3.6 Ecological isolation and ecosystem interconnectivity

The seasonal variation on IC_h was compared with the ecological isolation factor described by Medina *et al.* (2007) for demersal fish assemblages (Figure 4.12). The temporal variation between these two ecological indices shows a significant negative correlation (r = -0.728; p = 0.007) witch suggest they evolve almost in an opposite way. On one hand, the decreasing of ΔD observed during the cold season between December and January corresponds to a period of strong IC_h, with apparently one-month delay. On the other hand, the period during which ecological isolation seems stable at high level (warm season between May and November) coincides with a period of hydrodynamic interconnectivity lower than the average. These analyses seem to confirm that the hydrodynamic processes play a key role in the ecosystem connectivity of the archipelago.

4.3.7 Geographical distance, bathymetry and ecosystem connectivity

Mantel tests correlations between C_h at three depth levels (C_{h0}, C_{h50} and C_{h100}), geographical distance d and average depth b were calculated (Table 4.1). All linear correlations between these matrices are positive and statistically significant except on surface between C_h and average depth ($r = 0.306$, $P = 0.060$).

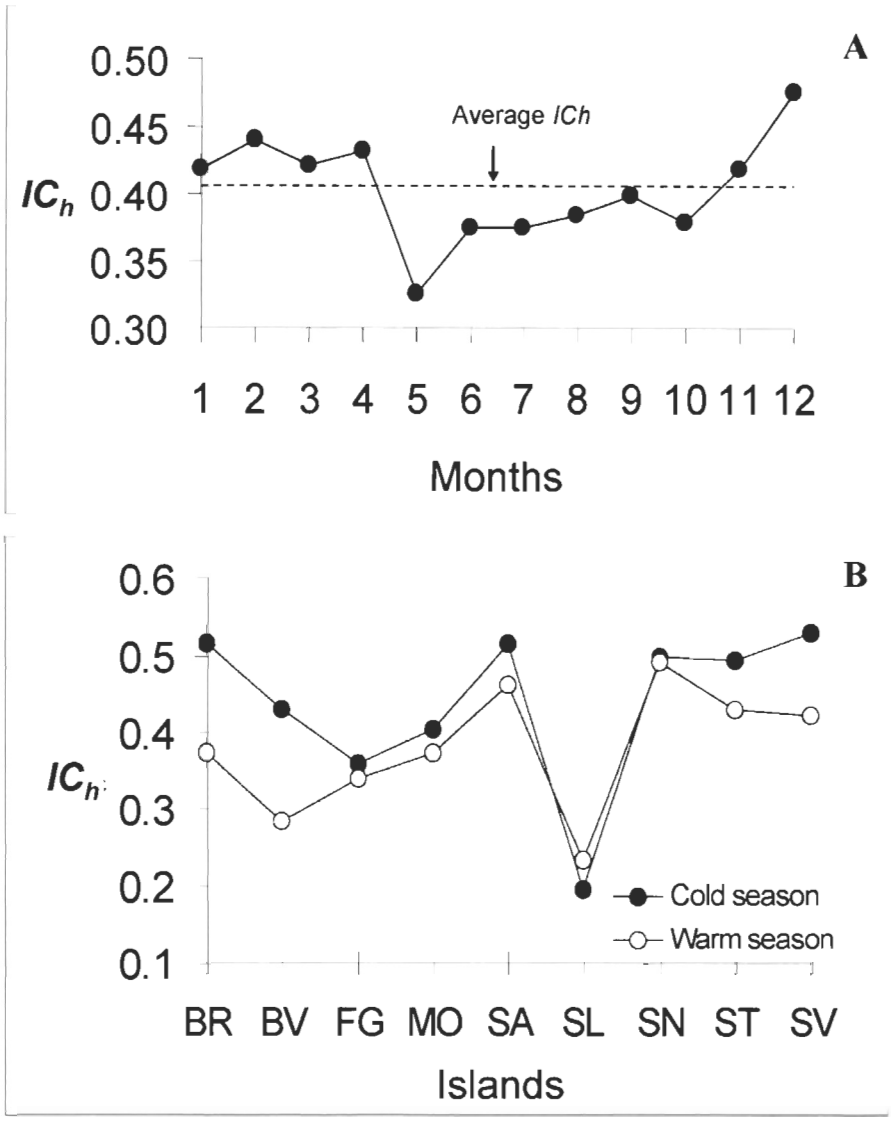

Figure 4.11

- Interconnectivité moyenne mensuelle entre les îles du Cap-Vert (A) et le patron saisonnier entre les îles (B).

- Monthly averaged interconnectivity among Cape Verde islands (A) and seasonal patterns among islands (B).

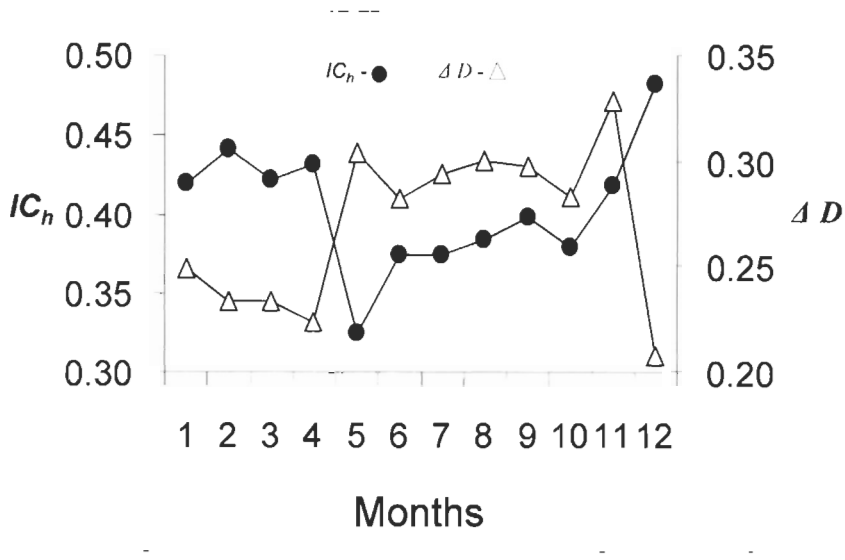

Figure 4.12

- Comparaison entre les patrons temporels de variation entre l'interconnectivité hydrodynamique (IC_h) et l'isolement écologique ($\triangle D$), celui-ci tel qu'estimé par Medina *et al.* (2007).

- Comparison between the temporal patterns on the variation between hydrodynamic interconnectivity (IC_h) and ecological isolation ($\triangle D$), the latter was estimated by Medina *et al.* (2007).

However partial correlation (when geographic distance remains constant) is strongly negative (r = - 0.87) and highly significant (P = 0.000). Such a statistical trend remains with depth suggesting that d and b interact as suppressor variables, masking a larger and significant correlation between each of them and C_h. The negative partial correlation indicates that hydrodynamic connectivity is stronger on surface and becomes weaker with depth, corroborating the previous results on islands connectivity.

4.3.8 Ecosystem connectivity and phenotypical variation

Linear correlation between C_h and the procrustes distance P_d (see Chapter 3) is not statistically significant when integrating local islands effect - P_{di} (Table 4.2 - upper panel) at all depth levels considered. Whenever suppressing the effect of distance and depth in a partial correlation (forcing I_{db} to remains constant) such relation between P_d and C_h still persist statistically non-significant. However the relationship between C_h and P_{da} (Table 4.2 - lower panel) shows a clear statistical significance that tends to be stronger with depth. The difference on statistical significance between linear and partial correlations at the surface r (C_0 x P_{da}) and r (C_0 x P_{da} | I_{db}) suggests that C_h and I_{db} are suppressor variables related to phenotypical traits. Since the connectivity decreases with depth, islands become more isolated and so, such a correlation between C_h and P_d suggests that a decrease in connectivity will be favourable to an increase of phenotypical variability.

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Tableau 4.1 Corrélations linéaires et partielles de première ordre à partir d'un test de Mantel effectué entre trois matrices symétriques [connectivité hydrodynamique à trois niveaux de profondeur - C_{h0} (surface), C_{h50} (50 m), C_{h125} (100 m); distance géographique – *(d)* et bathymétrie moyenne *(b)* entre îles]. Les tests on été effectués avec un nombre exhaustif de permutations et l'hypothèse nulle a été considérée pour alpha = 0.05.

