Variabilité spatiale multiéchelle du zooplancton dans un lagoon récifal côtier (Multiscale spatial variability of zooplankton in a coastal reef lagoon)

Carol Avois-Jacquet

To cite this version:

Carol Avois-Jacquet. Variabilité spatiale multiéchelle du zooplancton dans un lagoon récifal côtier (Multiscale spatial variability of zooplankton in a coastal reef lagoon). Autre. Université Pierre et Marie Curie - Paris VI, 2002. Français. NNT : . tel-00001767

HAL Id: tel-00001767
https://theses.hal.science/tel-00001767

Submitted on 4 Oct 2002

THÈSE DE DOCTORAT
DE l'UNIVERSITÉ PARIS 6
ET DE l'UNIVERSITÉ DE MONTRÉAL

Spécialité

Océanologie Biologique – Environnement Marin – Écologie Numérique

Présentée par

Carol AVOIS-JACQUET

Pour obtenir le grade de

DOCTEUR de l'UNIVERSITÉ PARIS 6
PHILOSOPHIÆ DOCTOR de l'UNIVERSITÉ DE MONTRÉAL

Sujet de thèse

VARIABILITÉ SPATIALE MULTIÉCHELLE DU ZOOPLANCTON DANS UN LAGON RÉCIFAL CÔTIER

Soutenue le 16 mai 2002 devant le jury composé de

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M. J. CLAVIER	Professeur, Université de Brest	Rapporteur
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Ce travail a été réalisé en cotutelle au sein du laboratoire de Biologie Marine de l'Université Antilles-Guyane (Guadeloupe) et au département de Sciences Biologiques de l'Université de Montréal (Canada).

REMERCIEMENTS

Je dois d'avoir pu mener à bien cette thèse d'une part aux soutiens financiers du Ministère de la Recherche et de l'Enseignement Supérieur (France), du Ministère des Affaires Étrangères (France), de la Société de Secours des Amis des Sciences (France), du Ministère des Relations Internationales du Québec (Canada) et du département de sciences biologiques de l'Université de Montréal et d'autre part, et non des moindres, aux personnes qui m'ont apportée leur aide et leur soutien tout au long de ces années. Pour leur assistance et leurs encouragements, je tiens à les remercier ici comme il se doit.

Je tiens, tout d'abord, à exprimer toute ma gratitude à **PIERRE LEGENDRE**, mon directeur de recherche. Dès mon D.E.A., il m'a donné l'opportunité de travailler dans l'un des "temples" de l'Écologie Numérique et je souhaite lui répéter la fierté qui est la mienne d'avoir fait partie de son équipe en espérant qu'il sera fier de ce travail réalisé dans son laboratoire. C'est sans conteste l'une des personnes qui m'a le plus inspirée par ses qualités intellectuelles autant scientifiques que philosophiques. J'en retiens sa vivacité d'esprit, son ingéniosité, sa connaissance et sa rigueur scientifiques, mais également son ouverture d'esprit et son "bouillon de culture". Il m'a permis d'élaborer et de poursuivre mes propres idées tout en me guidant et en me ramenant sur le juste chemin au cours de mes travaux. Ses commentaires et ses suggestions sont et seront toujours appréciés. Toute ma reconnaissance lui est adressée ici non seulement pour son enseignement et sa disponibilité, mais également pour la confiance qu'il m'a témoignée, pour son soutien et sa compréhension. Merci pour tout, πr.

Toute ma considération est exprimée à **MAX LOUIS**, mon codirecteur de thèse. Si mon projet de recherche était élaboré, il m'a donné la possibilité de le réaliser dans un milieu qui ne pouvait être plus adéquat. Je lui suis reconnaissante pour son accueil, son aide et pour les moyens qu'il a mis à ma disposition lors de mes séjours à l'Université des Antilles et de la Guyane (Guadeloupe). Son enthousiasme n'avait d'égal que l'espoir qu'il plaçait dans mon travail. Merci, Max.

Je n'aurais pas eu le privilège d'étudier à l'étranger sans l'appui renouvelé à maintes occasions du Professeur **PAUL NIVAL**, responsable de l'école doctorale à l'Université Paris 6. Qu'il trouve ici le témoignage de la confiance qu'il a mis en moi dès ma Maîtrise puis lors de mon DEA et de mon doctorat. Ce fut incontestablement une expérience scientifique et humaine, ô combien, stimulante et enrichissante dont je mesure quotidiennement l'importance. Veuillez accepter, Monsieur Nival, l'expression de toute ma considération.

Je tien à adresser mes remerciements à certains scientifiques qui, en m'accordant de leur temps, m'ont beaucoup éclairé sur leur domaine respectif. Mes pensées sont, en premier lieu, pour le Dr **JOHN C. ROFF** de l'Université de Guelph (Ontario, Canada) qui a toujours suivi avec intérêt mon travail. Avec son aide et celui de ses étudiants, j'ai pu enrichir mes connaissances dans ces vastes domaines que sont la biologie et la taxonomie du zooplancton. J'ai beaucoup appris à ces côtés et je garde un très bon souvenir de mon séjour dans son laboratoire. Qu'il soit certain que ces commentaires et ses suggestions toujours très pertinents ont été une source d'inspiration très précieuse. Je tiens à vous exprimer Monsieur Roff toute ma gratitude. Une grande partie de mon travail n'aurait pu aboutir sans l'aide et la collaboration du Dr **DANIEL BORCARD** que j'ai eu le plaisir de côtoyer dans le laboratoire de Pierre Legendre. Il m'a toujours montré beaucoup de considération et m'a offert son assistance à des moments décisifs alors que je scrutais le “No Man's Land” des analyses multivariées (je me souviens encore de la veille de mon examen pré-doctoral !). Daniel, trouves ici l'expression de ma profonde reconnaissance. Toute ma reconnaissance est également présentée au Dr **BERNADETTE PINEL-ALLOUL** avec qui j'ai eu l'occasion de collaborer lors de mon DEA réalisé à l'Université de Montréal et qui a fait l'honneur d'être la présidente de mon jury d'examen pré-doctoral. Je lui exprime toute mon admiration pour avoir si bien su associer carrière scientifique et vie familiale et lui adresse mes remerciements les plus chaleureux. Enfin, je ne pourrais oublier le Dr **CLAUDE BOUCHON** et le Dr **YOLANDE NAVARRO-BOUCHON**, pour lesquels les mers tropicales, leurs poissons et leurs coraux n'ont plus de secrets, pour l'aide et les conseils qu'ils m'ont offerts lors de mes séjours en Guadeloupe. Merci à vous deux.