Table 4.1 Linear and first-order partial correlations from a Mantel test computed between three symmetrical matrices [hydrodynamic connectivity at three depth levels - C_{h0} (surface), C_{h50} (50 m), C_{h100} (125 m); geographical distance – *(d)* and average depth *(b)* between islands]. Tests were performed for an exhaustive number of permutations and the null hypothesis was considered for alpha = 0.05.

Matrices	Linear correlation	Partial correlation	*P*
$C_{h\,0}$ *x b*	0.306	-	0.060
$C_{h\,0}$ *x d*	0.463	-	**0.014**
$C_{h\,0}$ *x b | d*	-	- 0.897	**0.000**
$C_{h\,50}$ *x b*	0.408	-	**0.013**
$C_{h\,50}$ *x d*	0.487	-	**0.001**
$C_{h\,50}$ *x b | d*	-	-0.305	**0.034**
$C_{h\,100}$ *x b*	0.540	-	**0.005**
$C_{h\,100}$ *x d*	0.641	-	**0.001**
$C_{h\,100}$ *x b | d*	-	-0.427	**0.004**

Tableau 4.2 Corrélations linéaires et partielles de première ordre à partir d'un test de Mantel effectué entre trois matrices symétriques [connectivité hydrodynamique à trois niveaux de profondeur - C_{h0} (surface), C_{h50} (50 m), C_{h125} (100 m); isolement physique (I_{db}) entre îles; distance procruste – P_d (au niveau d'île - P_{di} et d'archipel - P_{da})]. Les tests on été effectués avec un nombre exhaustif de permutations et l'hypothèse nulle a été considérée pour alpha = 0.05.

Table 4.2 Linear and first-order partial correlations from a Mantel test computed between three symmetrical matrices [hydrodynamic connectivity at three depth levels - $C_{h\ 0}$ (surface), $C_{h\ 50}$ (50 m), $C_{h\ 100}$ (100 m); physical isolation (I_{db}) between islands; procruste distance - P_d (at island level – P_{di} and archipelago level – P_{da})]. Tests were performed for an exhaustive number of permutations and the null hypothesis was considered for alpha = 0.05.

Matrices	Linear correlation	Partial correlation	*P*
$C_{h\ 0}\ x\ P_{di}$	-0.372		0.051
$C_{h\ 0}\ x\ P_{di} \mid I_{db}$		-0.347	0.059
$C_{h\ 50}\ x\ P_{di}$	-0.216		0.220
$C_{h\ 50}\ x\ P_{di} \mid I_{db}$		-0.328	0.105
$C_{h\ 100}\ x\ P_{di}$	-0.149		0.286
$C_{h\ 100}\ x\ P_{di} \mid I_{db}$		-0.245	0.169
$C_0\ x\ P_{da}$	-0.371		0.058
$C_0\ x\ P_{da} \mid I_{db}$		-0.374	**0.048**
$C_{h\ 50}\ x\ P_{da}$	-0.463		**0.015**
$C_{h\ 50}\ x\ P_{da} \mid I_{db}$		-0.485	**0.011**
$C_{h\ 100}\ x\ P_{da}$	-0.416		**0.017**
$C_{h\ 100}\ x\ P_{da} \mid I_{db}$		-0.434	**0.013**

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4.4 Discussion

Archipelago systems present a heterogene topography that breaks the large oceanic flows and produces various mesoscale circulation features. The Cape-Verde archipelago is located in a bordering and transitional zone between two large-scale oceanic circulation systems, the North Atlantic subtropical gyre (Canary Current) in the north, and the northern limit of the Equatorial Counter-Current in the south. This archipelago represents a particular case, which has received, until now, very little attention. The seasonal variation on the two major systems of oceanic currents is related to variations on the intensity of the Azores anticyclone in the North Atlantic and the Santa Helena island's anticyclone in the South Atlantic (Soares & Vasconcelos 1962) affecting the circulation of the surface layer down to 200 m of depth (Stramma & Siedler 1988). However, the variations of the water flows at spatial (islands) and temporal scales (month and season) are not known.

In order to address those issues, the present work takes advantages of a modern ocean modeling approach. Specifically, the *Mercator Ocean* operational system describes the state of the ocean at any given time and place and provided for the study area a considerable amount of high-resolution oceanographic data, which were successfully validated by independent information. The methodological approach of the present work is based on multivariate statistics such as Complex Empirical Orthogonal Function analyses (CEOF) to identify and describe main hydrodynamic patterns, and Lagrangian stochastic modeling (LSM) to investigate ecosystem connectivity, which have proven to have enough discriminating and analytical power. CEOF analysis present known shortcomings (Korres *et al.* 2000; Fernandes *et al.* 2005; Hannachi *et al.* 2007) and the two-dimensional LSM

approach presents limitations, as it does not consider vertical advection of particles. Despite those caveats, the present results appear robust and coherent with other research undertaken in other insular areas (below in the discussion). Therefore, the phenomena and processes described here at different spatial and temporal scales represent a new contribution for the understanding of the overall functioning of this tropical insular marine ecosystem.

From the two large oceanic circulation systems, the Canary Current appears to be the main contributor to the archipelago circulation system. That current presents velocities of about 10 to 15 $cm.s^{-1}$. At the latitude of Cape Verde islands, it is get strengthened by the effect of northeasterly Trade Winds and reaches velocities of 20 to 30 $cm.s^{-1}$. When reaching the islands, the Canary Current becomes stronger and it is divided in several branches. Two of them go round the archipelago, one along the northern limit and another along the southern one. Other branches enter the archipelago system and are responsible of the small-scale (60 to 120 km) circulation patterns and of the east-west and north-south transport of a considerable amount of water.

The circulation between islands is dominated by an intensification of the currents downstream, with the formation of several small-scale circulation structures such as eddies and local currents. This increase of currents velocity downstream from the islands can be explained by the conservation of the potential vorticity due to topographic effects (Hamner & Hauri 1981; Metzner & Hennings 1995; Spall 2000). In the northern area, these hydrodynamic changes generate, in the south of Santo Antão, Sao Vicente, Santa Luzia and Sao Nicolau, a system of swirling asymmetrical circulation with the formation of a cyclonic eddy towards the west and a anticyclonic eddy towards the south. The consequent

ascending or descending rotational movement of water masses produces respectively a reduction and an increase in the relative vorticity. Similar circulation patterns were observed in insular and coral reef regions as Pandora Reef (Hamner & Hauri 1981), Canary Islands (Aristegui *et al.* 1994), Barbados Island (Bowman *et al.* 1996) and Azores Islands (Richardson & Tychensky 1998), and were recently reproduced in laboratory by numerical simulations (Dong *et al.* 2007). The stability and lifespan of the observed small-scale structures are depending on the seasonal variation. The anticyclonic eddy appears to be consistently longer and more stable than the cyclonic one. However, during the cold season, it appears to be better established and closer to the islands. During the warm season, when current speed increases beyond a critical value (> 40 $cm.s^{-1}$ in June), vorticity becomes localized in the anticyclonic eddy, which seems to be stretched in the direction of dominant currents. This dynamic behaviour is consistent with field observations (Hamner & Hauri 1981; Kamenkovich 1986) and laboratory simulations (Dong *et al.* 2007). The dimension and the lifespan of such small-scale circulation structures suggest that they play an important role in the biological functioning of the archipelago. Spatial features of 60 to 120 km and events periods of 120 days are sufficient scales to influence biological events such as depletion of nutrients, increased productivity and depletion of phytoplankton due to increased grazing and elimination of small grazers by larger predators, in a context of well coupled surface and mid-water processes (Hamner & Hauri 1981).

A north-south current is another important small-scale circulation structure observed. It transports a significant amount of water from northern to southern islands in the leeward of the archipelago, mainly from December to June. When reaching the south waters, it

forms a cyclonic movement around Brava, Fogo, Santiago and Maio islands, completely wrapping them, before taking the dominant large-scale current, in westward direction. At the same time, a corresponding anticyclonic eddy is generated in the south of the archipelago. Once again, this asymmetric circulation system, despite its short lifespan, seems to play important role in the hydrodynamic connection among the southern islands with the same biological consequences as suggested for the asymmetric system on the north.

A dynamic comprehension of the circulation within the archipelago can be assimilated as the result of complex interactions between the climate seasonality in the archipelago (De Brum Ferreira 1989), the large-scale oceanic circulation systems (Stramma & Siedler 1988; Stramma & Schott 1999; Lázaro *et al.* 2005) and the local small-scale effects of islands morphology and topography.

The small-scale circulation patterns and the corresponding spatial and temporal variability drive a complex mechanism of islands connectivity. The detailed analysis of trajectories of fluid particles in a two-dimensional LSM shows five main dynamic trajectories, which play different roles in the whole ecosystem connectivity and population structure.

A first type of trajectory corresponds to local retention at island scale. This process is very important for the preservation of local populations and biodiversity of each island, and enhances ecological isolation. Local retention is a dominant factor at the surface for Sao Vicente and Santa Luzia islands, Raso and Branco islets. Retention can be induced either by local coastal currents or by eddies circulation structures. It corresponds to the "islands

mass" effect (Hamner & Hauri 1981; Sander 1981; Boden 1988; Rissik *et al.* 1997) where it is possible to observe a passive homing behavior of particles in all release sites after a varying dispersal time.

The trajectories favouring islands exchanges, either in one or in two senses by import and export processes, potentially preserve populations and biodiversity at the scale of the archipelago system, at a higher scale than one island. Furthermore, import/export processes may favour genetic mixing among marine populations. These two types of islands connections are thus important as well in the spatial flows of energy as of materials and organisms across islands boundaries within the archipelago. Import and export processes are not symmetrical within the archipelago. Sal Island appears to be a net exporter, receiving very few particles from other islands. It can be then considered as a "source" population, which makes this island very vulnerable to recruitment failure but very important for recruitment at other islands. Some islands are net importers, such as São Vicente, Santa Luzia, the islets Raso and Branco and Santo Antão. Those islands are also the most favourable for larval retention almost all year round, as observed in the field (Marques *et al.* 1997). As they are fed by several other islands, they may have more stable and sink populations. Finally, islands such as Boa Vista and Brava present a kind of equilibrium between import and export. Such observations corroborate researches on the life cycle of marine species, which state the role of hydrodynamic conditions as the major factor favoring larval settlement in islands and coral reefs after a more or less long adaptive residence in the open ocean (McCormick & Makey 1997; Lecchini *et al.* 2004; Ribergaard *et al.* 2004).

Other trajectories correspond to advection by current or transport by eddies out of the archipelago. Those trajectories imply losses for the system but play a role in the connection of the archipelago with the whole North Atlantic Ocean ecosystems through the large-scale currents systems. These hydrodynamic connections can be of crucial importance in the analysis of biogeographic hypotheses that place de Cape Verde archipelago in the highway of transatlantic ecosystems colonization as suggested for the Loggerhead Sea Turtle, *Caretta caretta* (Bolten *et al.* 1998) and the Gastropod, *Littorina stiata* (De Wolf *et al.* 2000). Similar scientific hypotheses have been recently proposed by Shank & Halanych (2007) for the genetic distribution of the deep-sea hydrothermal vent tubeworm *Riftia pachyptila* in the Pacific Ocean.

The "larval" balance estimated for the archipelago is based on a dynamic comprehension of particles trajectories, *i.e.* the quantification particles transport simulated by weighing the average number of particles against their average residence period when moving from one site to another. As highlighted by research on passive dispersal modeling (Engie & Klinger 2007) larval of longer planktonic duration are more likely to disperse between sites but are also more likely to be exported beyond the boundaries of the system. Therefore, such an approach enables to propose a conceptual framework for the assessment of the dynamic relationships (retention, import, export and loss) between several geographic compartments of an insular marine system. It allows making a diagnosis of functioning conditions of the system and subsequently simulates various scenarios in term of marine population's structure and dynamics, at the larval stage.

The ecological indices we propose to measure the ecosystem hydrodynamic connectivity C_h and interconnectivity IC_h in an archipelago system are based on classical approaches in numerical ecology, which integrate concepts of ecological distance, similarity and biological diversity (Legendre & Legendre 1998). They can be applied to quantitative data (continuous or not) and their use is not affected by doubles zeros, making it possible to simulate the exhaustiveness of scenarios on the hydrodynamic exchange between ecosystem compartments, either two by two or between each one and the whole system. These two levels of ecosystem connectivity have different implications in terms of population structure. While the first concept refers to a two-by-two relationship, the second one aims at measuring the strength by which a particular compartment (*i.e.* island) is connected with the whole. The implementation of such indices in the present work in a statistical multivariate context, allowed studying the Cape Verde islands ecosystem connectivity and its sensitivity variation with depth. A suppressor effect between distance and depth related to hydrodynamic connectivity was observed. The same statistical behaviour between physical isolation and hydrodynamic connectivity was also observed related to phenotypical variability, *i.e.* they interact as suppressor variables masking a larger and negative significant correlation between each one and phenotypical distance. It was thus possible to demonstrate a significant negative correlation between hydrodynamic connectivity and phenotypical traits for a demersal fish (Serranidae – *C. taeniops*) widely distributed among the Cape Verde Islands (this thesis, Chapter 3). This correlation becomes stronger with depth and follows hydrodynamic seasonal variations on surface. The same correlation had already been observed by Medina *et al.* (2007) between geographic

distance, average depth and ecological variability of demersal fish assemblages among islands. Hydrodynamic connectivity decreases with depth and islands become more isolated suggesting that a decrease in connectivity will be favourable to an increase of phenotypical variability. Since during their development, larvae tend to become benthic, such an outcome seems coherent, as benthic forms rapidly become capable of settling and thus they take the phenotypic signal driven by the local environment. However, we do not know when the determination of phenotypic differentiation takes place because young and larval stages were not studied. Thus, before making any ecological inference between hydrodynamics in the archipelago and marine species phenotypical traits, we recommend, in future research, to extend such exercise to other species and taxonomic branches. Northern islands (Santo Antão, São Vicente, Santa Luzia and São Nicolau) are well isolated from the eastern and southern ones (excepting Sal island), which are well connected among them by dominant currents. These results highlight an important role of hydrodynamics in the ecosystem connectivity at the surface.

The proposal of such ecological indices in the present work aims to provide decision makers with practical tools to facilitate the implementation of marine resources management and conservation policies. In the application of these ecological indices, we highlighted the almost extreme hydrodynamic vulnerability of eastern islands, upstream of the dominant currents, more particularly the Sal Island, concerning ecological awareness on larval retention and subsequent recruitment processes. The strength of dominants currents and their east-west direction favour a consistent unidirectional transport, suggesting that larvae are exported from the eastern side of the archipelago. Such ecological findings explain quite well some of the major reasons of the non recovery of lobster resources on

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Sal and Santiago islands (Medina *et al.* 2003), for more than a decade from now, despite the absence of target fisheries. The approach we developed in the present work represents an important contribution in the understanding of marine populations' structure in archipelago systems. Therefore, according to the general lack of scientific information on larval dynamics in the archipelago we suggest that the present results can be taken as a reference guide in all attempts to construct a functional network of Marine Protected Area as well as to design fisheries management plans. Further, it would be interesting to test the hydrodynamic and ecological approaches we propose here and evaluate the applicability of the ecological tools in a broader context of archipelagos that have common physical, geomorphological and geographical features with Cape Verde archipelago.

Among significant scientific issues to be addressed related to ocean circulation and larval dynamics, it would be interesting to investigate the main biological processes in the localized asymmetric eddies circulation in the archipelago. We are fully conscious that the oceanographical and ecological processes elucidated in this research are, in addition to the monthly and seasonal variations, subjected to annual variations. However, we could not address those longer-term variations as only two years of data were available. Thus, it leaves open an interesting continuation of this work, for example, by analysing a longer series of Mercator output as given by ocean reanalysis which applicability is already validated for this archipelago. It could be done by developing a more sophisticated individual based model (Moullon *et al.* 2003) that could integrate a vertical dimension and some real larvae behaviour (*i.e.* buoyancy, active movement, morphology) in order to predict where, when and how larvae from different species are going to be recruited in a given island or habitat in the archipelago.