Ce travail n'aurait pas été réalisable sans l'assistance et le support logistique que m'ont accordés de nombreuses personnes. J'adresse mes remerciements les plus sincères à **ROBERT HAMPARIAN**, ingénieur-technicien à l'Université des Antilles et de la Guyane, dont la collaboration à toutes mes campagnes d'échantillonnages (week-ends, vacances et jours fériés inclus) a largement contribué à l'accomplissement de ce travail. Marin hors-pair, il m'a permis d'échantillonner dans des endroits dits inaccessibles et son ingéniosité m'a souvent sorti de l'impasse. Après un temps d'adaptation à son accent québécois, j'ai pu enfin comprendre toutes les explications que **GINETTE METHOT**, assistante de recherche dans le laboratoire du Dr Bernadette Pinel-Alloul, me donnaient sur les techniques en laboratoire. Ses conseils et sa disponibilité ainsi que sa joie de vivre et ses suggestions de romans québécois ont toujours été appréciés. Ginette, trouve ici l'expression de mon amitié la plus sincère. Enfin, un grand merci à Monsieur **ZINZOU** de l'Université des Antilles et de la Guyane et à Monsieur **JEAN-YVES ANCTIL** du Groupe Interuniversitaire de Recherches Océanographiques du Québec (GIROQ) à l'Université Laval pour le matériel qu'ils ont mis à ma disposition. Un grand merci à **ALAIN PATOINE** pour le temps qu'il m'a consacré devant l'OPC, à **MARIE-JOËLLE** pour son aide précieuse les jours précédents mon départ en Norvège et à **METEO-FRANCE** (Le Raizet, Guadeloupe).

Loin de la scolarité et des couloirs de l'Université Paris 6, il n'était pas aisé sans l'aide d'**ALAIN NIERGA**, secrétaire du DEA d'Océanologie Biologique et d'Environnement Marin, d’effectuer les démarches administratives et d’être informé des opportunités scientifiques si utiles pour un doctorant. Sa disponibilité, sa patience et son efficacité ont été plus qu’appréciés. Je tiens également à remercier tous les membres administratifs du département de sciences biologiques et le personnel de la bibliothèque EPC-Bio de l’Université de Montréal pour leurs compétences, leur accueil et leur jovialité. Une pensée particulière est pour **CLAUDETTE BLANCHARD**, secrétaire du Groupe de Recherche Interuniversitaire en Limnologie (GRIL). Ses compétences, son efficacité et son dévouement m’ont fait gagner un temps précieux, spécialement dans les moments les plus pressants. Mais c’est en tant qu’amie que je tiens à lui exprimer toute ma reconnaissance pour son soutien moral et sa bienveillance. Merci pour “tout”, Claudette.

Pendant deux années, j’ai eu le plaisir d’être assistante d’enseignement à l’Université de Montréal. Bien que n’ayant aucun rapport avec mon travail de thèse, cette expérience a été très intéressante et très enrichissante autant pour ces aspects pédagogiques que pour les satisfactions que sont celles de transmettre des connaissances et de stimuler les intérêts des étudiants. Je n’aurais pas eu l’opportunité de dispenser ces cours sans la confiance que m’ont manifestée les professeurs **P. NEUMANN**, **M. FAMELART** et **D. BORCARD**. Trouvez ici, Messieurs, l’expression de ma profonde reconnaissance.

Que soient remerciés comme il se doit, il ne pourrait en être autrement, mes ami(e)s : leurs encouragements et leur soutien furent sans faille. Merci à ceux qui ont partagé le même “univers statistique”, **ELAINE HOOPER, MATTHEW NORTON, YVES DESDEVISES** et **PHILIPPE CASGRAIN**, le grand manitou de l’informatique au sein du laboratoire de Pierre Legendre dont les talents et la disponibilité m’ont épargné plus d’une fois des désagréments. Merci pour votre aide, vos conseils et vos encouragements, mais aussi pour tous les bons moments “extralab”. Merci à mes ami(e)s québécois(es) qui m’ont fait passer des moments merveilleux long de chez moi, **ANAS** “My Friend”, **FRED** “Ma Sauterelle”, **AUDREY**, **CAROLINE**, **J.-C.** Une pensée particulière est pour **LOUISE CLOUTIER** qui fut plus qu'une amie, mais une véritable mère pour moi. Elle a toujours suivi avec attention mon travail et a fait preuve à mon égard d'une grande sollicitude. Merci de tout cœur Mam'Sub pour tes conseils, ton affection et ta bienveillance. Merci à mes ami(e)s norvégien(ne)s, "les Gadjos", **HERVE**, **FRED** et **ÉRIC** ainsi que **TONJE** et **SOPHIE**. Et merci à **VERO** mon amie de toujours (ou presque !). Trouvez ici l'expression de mon amitié la plus sincère. Vous êtes tous supers !

J'adresse enfin mes remerciements aux membres du jury pour la lecture et la critique de ce manuscrit. Leur travail et leur présence m'ont permis de soutenir ma thèse.

Je souhaite terminer en dédiant ce travail à deux personnes exceptionnelles. Je dois à ma maman, **MARTINE MOREL**, de m'avoir donné les moyens de réaliser mes rêves, même les plus fous, et de n'avoir jamais remis en considération mes choix de vie même dans les moments difficiles. Je pense à ma décision de quitter l'école d'infirmière pour entreprendre des études en biologie, de mon départ au Canada puis en Norvège. L'amour et la confiance qu'elle m'a toujours témoignés m'ont permis non seulement de traverser ces dernières années d'études, mais également d'effacer mes doutes et d'acquérir une vision réaliste de la vie. Son soutien et son enthousiasme n'avaient d'égal que l'amour qu'elle me portait. Merci, Maman. Je ne serais pas parvenu à finaliser ce travail sans le total dévouement de **STEPHAN JACQUET**. Sa compétence en tant que scientifique averti a souvent été sollicitée et c'est toujours sans aucune hésitation qu'il m'a consacré une partie de son temps et toutes ses attentions. Ses encouragements et sa présence ont été (et sont) indispensables. Qu'il trouve ici (bien que ces mots soient dérisoires) le témoignage de toute mon Estime et de tout mon Amour. Merci infiniment, Zizou. Tu es simplement le meilleur !

Carol AVOIS-JACQUET
Thonon-les-Bains, le 23 mars 2002.

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CHAPITRE

1

INTRODUCTION GENERALE

1.1 Introduction

La prise en compte de l'espace et de l'hétérogénéité spatiale a mené les problèmes d'échelle au cœur de la réflexion écologique. Le développement de l'écologie spatiale, en mettant en avant le rôle de l'espace dans le contrôle des patrons et des processus écologiques, souligne l'importance de l'échelle spatiale sur la perception des phénomènes et la recherche des causalités. Puisque les patrons et les processus écologiques sont des phénomènes échelle-dépendants, déterminer les échelles de dépendance spatiale des patrons et des processus écologiques est l'un des objectifs de recherche en océanographie. Dans cette perspective, l'approche multiéchelle a été utilisée pour identifier et caractériser la variabilité spatiale du zooplancton marin associé aux régions tempérées et aux régions tropicales océaniques. Bien que les écologistes reconnaissent l'importance des organismes zooplanctoniques dans la structure et la dynamique des écosystèmes tropicaux côtiers, les causes et les conséquences des patrons du zooplancton à travers les échelles spatiales n'ont jamais été abordées. Il est pourtant évident que l'identification et la compréhension des changements échelle-dépendants dans les patrons et les processus écologiques doivent être un pré-requis pour prédire les conséquences des changements, induits par les perturbations naturelles et anthropiques de l'environnement, qui peuvent survenir dans les écosystèmes tropicaux côtiers. De multiples mécanismes (physiques et biologiques) contrôlent la dynamique des entités écologiques (i.e. individus, espèces, populations, communautés). Comprendre comment une entité écologique répond à l'hétérogénéité environnementale requiert la connaissance des processus impliqués et l'échelle spatiale à laquelle ils opèrent.