DISCUSSION GÉNÉRALE

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Les archipels sont des écosystèmes avec des limites spatiales clairement établies, caractérisés par des interactions multiples entre de nombreux facteurs physiques comme la topographie, la morphologie des côtes, l'étendue des plateaux, la distance géographique et la bathymétrie entre les îles. Ces interactions, liées à des patrons très variables de circulation océanique à petite et à grande échelle, sont à l'origine d'une diversité écologique qui influence la structure et la dynamique des populations marines. Le Cap-Vert représente un cas de ce genre de système où l'on a pu mettre en évidence la fragmentation physique par la distance géographique et la bathymétrie, à laquelle s'associe un hydrodynamisme complexe induit par des variations saisonnières dans la circulation océanique à grande échelle qui affecte la région, essentiellement la gyre Nord-Atlantique et le Contre-Courant Équatorial.

L'étude présentée dans le chapitre 1 de cette thèse (Medina *et al.* 2007) fait ressortir l'effet combiné de la distance géographique et de la bathymétrie moyenne dans la variabilité écologique des populations démersales de poissons entre les îles. Cet effet présente des variations saisonnières. Il est plus intense et stable entre mai et novembre et, plus faible et variable entre décembre et avril. Le présent travail montre qu'il existe un isolement écologique des différentes îles, ou groupes d'îles, à l'intérieur de l'archipel régulé, entre autres, par une corrélation entre la bathymétrie moyenne, la distance entre les îles et les conditions hydrodynamiques (Medina *et al.* 2007). Ces résultats sont appuyés par les travaux récents sur l'hydrodynamisme autour d'îles (Spall 2000; Jirka 2001; Palacios 2002; Johnston & Merrifield 2003), pics sous-marins et récifs coralliens (Cowen 2002). Cet

isolement écologique aussi été mis en évidence dans l'étude de la variation phénotypique de la forme du corps du mérou à point bleu (*C. taeniops*) en fonction d'une fragmentation induite par ces mêmes facteurs d'isolement physique (chapitre 3 de cette thèse). *A posteriori*, l'étude de la circulation océanique et de la connectivité hydrodynamique à l'intérieur de l'archipel, entre les îles (chapitre 4) nous a permis de corroborer ces constatations. En fait, la distance géographique et la bathymétrie jouent un rôle significatif aussi bien dans la variabilité écologique que dans la connectivité hydrodynamique entre les îles. L'effet de la connectivité hydrodynamique sur la variation phénotypique à l'échelle de l'archipel a aussi été constaté. Par contre, à plus petite échelle spatiale (île) cet effet n'a pas pu être démontré, suggérant ainsi une plus forte influence des conditions locales sur l'expression phénotypique. Dans les circonstances où un effet de l'hydrodynamisme est observé, cet effet peut être potentiellement masqué par l'isolement physique, suggérant qu'une interprétation adéquate de l'effet des facteurs d'isolement physique et de l'hydrodynamisme sur l'expression phénotypique requiert un dépistage préalable des effets suppressifs de l'une et l'autre source de variation.

Les échelles spatiales et temporelles des processus et phénomènes étudiés au niveau écologique (chapitres 1 et 2), phénotypique (chapitre 3) et hydrodynamique (chapitre 4) varient à l'intérieur de l'archipel et n'affectent pas les différents niveaux organisationnels (gamètes, œufs et larves, espèces et assemblages) de la même façon et avec la même intensité. En milieu marin, l'appréhension et la maîtrise de ces échelles de variation représentent une condition indispensable à la compréhension de la dynamique et de la structure des populations en fonction de la complexité de différents phénomènes: dérive,

rétention, migration, advection et diffusion, induits et contrôlés par des facteurs biotiques et abiotiques.

1 Structure écologique

L'effet combiné de la distance géographique et de la bathymétrie sur la structure écologique des communautés de poissons démersales induit une organisation des îles selon un patron géographique en fonction de différents degrés d'isolement physique (Figure 1-A). Les populations des îles du Nord (Santo Antão, São Vicente, Santa Luzia, îlots Raso, Branco et São Nicolau) présentent une structure écologique similaire dominée par les espèces moins sensibles aux effets de l'isolement écologique comme *Apsilus fuscus*, *Lutjanus agennes*, *Pseudupeneus payensis*, *Scarus hoefleri* et *Scorpaena scrofa*. On y trouve, encore avec un certain poids dans la structure écologique, un assemblage mixte d'espèces plus (*Parapristipoma humile*) et moins sensibles (*Galeoides decadactylus* et *Acanthurus monroviae*) à l'isolement écologique. Les populations des îles orientales (Sal, Boavista et Maio) présentent une structure écologique dominée à la fois par des espèces moins sensibles (*Bodianus scrofa et Lethrinus atlanticus*) et par des espèces plus sensibles (*Virididentex acromegalus*, *Epinephelus marginatus* et *Cephalopholis taeniops*). Au sud de l'archipel, les populations de l'île de Brava et les îlots voisins sont caractérisées par des espèces plus sensibles à l'isolement écologique dont *Serranus atricauda*, *Pomadasys incisus*, *Priacanthus arenatus* et *Seriola dumerili*. Au niveau de similarité écologique où ces populations se trouvent structurées, les îles de Fogo et de Santiago restent relativement isolées l'une de l'autre. D'une part, les populations de l'île de Fogo présentent une structure

écologique proche de celles de Brava et des îlots voisins tandis que les populations de Santiago s'approchent plus de celles du nord de l'archipel. Dans l'un et l'autre cas les niveaux de similarité entre ces assemblages sont très faibles.

2 Dynamique spatiale

Les populations démersales de poissons de l'archipel révèlent essentiellement deux modes d'occupation de l'espace, indépendants de la densité, liés à la disponibilité de l'espace qui semble être un facteur important. D'une part les populations des îles à plateaux insulaires relativement plus étendus comme São Vicente, Santa Luzia et îlots voisins au nord, Boavista et Maio à l'est, Brava et îlots voisins au sud, tendent à présenter une variation différentielle de densité avec la variation d'abondance. Ces îles se trouvent sensiblement dans le même plateau insulaire jusqu'à l'isobathe de 100 m (figure 5.1). D'autre part, les populations confinées par l'étroitesse des plateaux insulaires c.-à-d. Santo Antão et São Nicolau au nord, Santiago et Fogo au sud et Sal à l'est, tendent à varier leur densité de façon proportionnelle à la variation de leur abondance. Ces sont des populations isolées des autres par des profondeurs supérieures à 500 m.

3 Structure phénotypique

Les individus de *C. taeniops* présentent des variations morphologiques suffisamment discriminantes pour séparer les populations des différentes îles. Cependant, certaines de ces populations présentent des similarités qui laissent supposer des échanges entre elles à un moment donné de leur cycle de vie. Les populations des îles du nord et celles des îles de

l'est de l'archipel sont plus similaires au niveau des variations de formes du corps tandis que celles des îles de Fogo et Santiago sont très éloignées (figure 5.1-B).

4 Structure hydrodynamique

Au niveau de l'hydrodynamisme de surface, les populations des îles du nord se trouvent bien connectées. De même, celles des îles de l'est et du sud se trouvent bien connectées dans le sens du courant résiduel dominant vers le sud-ouest de l'archipel. L'île de Sal se trouve complètement isolée du reste de l'archipel (figure 5.1-C). Ces patrons laissent supposer des échanges entre ces populations, encore au stade de développement larvaire des espèces, ces échanges pouvant résulter ou non en différentiation phénotypique, en fonction de la selection naturelle induite par les environnements locaux autour des îles et groupes d'îles.