La problématique de mon travail de thèse a été centrée sur la variabilité spatiale multiéchelle du zooplancton tropical dans un lagon récifal côtier. Les patrons de biomasse et d'abondance de deux classes de taille de zooplancton (190–600 µm et > 600 µm) ont été mis en relation, à travers les échelles spatiales, avec l'hétérogénéité spatiale de l'environnement et notamment celle générée par le type et la structure de l'habitat, les influences océaniques et côtières, l'hydrodynamique locale, la distribution spatiale de la nourriture (i.e. phytoplancton) et le comportement du zooplancton. Mon approche a combiné les observations quantitatives/qualitatives et l'analyse multiéchelle afin d'établir les relations spatiales multiéchelles entre les patrons du zooplancton et les processus environnementaux. Le travail de recherche présenté dans ce manuscrit a montré comment le changement d'échelle spatiale, dans le cadre de l'analyse multiéchelle, met en évidence divers niveaux d'organisation de la communauté zooplanctonique. La communauté zooplanctonique étudiée s'est avéré être caractérisée par une variabilité spatiale multiéchelle en réponse à plusieurs processus physiques et biologiques dont la nature et les effets sont dépendants de l'échelle spatiale.

1.2 Hétérogénéité et Échelle Spatiales

L'un des problèmes fondamentaux de l'analyse actuelle des écosystèmes concerne leur stratégie d'occupation de l'espace-temps, et ce à toutes les échelles d'observation. L'écosystème étant un système complexe d'interactions, l'étude de la structure et de la dynamique des êtres vivant en son sein, eux-mêmes structurés dans l'espace-temps, est une étape fondamentale préalable à l'étude de cet écosystème et de son fonctionnement.

Tous les écosystèmes sont hétérogènes dans l'espace et dans le temps et plusieurs processus dans l'environnement (forçage physique, dynamique des populations et des communautés) sont sources d'hétérogénéité (Roughgarden et al. 1989, Kolasa & Pickett 1991, Peterson & Parker 1998). Cette hétérogénéité écologique est fondamentale dans la structure et le fonctionnement des écosystèmes (Levin 1992) qui s'organisent le long d'un continuum d'échelles spatiales, temporelles et fonctionnelles. Le comportement dynamique des écosystèmes qui en résulte est caractérisé par une variabilité spatio-temporelle. Dès les années 1960, Goodhall (1962) écrivait déjà : « Dans les écosystèmes, l'hétérogénéité spatiale est intrinsèque et inséparable de leur mode de fonctionnement ». Cependant McArthur (1972) déplorait encore, dix ans plus tard, la tendance de beaucoup d'écologistes à étudier les organismes dans un univers "homogénéisé" et il recommandait pour de telles études de considérer la structure de l'environnement et l'effet des patrons spatiaux et temporels. La variabilité spatiale considérée pendant longtemps comme une nuisance statistique (Steele 1976) est maintenant reconnue comme une caractéristique écologique des écosystèmes (Legendre 1993).

L'étude des patrons spatiaux et temporels des entités écologiques est devenue un sujet courant de recherche (Thrush 1991, Legendre et al. 1997, Piontkovski et al. 1995a, Currie et al. 1998, Roman et al. 2001). Concomitante avec ces études est la notion que les patrons de variabilité spatiale dépendent de l'échelle d'observation (Levin 1992, Legendre et al. 1997, Dungan et al. 2002). En effet, les patrons et les processus écologiques sont des phénomènes échelle-dépendants (Wiens 1989, Schneider 1994) et de nouvelles propriétés écologiques peuvent apparaître à différentes échelles d'observation (Mackas et al. 1980, Wiens 1989, Allen & Hoekstra 1991). Ces faits dépendent, d'une part, des individus eux-mêmes qui expérimentent l'environnement à des échelles spatio-temporelles spécifiques (Figure 1.1 ; Denman & Platt 1975, Mackas & Boyd 1979, Legendre et al. 1986, Levin 1992) et d'autre part, des processus physiques et biologiques qui varient avec l'échelle (Haury et al. 1978, Legendre & Demers 1984, Pinel-Alloul 1995).

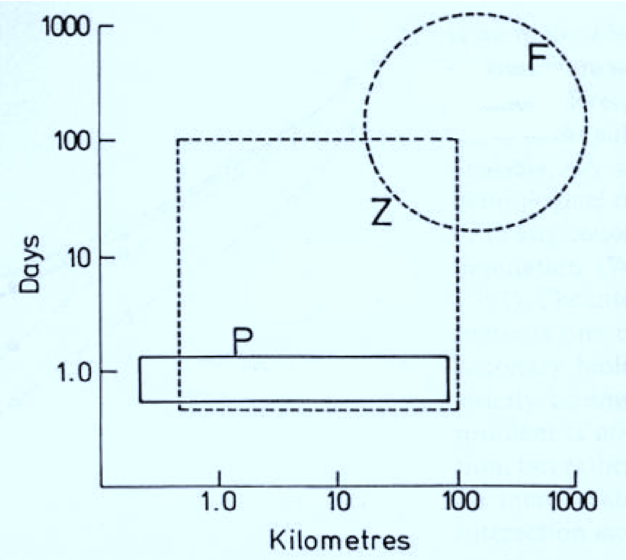


Figure 1.1 Échelles auxquelles la variabilité spatio-temporelle du phytoplancton (P), du zooplancton (Z) et des poissons (F) peut être observée (modifié d'après Steele 1978).

Ces deux propriétés écologiques renforcent l'évidence qu'il n'existe pas une seule échelle à laquelle nous pouvons décrire la structure et la dynamique des populations, communautés et écosystèmes (Wiens 1989, Levin 1992). Si les différences d'échelle ne sont pas prises en considération, des erreurs quantitatives et d'interprétation peuvent survenir (Ricklefs 1987, Allen & Hoekstra 1991). Non seulement les processus physiques et biologiques ainsi que la réponse des individus à l'hétérogénéité environnementale changent avec l'échelle, mais les phénomènes corrélés positivement à une échelle peuvent être corrélés négativement à une autre échelle (Mackas et al. 1980, Wiens 1989, Allen & Hoekstra 1991). Par exemple, la dynamique proie-prédateur peut apparaître comme négative à petite échelle (Figure 1.2), mais positive à grande échelle comme la réponse des deux entités aux mêmes conditions environnementales (Fiedler 1983, Rose & Leggett 1990). Dans ce cas, un changement du signe de la corrélation implique le plus souvent un changement d'échelle (Allen & Hoekstra 1991). Par conséquent, la perception et l'étude de la variabilité écologique (i.e. la variabilité non-aléatoire des individus, espèces, populations, communautés, écosystèmes) conduit à un nouveau concept : l'échelle. L'échelle est une composante intrinsèque de l'hétérogénéité écologique (Dutilleul 1998a). En plus de reconnaître l'hétérogénéité, il est donc essentiel de considérer son échelle.

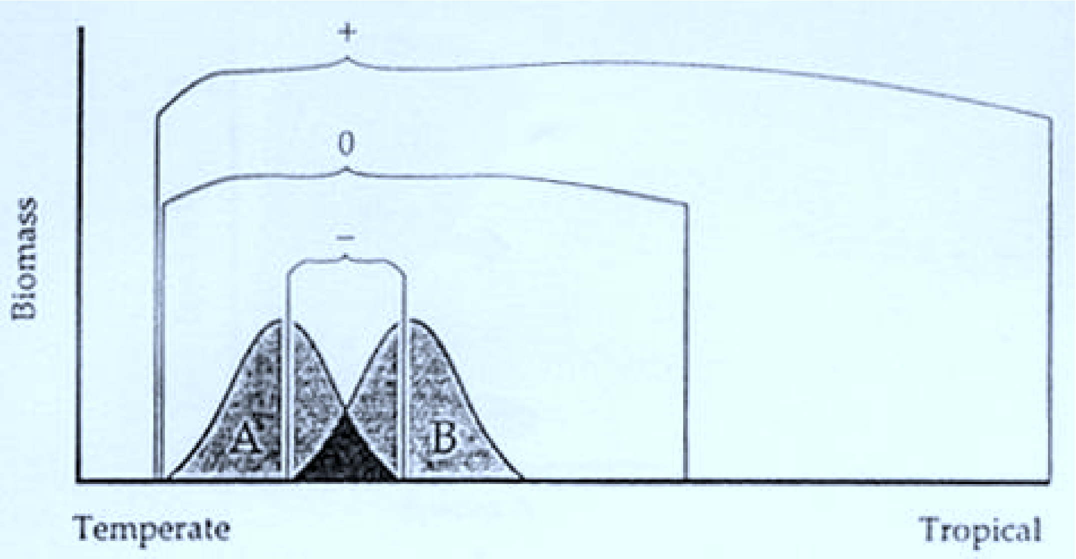


Figure 1.2 Le long d'un gradient allant des régions tempérées aux régions tropicales, la corrélation entre les espèces A et B change selon l'échelle considérée. À petite échelle (localement), la corrélation entre les deux espèces est négative ce qui peut impliquer une relation de compétition ou de prédation. À moyenne échelle, il n'existe pas de relation entre les espèces A et B, les deux étant présentes simultanément dans la région. À grande échelle, les deux espèces se distinguent le long du gradient comme espèces des régions tempérées et sont positivement corrélées (modifié d'après Allen & Hoekstra 1991).

Un problème central en écologie est donc celui des échelles spatiales et temporelles de la structure et de la dynamique des entités écologiques (Wiens 1989, Levin 1992) ; le but de l'écologie spatiale étant de déterminer comment l'espace et l'échelle spatiale influencent la structure et la dynamique des individus, espèces, populations et communautés. En écologie aquatique, l'intérêt porté aux effets de l'échelle dans l'étude de la structure et de la dynamique des entités écologiques a augmenté (Rose & Leggett 1990, Legendre et al. 1997, Claustre et al. 1999, Guichard et al. 2001) et les patrons et les processus écologiques ont été étudiés à différentes échelles d'espace et de temps (Haury & Yamazaki 1995, Solow & Steele 1995, Dunstan & Johnson 1998, Attayde & Bozelli 1999, Blanchard & Bourget 1999, Murdock & Aronson 1999, Petersen et al. 1999, Huntley et al. 2000, Huskin et al. 2001). Dans cette perspective, l’approche multiéchelle est utilisée pour identifier et caractériser les échelles de dépendance spatiale des patrons et des processus (Piontkovski and Williams 1995, Seuront & Lagadeuc 1997, 2001, Seuront et al. 1999, Lovejoy et al. 2001) ce qui permet d’apprécier la nature et l’importance des sources de variabilité, de comprendre les processus physiques et biologiques sous-jacents et enfin d’établir des stratégies d’échantillonnage adéquates. Plusieurs méthodes statistiques ont été développées pour analyser les patrons et les processus en fonction des échelles (se référer à Horne & Schneider 1995, Dutilleul 1998b, Gardner 1998, Seuront et al. 1999, Dale et al. 2002 pour une revue exhaustive). Trois méthodes sont fréquemment utilisées comme analyse multiéchelle par les océanographes et les limnologues. Il s’agit de l’analyse spectrale (Platt & Denman 1975, Mackas & Boyd 1979), de l’analyse multifractale (Pascual et al. 1995, Seuront & Lagadeuc 1997) et de l’analyse multifractale universelle (Marguerit et al. 1998, Seuront et al. 1999, Lovejoy et al. 2001). Cependant ces méthodes ne peuvent pas être appliquées sans prendre en considération certaines conditions théoriques et pratiques (Dutilleul 1998b, Seuront et al. 1999). Elles requièrent des observations continues et simultanées des variables considérées, alors que les données biologiques ne proviennent pas toujours de séries temporelles et/ou spatiales appropriées et qu’elles enfreignent souvent les hypothèses concernant l’intervalle régulier de l’échantillonnage et la stationnarité des moyennes. Une nouvelle forme d’analyse multiéchelle a donc été utilisée pour mon travail de recherche : la méthode des coordonnées principales des matrices de voisin (PCNM) développée par Borcard & Legendre (2002). Cette méthode, basée sur les relations des plus proches voisins entre les sites d’échantillonnage, permet de détecter et de quantifier les patrons spatiaux des entités écologiques le long d’un continuum spatial. Les données mesurées en continue ne sont pas nécessaires et la méthode peut être utilisée avec des données mesurées à intervalle irrégulier. Cependant comme toutes les méthodes citées précédemment, le degré avec lequel la PCNM détecte les patrons spatiaux est sensible à l’échelle d’observation (i.e. le grain et/ou l’étendue de l’échantillonnage).

1.3 Variabilité Spatiale du Zooplancton Marin

Les premières études sur la structure spatiale du zooplancton remontent à la fin du 19^e siècle (Hensen 1884, Haeckel 1891). Elles se sont multiplié depuis les années 1960 (Cassie 1963, Frontier 1973, Fasham et al. 1974, Lewis 1978) en se basant sur le concept du patron spatial développé par Hutchinson (1953) qui utilise les termes de sur-dispersion et sous-dispersion pour décrire la structure spatiale du plancton. Il est maintenant reconnu que les organismes zooplanctoniques ne sont pas répartis uniformément ou aléatoirement dans leur milieu, mais qu’ils forment des taches, c’est-à-dire des agrégats, des essaims et des bancs (Emery 1968, Wiens 1976, Roughgarden 1977, Hamner & Carleton 1979, Haury & Wiebe 1982, Omori & Hamner 1982, Haury & Yamazaki 1995, Leising & Yen 1995) ou des gradients (Johnson 1949, Michel 1969, Moore & Sander 1976, Archambault et al. 1998, Hassett & Boehlert 1999). Ces structures, appelées patrons, sont particulièrement bien développées dans l’environnement marin (Steele 1978, Hamner & Carleton 1979, Haury & Wiebe 1982, Mackas et al. 1985, Lewis & Boers 1991, Swartzman et al. 1999, Turner et al. 1999 ; Franks & Jaffe 2001). Elles ont été observées à différentes échelles spatiales et temporelles (Haury et al. 1978, Mackas et al. 1985, Legendre et al. 1986, Pinel-Alloul 1995, Currie et al. 1998) et les études montrent que la taille des agrégats varient de quelques centimètres (micro-agrégats) à plusieurs milliers de kilomètres (structures biogéographiques).