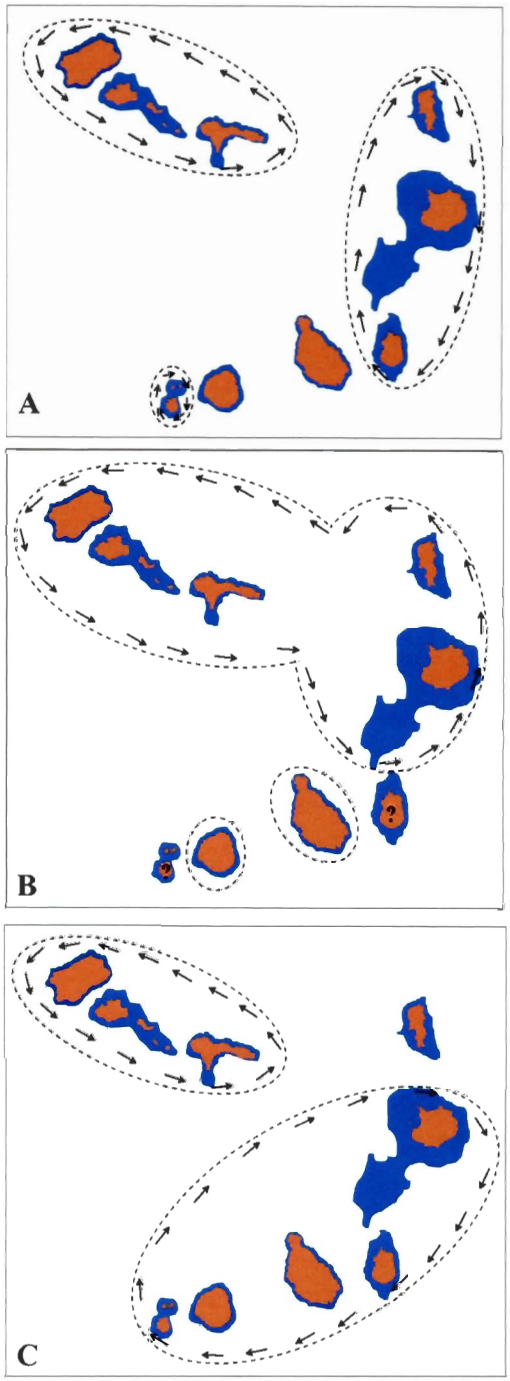

Figure 5.1 Structure des populations démersales de poissons de l'archipel du Cap-Vert tel qu'extrait de la variabilité écologique (A), phénotypique (B) et connectivité hydrodynamique de surface (C). Les îles sont entourées des plateaux insulaires respectifs jusqu'à l'isobathe des 100 m (en bleu sombre). Les contours en pointillés délimitent les zones à l'intérieur desquelles s'établissent des échanges (flèches noires) entre les différentes unités de populations.

5 Un modèle écologique de structure des populations démersales

Les informations issues des différentes approches d'étude de la structure des populations démersales c.-à-d. 1) étude de la structure écologique et de la dynamique spatiale à partir des données de pêche artisanale; 2) étude de la structure phénotypique à partir d'une des espèces de poissons démersales plus abondante et plus largement distribuée dans l'archipel; 3) étude de la connectivité hydrodynamique entre les populations des îles, ont été intégrées dans la figure 5.2.

Cet exercice de synthèse nous permet de présenter les populations démersales des plateaux insulaires de l'archipel du Cap-Vert comme une grande metacommunauté constituée essentiellement de trois metapopulations – la metapopulation des îles du Nord, la metapopulation des îles de l'Est et la metapopulation des îles du Sud (Figure 5.2). Chaque metapopulation est constituée d'un ensemble de populations typiques de chaque île ou îlot à l'intérieur de laquelle il peut exister des échanges dont l'intensité et l'échelle dépendent du degré de fragmentation de l'écosystème. Les échanges par migration d'adultes et de juvéniles peuvent se produire entre populations qui se trouvent sur les mêmes plateaux à des profondeurs inférieures à 100 m, tandis que des échanges de gamètes, œufs et larves peuvent se produire par effet hydrodynamique à des échelles spatiales supérieures.

Au niveau des metapopulations, les échanges peuvent se produire à tous les niveaux biologiques d'organisation, depuis les gamètes jusqu'à l'individu adulte et sont suffisamment constants dans l'espace et dans le temps pour produire un effet sur la structure écologique, le phénotype et la génétique des populations.

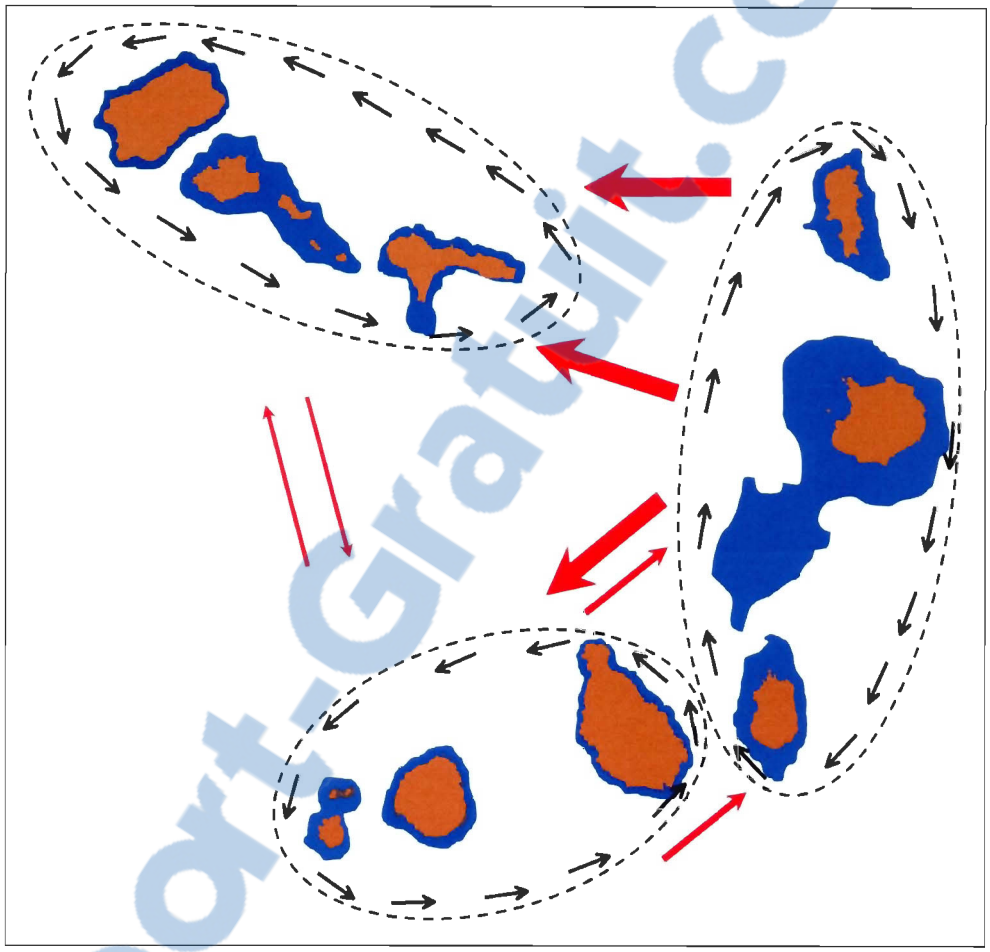

Figure 5.2 Représentation synthétique de la structure des populations démersales de poissons de l'archipel du Cap-Vert tel que déduit des connaissances complémentaires apportées par la structure écologique des principales espèces exploitées, la structure phénotypique du Mérou à point bleu (*Cephalopholis taeniops*) et l'hydrodynamisme dominant de surface. Les îles sont entourées des plateaux insulaires respectifs jusqu'à l'isobathe des 100 m. Les contours en tirés délimitent les zones à l'intérieur desquelles s'établi des échanges (flèches noires) entre les différentes unités de populations. Les flèches rouges, plus épaisses et en ligne continue représentent les échanges dominants entre les metapopulations de l'Est, du Nord et du Sud de l'archipel (l'épaisseur donne un ordre de grandeur sur l'intensité des échanges)

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Au niveau de la metacommunauté (l'ensemble de l'archipel), les échanges sont essentiellement limités aux premiers stades de développement des espèces et ne sont pas efficaces au niveau de la structure écologique et phénotypique, à court et moyen terme (échelle de quelques générations).