D’après Longhurst (1981), l’agrégation du zooplancton est une condition nécessaire à la vie dans les milieux aquatiques et c’est probablement pour cette raison que les processus responsables de la variabilité du zooplancton sont étudiés. De nombreuses études ont montré que les patrons spatiaux du zooplancton sont générés et maintenus, d’une part, par des processus physiques (courants et fronts océaniques, upwelling, tourbillons, vagues internes, circulation de Langmuir, turbulence) qui sont principalement induits par les régimes climatiques et hydrodynamiques combinés à la topographie du milieu (Haury et al. 1978, Legendre & Demers 1984, Davis et al. 1991, Piontkovski et al. 1995b, Leising & Yen 1997, Noda et al. 1998, Huntley et al. 2000, Roman et al. 2001) et, d’autre part, par des processus biologiques (migrations verticales, prédation, broutage, compétition, reproduction) associés aux comportements individuels des organismes zooplanctoniques (Hamner & Carleton 1979, Haury & Wiebe 1982, Mackas et al. 1985, Tiselius 1992, Ribes et al. 1996, Buskey 1998, Folt and Burns 1999, Rollwagen-Bollens & Landry 2000, Bullard & Hay 2002).

Les organismes zooplanctoniques ont longtemps été considérés comme des membres passifs (Omori & Ikeda 1984, Castel &Veiga 1990) des agrégats qui étaient le produit de processus physiques opérant à grande échelle (Pinel-Alloul 1995). Ce point de vue a changé en acceptant que les processus biologiques contribuaient significativement à la formation des patrons spatiaux du zooplancton (Folt & Burns 1999). De récentes études ont souligné la contribution relative des processus physiques et biologiques dans la formation et le maintien des structures spatiales du zooplancton (Lewis & Boers 1991, Hill 1995, Wiafe & Frid 1996, Alvarez-Cadena et al. 1998, Smith et al. 2001) et de quelle manière les processus biologiques pouvaient neutraliser l’effet des processus physiques sur ces patrons spatiaux (Emery 1968, Hamner & Carleton 1979, Lewis & Boers 1991, Davis et al. 1991, Alvarez-Cadena et al. 1998, Tiselius 1998). Cependant, l’approche n’est pas de considérer les processus physiques et biologiques séparément, mais sous l’hypothèse des forces motrices multiples (multiple driving forces hypothesis ; Pinel-Alloul 1995). Ni les processus physiques ni les processus biologiques considérés seuls ne peuvent expliquer l’hétérogénéité spatiale du zooplancton. Les patrons spatiaux sont la conséquence du couplage des mécanismes physiques et biologiques et cela à toutes les échelles spatiales. L’hypothèse des forces motrices multiples énonce la dominance des processus abiotiques (chimiques et physiques) à grandes échelles alors que les processus biotiques prédominent à petites échelles (Pinel-Alloul 1995). En d’autres termes, l’importance relative des processus physiques et biologiques impliqués dans la variabilité spatiale du zooplancton peut être vue comme un gradient de leurs effets le long d’un continuum spatial (Figure 1.3).

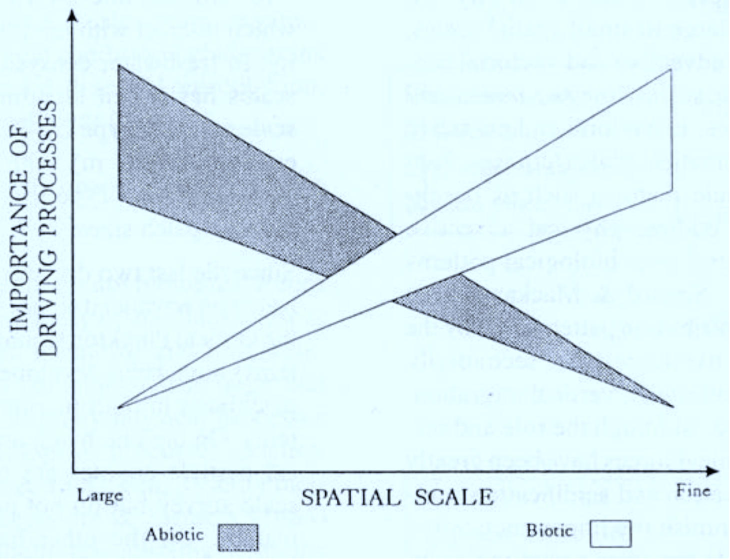


Figure 1.3 Illustration de l’hypothèse des forces motrices multiples montrant la relation entre les échelles spatiales et la contribution relative des processus abiotiques et biotiques (d’après Pinel-Alloul 1995).

Tous les processus physiques et biologiques opèrent à des échelles spatiales et temporelles spécifiques (Haury et al. 1978, Legendre et al. 1986) et ils génèrent une variabilité multiéchelle du zooplancton (Figure 1.4). Cela explique qu’il existe une relation étroite entre les échelles spatiales et temporelles des différents processus physiques et biologiques et les aspects de l’hétérogénéité biologique qui leur sont associés (Denman & Powell 1984). Puisque les patrons spatiaux du zooplancton et les processus sous-jacents sont des phénomènes échelle-dépendants, considérer l’échelle spatiale est une nécessité pour examiner la variabilité spatiale du zooplancton et déterminer les processus qui génèrent et maintiennent une telle variabilité. Cette exigence est renforcée par les faits que les échelles spatiales et l’amplitude de la variabilité spatiale du zooplancton changent avec la taille des organismes (Mackas & Boyd 1979, Mackas et al. 1985, Piontkovski et al. 1995a) et leur motilité (Hamner et al. 1988, Piontkovski & Williams 1995) et que les échelles spatiales de variabilité diffèrent entre la composition de la communauté zooplanctonique et la biomasse zooplanctonique (Figure 1.5 ; Mackas 1984, Powell 1989). Cela suppose que les processus environnementaux impliqués dans la variabilité spatiale du zooplancton diffèrent non seulement selon l'échelle spatiale, mais également selon les organismes et la variable-réponse considérée (i.e. biomasse, abondance, composition en espèces).