Metapopulation du Nord. Cette metapopulation est constituée de cinq unités de populations chacune correspondant à une île ou îlot. La migration de juvéniles et adultes est possible entre les populations de São Vicente, Santa Luzia, îlots Raso et Branco, car elles se trouvent sous le même plateau insulaire de 50 m. Cette caractéristique permet à ce noyau de populations de jouer un rôle de population-source qui se rapproche de la conception de metapopulation mixte de Harrison (1991). Par contre, les échanges avec les populations des îles voisines de Santo Antão et São Nicolau se résument à des processus de dispersion hydrodynamique de gamètes, œufs et larves. Ces processus sont suffisamment intenses et constants pour induire des similarités écologiques, phénotypiques et probablement génétiques.

Metapopulation du Sud. Cette metapopulation est constituée par quatre populations (Santiago, Fogo, Brava, îlots Grande). La possibilité de migration de juvéniles et adultes semble faible, car les populations sont séparées par des profondeurs supérieures à 1000 m, à l'exception du chenal entre Brava et îlots Grandes qui pourrait permettre un tel échange. L'espace est très fragmenté et les échanges principaux sont certainement hydrodynamiques.

Metapopulation de l'Est. Constituée par les populations des îles de Sal, Boavista et Maio, il s'agit de la metapopulation la plus petite en nombre d'unités, mais aussi les moins fragmentées, formée par des populations relativement plus grandes. À cause de l'étendue

particulièrement importante du plateau insulaire de l'île de Boavista jusqu'à l'isobathe de 100 m (environ 1 779 km2), ses populations semblent jouer un rôle de population-source. Les principaux échanges sont de nature hydrodynamique, les migrations de juvéniles et d'adultes étant très peu probables à cause des profondeurs qui séparent les plateaux.

La metapopulation de l'Est est la plus instable de l'archipel, car elle se trouve en amont des courants dominants, servant à alimenter la metapopulations du Nord et celle du Sud par des flux hydrodynamiques de gamètes, œufs et larves. Elle entretient une inter-connectivité hydrodynamique avec la metapopulation du Sud mais cet échange est relativement faible et temporellement instable, se limite à sa composante plus au sud (les populations de l'île de Maio). La metapopulation du Nord de l'archipel est la plus stable, car elle est fortement alimentée via l'hydrodynamisme, par la population de l'Est et s'auto-alimente à partir de sa propre population-source du plateau insulaire de São Vicente, Santa Luzia, îlots Raso et Branco. L'interconnectivité hydrodynamique qu'elle entretient avec la metapopulation du Sud n'est ni suffisamment intense, ni assez constante pour représenter un échange efficace entre les deux structures de population. La metapopulation du Sud est instable, car elle s'auto-alimente peu, ne disposant pas de population-source locale, et bénéficie quasi exclusivement des apports hydrodynamiques de la metapopulation de l'Est en amont.

L'ensemble de ces metapopulations, qui forment la grande metacommunauté de poissons démersaux des plateaux insulaires du Cap-Vert, se trouve dans une zone hydrodynamique très variable, résultat de la variabilité spatio-temporelle des principaux systèmes de courants de l'Atlantique Nord-Ouest (gyre Nord-Atlantique et Contre-Courant

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Équatorial). Cette variabilité de l'hydrodynamique est à l'origine d'importantes pertes directes de matière biologique à partir de l'archipel (environ 40 %, estimé par simulation LSM). Néanmoins, cette perte pour l'archipel peut représenter un flux important de matière biologique vers d'autres écosystèmes Nord-Atlantique.

Les modes de gestion actuels au Cap-Vert sont encore basés généralement sur le principe de stocks uniques pour l'ensemble de l'archipel. Les résultats obtenus ici démontrent que les populations sont hétérogènes et que chaque île pourrait être considérée comme une entité écologique qui pourrait être gérée de façon distincte. On constate aussi que les îles ne sont pas également vulnérables à l'exploitation par la pêche. Les îles orientales, c.-à.d. Sal, Boavista et Maio, de par leur localisation en amont des vents et courants océaniques dominants, représentent une région très sensible, en raison d'un flux de matière biologique quasi unidirectionnel vers l'ouest. Elles agissent comme populations sources pour les autres îles mais sont faiblement auto-suffisantes. Si l'on envisage, par exemple, la mise en place d'activités de réensemencement d'espèces ou la définition d'aires marines protégées, il semble logique de se concentrer sur la metapopulation de l'est, en sachant qu'il y aura peu de résultats au niveau local mais que cela pourra avoir des effets bénéfiques, à moyen terme, sur les autres metapopulations en aval. Dans la même logique d'utilisation des connaissances hydrodynamiques, il semble peu efficace, du point de vue écologique, de concentrer des efforts de conservation sur la metapopulation du sud, essentiellement constituée de populations puits. Les résultats sur la dynamique spatiale des communautés soulignent une variation différentielle de la densité locale liée à des effets environnementaux. Cela implique une grande sensibilité à la surexploitation locale et

suggère des modes de gestion qui éviteraient une concentration exagérée de la flottille de pêche sur certains bancs.

Même si les résultats exposés dans cette thèse peuvent servir de point de départ pour la mise en place de mesures de gestion et de conservation, on constate de nombreuses lacunes dans la connaissance de l'écologie marine de l'archipel du Cap-Vert. En effet, jusqu'à présent, il n'y a pas eu d'autres recherches scientifiques sur la structure des populations démersales en rapport avec les effets de l'exploitation sur les ressources génétiques et la biodiversité. On constate également un manque général d'informations scientifiques sur la dynamique des premiers stades de développement des espèces dans l'archipel. Les résultats exposés dans cette thèse ne représentent qu'une première étape dans la connaissance de la dynamique des espèces démersales de l'archipel du Cap-Vert.

CONCLUSIONS GÉNÉRALES

ET

PERSPECTIVES DE RECHERCHE

CONCLUSIONS GENERALES

L'objectif général de recherche de cette thèse était de définir et de modéliser le fonctionnement d'un écosystème marin insulaire tropical. On cherchait à analyser la structure et la dynamique des populations de poissons démersaux, en tenant compte des principales variables qui influencent la variation spatiale et temporelle de la distribution et de l'abondance des espèces. De par ses caractéristiques géologiques, géographiques et hydrodynamiques, le Cap-Vert a été utilisé comme un modèle d'archipel où les frontières spatiales sont clairement établies. Ce modèle d'archipel océanique nous a permis de valider les hypothèses de recherche et atteindre les objectifs spécifiques fixés au départ.

1. *L'analyse de l'importance de la fragmentation induite par la distance géographique et par la bathymétrie dans la structure spatio-temporelle et la variabilité écologique des communautés de poissons démersaux a permis de valider l'hypothèse selon laquelle la fragmentation des habitats se traduit par une structure spatiale des populations démersales, propre à chaque île ou groupe d'îles.*

À partir de scénarios de covariance, nous avons mise en évidence un facteur d'isolement physique qui intègre à la fois l'effet de la distance géographique et de la bathymétrie moyenne entre les îles. Ce facteur explique l'isolement et la variabilité écologique entre les îles.

Nous avons aussi mise en place un indice de structure de communauté qui mesure la distance écologique entre les îles deux à deux, basé sur la dominance relative des espèces. L'étude de la relation entre l'indice d'isolement et celui de structure de communauté nous a

permis de mettre en évidence un effet de niche écologique comme élément structurant les assemblages démersaux de poissons. D'une part, une augmentation de la distance géographique pour une profondeur moyenne constante, signifie plus d'espace disponible et améliore donc le fitness général de l'habitat, pour des espèces potentiellement dominantes, dans un secteur particulier. Par conséquent, les dominances relatives augmenteront. D'autre part, une augmentation de la profondeur moyenne pour la même distance géographique diminuerait l'espace disponible et réduirait le fitness général de l'habitat. Par conséquent, les dominances relatives diminueront car les espèces auront moins d'espace disponible pour exercer leur dominance. Du point de vue écologique, puisque la disponibilité de l'espace est le support physique des conditions biotiques et abiotiques à l'intérieur desquelles les espèces peuvent exister, un tel effet de niche semble être important dans la dynamique d'utilisation de l'espace par les espèces, dynamique liée aux partages des ressources de l'écosystème.