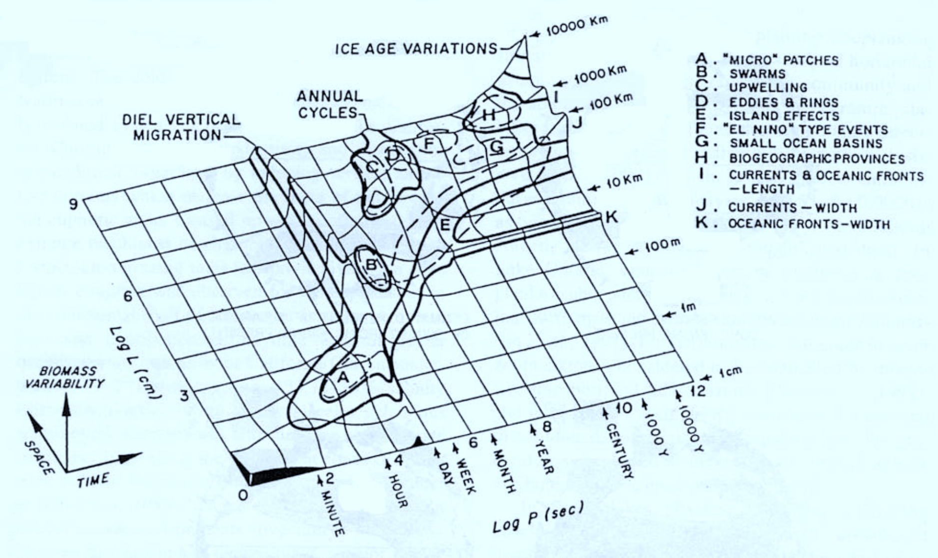


Figure 1.4 Diagramme de Stommel : échelles spatiales et temporelles de la variabilité de la biomasse du zooplancton marin et des processus physiques et biologiques impliqués (d'après Haury et al. 1978).

Dès lors, la variabilité spatiale du zooplancton conduit non seulement à considérer l'échelle spatiale, mais également à adopter une approche multiéchelle. Dans ce contexte, l'hypothèse des forces motrices multiples est d'autant plus justifiée qu'elle implique l'approche multiéchelle. L'idée de considérer la variabilité spatiale des communautés planctoniques comme un processus multiéchelle n'est pas nouvelle. Elle a été développée et élaborée, suite aux travaux de Platt & Denman (1975), au niveau du concept qui peut être considéré maintenant comme la variabilité spatio-temporelle multiéchelle des écosystèmes marins. Récemment, des études sur la variabilité spatiale du zooplancton ont adopté une approche multiéchelle (Pascual et al. 1995, Piontkovski and Williams 1995, Currie et al. 1998, Seuront & Lagadeuc 2001), mais elles ne concernent que les organismes associés aux régions tempérées et aux régions tropicales océaniques. La variabilité spatiale multiéchelle du zooplancton marin vivant dans les environnements tropicaux côtiers n'a fait l'objet d'aucune étude à ce jour et il est clair que les processus environnementaux qui contrôlent les patrons spatiaux du zooplancton ne peuvent pas être simplement extrapolés des régions tempérées et des régions tropicales océaniques aux régions tropicales côtières.

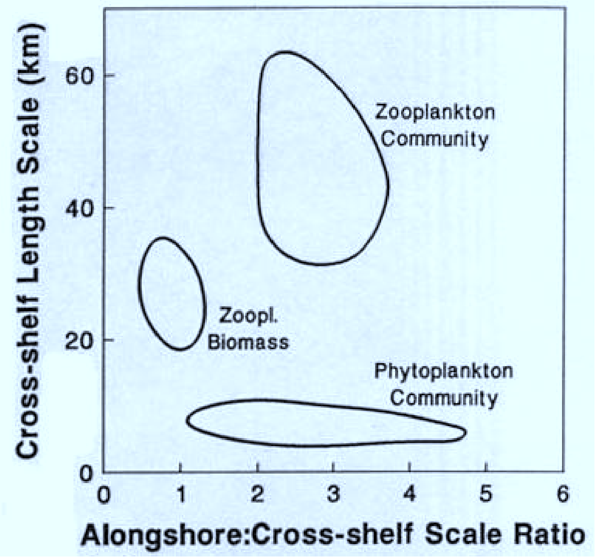


Figure 1.5 Échelles de variabilité de la biomasse du zooplancton et de la composition des communautés phytoplanctonique et zooplanctonique rencontrés le long des côtes de la Colombie britannique, Canada (d'après Mackas 1984).

1.4 Zooplancton Marin des Eaux Tropicales Côtières

Kramer (1897) réalisa la première étude quantitative sur le zooplancton vivant dans un récif corallien. Il observa que la communauté zooplanctonique récifale était composée d'espèces océaniques et endémiques et que l'abondance du zooplancton était plus élevée dans les eaux récifales que dans les eaux océaniques avoisinantes. Par la suite, le zooplancton tropical fut l'objet de nombreuses études tant en milieu océanique (Yoshioka et al. 1985, Piontkovski & Williams 1995, Webber & Roff 1995a, b, Le Borgne & Rodier 1997) qu'en milieu néritique-côtier (Moore & Sander 1976, 1979, Youngbluth 1980, Le Borgne et al. 1989, Chisholm & Roff 1990a, b, Renon 1993, Rios-Jara 1998, Súarez-Morales & Gasca 2000).

Dans les eaux tropicales côtières, les travaux ont porté sur la production secondaire et le taux de croissance des copépodes (Le Borgne et al. 1989, Chisholm & Roff 1990a, b, McKinnon & Thorrold 1993, Hopcroft et al. 1998a, b), les migrations verticales (Alldredge & King 1980, Robichaux et al. 1981, Ohlhorst 1982, Walters & Bell 1986, 1994), la variabilité saisonnière, annuelle ou interannuelle (Moore & Sander 1979, Youngbluth 1980, Lewis & Boers 1991, Zaballa & Gaudry 1996, Rios-Jara 1998) et la diversité spécifique (Emery 1968, Moore & Sander 1976, 1979, Hamner & Carleton 1979, Alvarez-Cadena et al. 1996, 1998, Morales & Murillo 1996). Ces études concernent les communautés zooplanctoniques associées aux différents habitats tropicaux côtiers comme les récifs coralliens (Emery 1968, Hamner & Carleton 1979, Robichaux et al. 1981, Ohlhorst 1982, Lewis & Boers 1991, Morales & Murillo 1996, Leichter et al. 1998, Suárez-Morales & Gasca 2000), les herbiers à phanérogames marines (Youngbluth 1980, Walters & Bell 1986, 1994, Conolly 1997, Rios-Jara 1998, Bullard & Hay 2002) et les mangroves (Youngbluth 1980, Ambler et al. 1991). Ces travaux ont permis de souligner le rôle des organismes zooplanctoniques i) dans la nutrition de nombreux invertébrés marins incluant les poissons (Emery 1968, Hamner & Carleton 1979, Alldredge & King 1980, Robichaux et al. 1981, Noda et al. 1998), les espèces coralliennes telles que *Montastrea annularis*, *Acropora sp.*, *Porites sp.* (Hamner et al. 1988, Sorokin 1993) et le zooplancton carnivore (Moore & Sander 1979) et ii) comme vecteur du transfert d’énergie dans les récifs coralliens (Roman et al. 1990) et à l’intérieur des lagons (Bishop & Greenwood 1994). Certains travaux avancent même que le zooplancton serait la source principale de proies pour les résidents des récifs coralliens (Hamner et al. 1988, Erez 1990, Sebens 1997) plutôt que le phytoplancton (Yahel et al. 1998) ; le zooplancton serait la source essentielle de carbone hétérotrophe dans ces systèmes (Le Borgne et al. 1989). Dues à leur proéminence dans les eaux océaniques et côtières et à leur distribution géographique, les organismes zooplanctoniques sont également des indicateurs biologiques importants dans l’environnement marin. En effet, les communautés zooplanctoniques sont souvent le plus sûr moyen de caractériser des masses d’eau d’origine différente (Johnson 1949, Renon 1993, Webber et al. 1996) et d’évaluer les influences océaniques et côtières dans l’environnement (Hopcroft & Roff 1990, Webber et al. 1992, Suárez-Morales et al. 1999). De plus, la production des copépodes, lesquels représentent 75 % de l’abondance totale du zooplancton dans les eaux tropicales côtières (Moore & Sander 1976, 1979, Morales & Murillo 1996, Alvarez-Cadena et al. 1998), mais également dans toutes les mers du monde (Raymont 1983), équivaudrait à celle des régions tempérées côtières (Chisholm & Roff 1990b). Des études récentes ont également mis en évidence l’importance des nauplii et des copépodites non pas en termes de biomasse (Hopcroft & Roff 1998, Hopcroft et al. 1998a), mais en termes d’abondance et de production (Hopcroft et al. 1998a, b) qui pourraient être aussi élevées que dans les écosystèmes tempérés. Non seulement les nauplii ont un rôle central dans la production secondaire dans les systèmes tropicaux, mais constituent également des intermédiaires importants entre le réseau trophique classique et la bouche microbienne (Roff et al. 1995).