Nous avons aussi démontré que, dans un système d'archipel, l'isolement physique se traduit par un isolement écologique qui affecte les espèces différemment, certaines étant plus sensible que d'autres. Pour l'archipel du Cap-Vert, cet isolement est plus marqué en saison chaude, entre mai et novembre (hydrodinamisme relativement faible), qu'en saison froide, entre décembre et avril (hydrodynamisme relativement forte). L'isolement physique induit une structure écologique des communautés d'espèces démersales selon un patron géographique qui regroupe les îles au nord, les îles au sud (à l'exception de Fogo et Santiago) et les îles orientales.

2. *L'analyse de la dynamique spatiale des populations démersales exploitées, selon différentes échelles spatio-temporelles (îles, saisons et années) et différents niveaux d'organisation écologique (espèce et communauté) a permis de renforcer les résultats obtenus dans la première approche.*

L'étude de la dynamique spatiale a démontré que dans les îles à plateau insulaire relativement large (São Vicente, Santa Luzia et îlots voisins; Boavista et Maio; Brava et îlots voisins), les communautés adoptent une dynamique spatiale de variation différentielle de la densité, principalement contrainte par des facteurs environnementaux. Au contraire, dans les îles ou les communautés démersales sont confinées par l'exiguïté des plateaux (Santo Antão, São Nicolau, Sal, Santiago et Fogo), l'occupation de l'espace se fait selon une dynamique à densité proportionnelle, indépendamment du niveau d'organisation écologique. Au niveau temporel, les espèces et les communautés adoptent la même dynamique spatiale d'une saison à l'autre et ce, à longueur d'année.

3. *La vérification de l'effet de la fragmentation d'habitat, résultant de la persistance de conditions d'isolement physique ou écologique entre les îles, sur l'isolement effectif des populations nous a permis de démontrer qu'effectivement l'isolement écologique induit une différentiation morphologique entre les individus de même espèce habitant chaque île ou groupe d'îles;*

Nous avons démontré une absence d'effet du sexe et le d'état ontogénique dans les variations de forme du corps du Mérou à point bleu (*C. taeniops*). Les variations phénotypiques inter-îles sont plus fortes que celles intra-îles et chaque île présente un

modèle allométrique particulier qui représente en moyenne 11.5 % de la variation totale de la forme du corps. Les îles du nord (Santo Antão, São Vicente et Santa Luzia) présentent une direction de changement ontogénique similaire à celle de l'île de Boavista à l'est tandis que, toutes les autres comparaisons deux à deux indiquent différents modèles ontogéniques entre les îles. L'isolement physique par la distance géographique et la profondeur est positivement corrélé avec la divergence morphologique entre populations des différentes îles et corrobore ainsi l'hypothèse selon laquelle la fragmentation insulaire dans l'archipel du Cap Vert peut être interprétée en termes de structure de populations marines.

4. *La définition et la validation d'un modèle hydrodynamique de connectivité de l'écosystème marin de l'archipel, tenant compte des objectifs antérieurs et des principaux phénomènes et processus océanographiques dominants nous a permis de confirmer que le régime hydrologique dans l'archipel contribue à l'isolement écologique et, probablement, génétique des îles.*

Le patron de circulation océanique entre les îles est dominé par une intensification des courants en aval, avec la formation de plusieurs structures de circulation tourbillonnaire à petite échelle (60 à 120 km), par des courants nord-sud et est-ouest, responsable pour le mélange des eaux à l'intérieure de l'archipel. La formation au sud-ouest de l'île de Santo Antão d'un système de circulation asymétrique tourbillonnaire composée d'un anneau cyclonique vers l'ouest et d'un anneau anticyclonique vers le sud ressort comme un phénomène persistant à la longueur de l'année. Pendant la saison froide, il semble être mieux établi et plus près des îles. Les dimensions d'ordre de 60 à 120 km et le temps de

résidence de telles structures, pouvant atteindre en moyenne 120 jours, représentent des échelles spatio-temporelles suffisamment grandes pour influencer des phénomènes et processus biologiques dans l'archipel.

La connectivité à l'intérieur de l'archipel est assurée par trois processus, guidés par différents types de trajectoires hydrodynamiques: 1) la rétention locale sur une île est induite par des courants côtiers ou par des tourbillon stables. Ce processus est très important dans la conservation des populations locales et de la biodiversité de chaque île et augmente l'isolement écologique à l'échelle de l'archipel. Elle est dominante en surface au niveau des îles São Vicente, Santa Luzia, îlots Raso et Branco; 2) des échanges entre îles se traduisent par des processus d'importation et d'exportation. Ce sont des processus importants pour la conservation de la biodiversité à l'échelle de l'archipel et représente un facteur potentiel de mélange génétique entre les populations marines; 3) l'advection hors de l'archipel est engendrée par les courants ou par des anneaux instables. Ce type de trajectoire implique des pertes pour l'archipel mais jouent un rôle dans sa connectivité avec d'autres écosystèmes de l'Océan Atlantique Nord par le biais des systèmes de courants à grande échelle. La quantification de ces processus permet de dresser un bilan larvaire hydrodynamique en fonction de la rétention, de l'importation/exportation entre îles et des pertes hors de l'archipel.

La connectivité hydrodynamique en surface révèle que, les îles de Santo Antão, São Vicente, Santa Luzia et São Nicolau sont bien isolées au nord. Les îles orientales (à l'exception de Sal), et les îles au sud sont aussi bien connectées entre elles. Ces patrons suivent des variations saisonnières et s'affaiblissent avec la profondeur où la distance

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géographique et la bathymétrie moyenne entre les îles deviennent des facteurs principaux de connectivité avec des effets opposés. Il a aussi été possible de démontrer une corrélation significative entre la connectivité hydrodynamique à différents niveaux de profondeur et les traits phénotypiques pour le Mérou à point bleu.

Une interprétation de l'ensemble des résultats nous a permis, dans une vision fonctionnelle, de présenter les populations démersales des plateaux insulaires de l'archipel du Cap-Vert comme une grande metacommunauté, constituée essentiellement de trois metapopulations – la metapopulation des îles du nord, la metapopulation des îles du sud et la metapopulation des îles de l'est. Chaque metapopulation est constituée d'un ensemble de populations typiques de chaque île ou îlot, à l'intérieur de laquelle il peut se produire des échanges dont l'intensité et l'échelle dépendent du degré de fragmentation de l'écosystème.

PERSPECTIVES DE RECHERCHE

La présente thèse de doctorat a été guidée par une démarche de recherche pluri-et interdisciplinaire qui cherchait, par une approche intégrée, à mettre plusieurs disciplines à contribution pour répondre à la problématique de recherche. De ce fait, en mettant en relation les différentes disciplines, une réflexion sur la dynamique du fonctionnement du système d'archipel étudié permet de dégager importants éléments de discussion qui pourront constituer autant d'éléments de recherche.

Dans l'étude sur les effets de la distance géographique et de la bathymétrie comme facteurs d'isolement écologique (chapitre 1), la science halieutique et l'écologie numérique ont été mises à contribution. Les résultats obtenus apparaissent robustes et cohérents pour comprendre la structure spatio-temporelle des communautés démersales de poissons de l'archipel mais ils ne tiennent pas compte de l'activité de capture. On peut émettre l'hypothèse que l'effet de la pêche sera suffisamment expressif pour interférer avec l'empreinte écologique mise en évidence. Il sera intéressant de mener une étude de même nature où l'on cherchera à discriminer entre le signal purement écologique et un éventuel signal de l'activité de pêche, contenu dans des données pêche.

Dans l'étude de la dynamique spatiale (chapitre 2), nous avons fait appel à la science minière – la géostatistique- pour modéliser les stratégies d'occupation de l'espace par l'espèce et la communauté à l'échelle d'île et d'archipel. L'interprétation des résultats de cette analyse nous a conduit à penser que la dynamique spatiale des poissons est un processus dépendant de l'échelle spatiale. Dans le contexte des théories récentes sur la distribution spatiale des espèces, dont la « distribution libre idéale », il sera opportun

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d'étudier, avec des données de même nature, la dynamique spatiale de l'espèce et de la communauté, à l'échelle du banc de pêche. Une telle étude pourra permettre de dégager des informations sur le comportement des espèces, importantes dans des études de la dynamique des populations marine exploitées.

L'étude phénotypique sur la variation de forme du corps du Mérou à point bleu (*C. taeniops*) a révélé la structure de population d'une espèce selon des unités géographiques indépendantes. Compte tenu de la robustesse et de la clarté du signal données par la géométrie morphométrique comme méthode d'étude de la structure des populations il serait très utile et opportun d'élargir cette étude à d'autres espèces démersales de poissons, mollusques et crustacées. De telles études fourniront des informations importantes pour la modélisation de la structure de population de chaque espèce ou communauté, en plus de représenter informations nouvelles sur la biodiversité de l'archipel. Des études récentes montrent une forte correspondance entre le signal phénotypique et le signal génétique sur plusieurs espèces dont *Sebastes sp.* (Valentin, 2006). Il serait donc intéressant de, dans des études futures sur *C. taeniops* ou d'autres espèces de l'archipel, d'intégrer, de façon conjointe, des approches phénotypiques et génétiques pour mieux identifier et décrire les structures des populations.

Dans un contexte d'environnement fragmenté, très variable et hétérogène, il serait intéressant de chercher à valider le modèle conceptuel de Swain & Foote (1999) qui vise à illustrer la relation entre l'environnement et la génétique dans l'expression du phénotype des espèces des différentes îles (Figure 6.1). De telles études seront fondées sur les principes selon lesquelles les variations des caractéristiques entre les espèces et populations sont dues à des effets génétiques et environnementaux, souvent liés à des variations géographiques et qui tendent à influencer le phénotype.

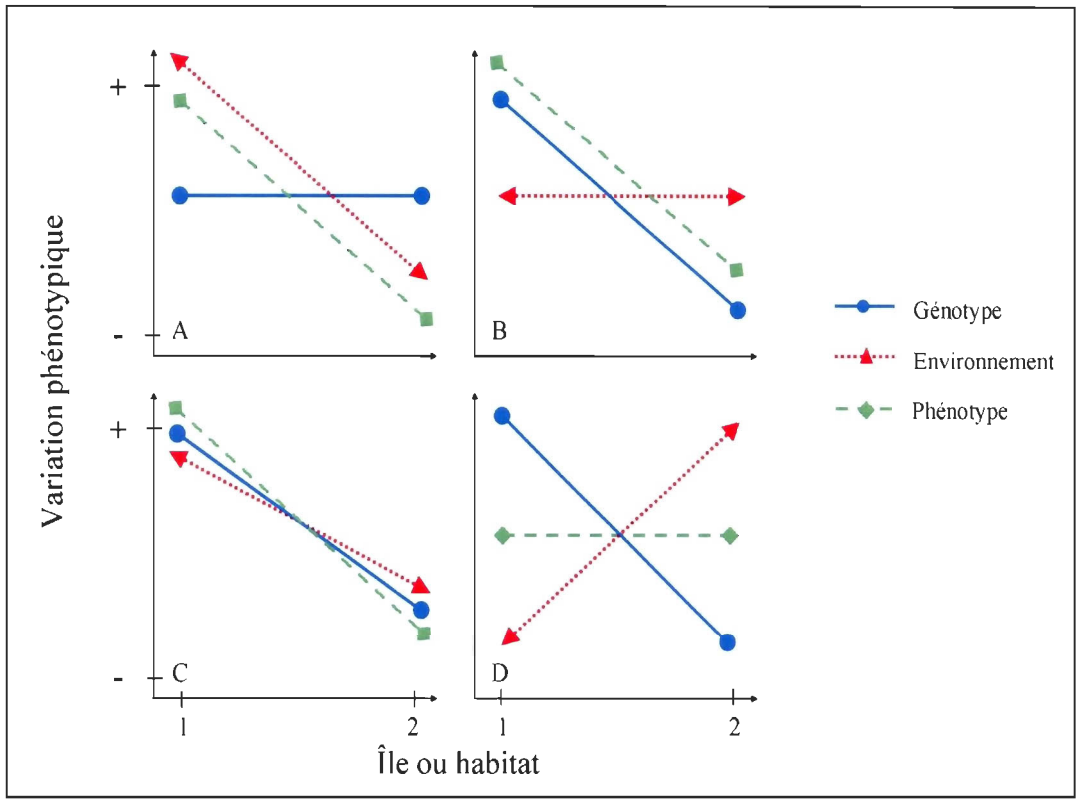

Figure 6.1 Relation conceptuelle entre le génotype et l'environnement dans l'expression de la variation du phénotype entre îles ou habitats. A) les variations phénotypiques sont induites par l'environnement local, la génétique n'ayant pas d'effet observable; B) les variations phénotypiques sont l'expression du génotype sans effet de l'environnement local; C) les variations phénotypiques sont le résultat d'une covariance entre l'environnement local et le génotype; D) l'environnement local exerce des effets pour contrecarrer ceux du génotype et réduire ou même éliminer les variations phénotypiques entre les îles (Adaptée de Swain & Foote 1999).

Bien que les différences phénotypiques ne soient pas des preuves directes d'isolement génétique entre populations, elles peuvent indiquer une séparation prolongée entre les stocks après les premiers stades de développement dans des régimes environnementaux différents (Begg & Waldman 1999). On parlera alors de plasticité phénotypique comme étant la capacité d'un simple génotype à produire plus qu'une alternative morphologique, état physiologique et ou de comportement en réponse à des conditions environnementales.

Au chapitre 4 de la thèse, dans la modélisation des patrons hydrodynamiques dominants nous avons identifié et décrit des structures de circulation tourbillonnaires à petite échelle, en aval des îles, soumises à des variations saisonnières. Nous avons aussi postulé qu'il s'agit de phénomènes importants dans les processus biologiques liés à la structure et à la dynamique des populations marines de l'archipel. Cela laisse ouverte une intéressante perspective de recherche qui devrait viser la caractérisation des principaux processus biophysiques liés à ces structures. On pourrait donc envisager une étude basée sur un échantillonnage biologique systématique sur toute la colonne d'eau et un suivi dynamique synchrone à partir des prévisions Mercator PSY2V2. Dans une telle étude, il serait souhaitable de considérer une plus longue période de sortie du modèle de façon à pouvoir étudier les variations à long terme, ce que nous n'avons pas pu résoudre, car nous ne disposions que de deux ans de données.

Avec l'étude sur la connectivité hydrodynamique entre les îles, nous avons réalisé un pas important vers une compréhension dynamique fonctionnelle des écosystèmes de l'archipel concernant la structure des populations marines. Cela nous a permis d'introduire une réflexion sur la vulnérabilité des différentes régions de l'archipel en terme de politiques

d'exploitation et conservation des ressources. Cependant, comme il s'agit d'une première étude du genre sur la région, nous nous sommes limités à dresser un cadre dynamique fonctionnel général sans aller jusqu'au niveau de l'espèce et de la population. Il serait donc intéressant de poursuivre cette ligne de recherche vers la conception de modèles IBM (modèles basés sur l'individu) de dynamique larvaire plus complexes et plus sophistiqués. Ces modèles tiendront compte, à la fois de la dimension verticale continue dans la distribution des larves et de leur comportement réel, c.-à-d. la flottabilité, le mouvement actif, la morphologie, etc. afin de prédire où, quand et comment les larves de différentes espèces sont recrutées dans une île ou habitat de l'archipel. Pour cela d'importantes initiatives de recherche en cours pourront servir de référence (Mullon *et al.* 2003; Miller *et al.* 2006; Let *et al.* 2006, 2007). Une telle démarche pourra être appliquée aux adultes afin de définir les aires et périodes de reproduction en fonction des conditions hydrodynamiques définies par les modèles.

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