Bien que les écologistes reconnaissent l’importance écologique du zooplancton dans les écosystèmes tropicaux côtiers et l’implication de la structure spatiale de ces organismes dans la structure et le fonctionnement des compartiments planctoniques et nectoniques, à travers la reproduction (Hamner & Carleton 1979, Ambler et al. 1991), la dynamique des populations (Alldredge & King 1980, Robichaux et al. 1981, Fiedler 1983, Walters & Bell 1994, Noda et al. 1998), les interactions proie-prédateur (Emery 1968, Hamner & Carleton 1979, Youngbluth 1980, McKinnon 1991, Bullard & Hay 2002) et la dynamique des récifs coralliens (Le Borgne et al. 1989, Erez 1990, Sorokin 1993, Sebens 1997), la variabilité spatiale du zooplancton dans les eaux tropicales côtières n’a jamais été réellement abordée. Toutes les études précédentes sur la distribution spatiale de l’abondance et/ou de la biomasse et/ou des espèces zooplanctoniques (Champalbert 1993, Moralez & Murillo 1996, Alvarez-Cadena & Segura-Puertas 1997, Carleton & Doherty 1998, Rios-Jara 1998, Suárez-Morales & Gasca 2000) se sont restreintes à un petit nombre de stations et les échantillons ont souvent été collectés dans un seul type d’habitat. Dans de telles études, les conditions minimums pour établir clairement la variabilité spatiale du zooplancton ne sont donc pas réunies. Les fortes variations observées dans les données suggèrent néanmoins une forte variabilité spatiale des communautés zooplanctoniques associées aux écosystèmes tropicaux côtiers et seul un échantillonnage avec une résolution spatiale suffisante permettrait de déterminer et d'interpréter correctement et précisément les patrons spatiaux du zooplancton.

Il semble que le zooplancton tropical côtier montre de fortes fluctuations écologiques induites par l'impact des influences océaniques et côtières (Webber et al. 1992, 1996, McKinnon & Thorrold 1993, Rios-Jara 1998) qui sont régulées par les patrons de précipitation et les courants induits par les vents (Youngbluth 1980, Yoshioka et al. 1985, Chisholm & Roff 1990b, Hopcroft & Roff 1990, Rios-Jara 1998). La disponibilité et la distribution du phytoplancton (Moore & Sander 1979, Webber et al. 1992, Riso-Jara 1998), le comportement du zooplancton impliqué dans la recherche de nourriture, dans la prédation et dans la reproduction (Emery 1968, Hamner & Carleton 1979, Ambler et al. 1981, Le Borgne et al. 1989, Lewis & Boers 1991, Alvarez-Cadena et al. 1998), les composantes épibenthique-endémique et planctonique-océanique des espèces zooplanctoniques (Emery 1968, Alldredge & King 1980), l'effet de la masse insulaire (Moore & Sander 1979, Alvarez-Cadena et al. 1998, Hassett & Boehlert 1999), l'hydrodynamique locale et le forçage du vent (Johnson 1949, Webber et al. 1996, Alvarez-Cadena et al. 1998), l'hétérogénéité de l'habitat (Hamner & Carleton 1979, Connolly 1997, Alvarez-Cadena et al. 1998, Rios-Jara & Gonzalez 2000) et l'intensification des relations entre les espèces et leur habitat (Emery 1968, Hamner & Carleton 1979, Walters & Bell 1994) sont également susceptibles d'expliquer les associations d'espèces zooplanctoniques et la distribution de ces organismes dans les écosystèmes tropicaux côtiers. Bien que les études précédentes aient décrit certaines structures spatiales du zooplancton (essaims, gradients) et mis en évidence l'importance de certains processus physiques et biologiques, les échelles de dépendance spatiale de ces patrons et des processus sous-jacents n'ont pas été considérées.

1.5 Objectif du Travail de Thèse

Il est actuellement reconnu que l'hétérogénéité spatiale du zooplancton joue un rôle important dans la compréhension et la modélisation de la dynamique des populations et de leurs interactions avec les autres compartiments planctoniques et nectoniques (Legendre & Demers 1984, Mackas et al. 1985, Wiens 1989, Levin 1992, Pinel-Alloul 1995). L'hétérogénéité spatiale du zooplancton a donc des implications importantes dans la structure et le fonctionnement des écosystèmes. S'il est nécessaire de gérer les écosystèmes tropicaux côtiers en évaluant les échelles spatiales et temporelles des dommages potentiels induits par les perturbations naturelles (ouragans, maladies) et anthropiques (sur-pêche, pollution, activités humaines) qui peuvent survenir (Hughes 1994, Eggleston et al. 1998, Sale 1999), l'étude de la variabilité spatiale multiéchelle du zooplancton est une étape fondamentale pour une compréhension précise de ses implications dans la structure et la dynamique des écosystèmes tropicaux côtiers. De telles études peuvent permettre de déterminer, par exemple, l'étendue de la détérioration de la qualité des eaux (effet bottom-up) ou l'impact de la sur-pêche (effet top-down).

L'objectif principal de ce travail de thèse a été de déterminer les échelles de dépendance spatiale des patrons du zooplancton associé à un lagon récifal côtier et des processus environnementaux sous-jacents. Dans ce contexte, mes objectifs ont été i) de quantifier les patrons de la variabilité du zooplancton dans l'espace, ii) de comprendre comment ces patrons changent selon l'échelle spatiale, et iii) de déterminer les processus physiques et biologiques responsables des patrons spatiaux du zooplancton. Mon approche a combiné des observations quantitatives/qualitatives et l'analyse multiéchelle afin d'établir les relations spatiales multiéchelles entre la variabilité du zooplancton et l'hétérogénéité environnementale. L'étude de ces relations m'a amené à poser certaines questions : i) comment les patrons du zooplancton varient-ils d'une échelle spatiale à une autre? ii) comment l'hétérogénéité des ressources et de l'habitat affecte-t-elle la variabilité spatiale du zooplancton? iii) quelle est l'importance respective du comportement du zooplancton et des processus hydrodynamiques dans la génération des patrons spatiaux du zooplancton? et iv) dans quelles conditions l'hétérogénéité environnementale et la variabilité spatiale du zooplancton sont-elles positivement ou négativement corrélées?

Pour répondre à ces questions, j'ai examiné la variabilité spatiale du zooplancton, distinguant deux classes de taille (190–600 µm et > 600 µm), pour deux variables-réponses, la biomasse et l'abondance, et plusieurs facteurs environnementaux dans le lagon du Grand Cul-de-Sac Marin (GCSM). Ce lagon tropical est le plus grand lagon récifal côtier des Petites Antilles et est localisé le long des côtes guadeloupéennes dans l'est de la Mer des Caraïbes (Figure 1.6). Le lagon du GCSM constitue une interface entre les écosystèmes marin (La Mer des Caraïbes) et côtier (les îles de la Guadeloupe) et il est très vulnérable aux perturbations naturelles comme les ouragans (Bouchon et al. 1991) et aux activités humaines comme la sur-pêche, la pollution ou le tourisme. En effet, un changement drastique et dramatique des espèces coralliennes dominantes en un système dominé par des algues charnues a été observé sur la barrière récifale (Louis, comm. pers.). Ces observations peuvent être associées aux apports d'eaux douces provenant des terres agricoles et au développement rapide de zones industriels (Bernard 1995, Bernard et al. 1996). Pour conserver et gérer le lagon du GCSM, des zones marines protégées ont été crées et plusieurs études ont été réalisées sur la structure et la dynamique des espèces coralliennes et des poissons associés à cet écosystème (Louis & Guyard 1982, Baelde 1990, Bouchon & Laborel 1990, Bouchon et al. 1991, Aliaume et al. 1993). La communauté zooplanctonique associée à ce lagon n'a fait l'objet d'aucune étude bien que les connaissances sur cette communauté pourraient contribuer à une meilleure compréhension des processus environnementaux impliqués dans la structure et la dynamique du lagon du GCSM, et de ce fait à une meilleure gestion et à une meilleure conservation.

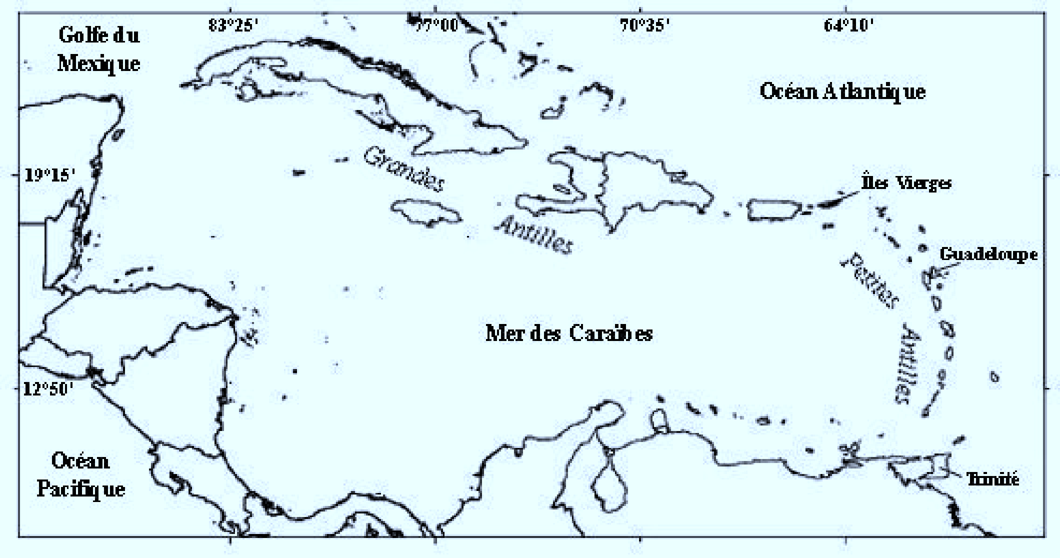


Figure 1.6 Carte de la Mer des Caraïbes localisant les iles de la Guadeloupe dans les Petites Antilles (West Indies). Les West Indies est une région qui inclut toutes les îles de l'extrémité de la péninsule de Floride au nord de l'Amérique du Sud (carte modifiée d'après NOAA, http://rimmer.ngdc.noaa.gov/coast/).

Mon travail de thèse s'insère dans le cadre des recherches concernant les échelles spatiales des patrons et des processus écologiques. L'originalité de cette étude a été de considérer la variabilité spatiale du zooplancton associé au lagon récifal côtier en fonction de la taille des organismes zooplanctoniques, de la distribution du phytoplancton, de l'hétérogénéité de l'habitat, de l'hydrodynamique locale, du forçage climatique, et ce sur un continuum spatial.

CHAPITRE

2

SITE DE L'ÉTUDE

2.1 Le Lagon du Grand Cul-de-Sac Marin

2.1.1 – Situation Géographique

Le lagon du Grand Cul-de-Sac Marin (61°34'W, 16°18'N) est un lagon récifal côtier peu profond (profondeur moyenne = 5 m, profondeur maximale = 30 m) localisé sur les côtes guadeloupéennes dans l'Est de la Mer des Caraïbes. L'archipel guadeloupéen (Figure 2.1) appartient à l'arc insulaire des Petites Antilles qui s'étend des Îles Vierges à l'île de la Trinité (Figure 1.6) et qui sépare l'Océan Atlantique à l'est de la Mer des Caraïbes à l'ouest. Les deux îles de la Guadeloupe constituent la charnière géologique des deux blocs des Petites Antilles. Grande-Terre (585 km^2) est un plateau continental calcaire d'origine océanique comme Marie-Galante, la Désirade et toutes les îles situées au nord. Basse-Terre (848 km^2) présente un relief montagneux d'origine volcanique à l'image des îles voisines situées au sud comme les Saintes, la Dominique, Montserrat (Starmühlner & Therezien, 1982). La séparation entre les deux îles n'excède pas 200 m de largeur matérialisée par un bras de mer, la Rivière Salée.

La situation géographique de la Guadeloupe lui confère un climat tropical maritime chaud et humide bien qu'il soit tempéré par le régime des alizés (vents de nord-est). Les températures à terre varient entre 25 et 28°C (Figure 2.2). Le climat est typique des zones tropicales avec l'alternance entre les saisons sèche et humide. La saison sèche, de décembre à mai, est caractérisée par des précipitations dépassant rarement les 120 mm par mois, surtout marquée pendant le carême (février-mars). La saison des pluies, de juin à novembre, est caractérisée par de fortes précipitations (valeurs mensuelles supérieures à 120 mm) et par des périodes cycloniques (Chaperon et al. 1985). Cependant il est à noter que les précipitations varient avec l’altitude et l’orientation. Grande-Terre reçoit approximativement 990 mm de pluie par an alors que les régions montagneuses de Basse-Terre reçoivent plus de 2500 mm de pluie par an.

Figure 2.1 Îles de la Guadeloupe dans les Petites Antilles (West Indies) et localisation géographique du lagon du Grand Cul-de-Sac Marin.

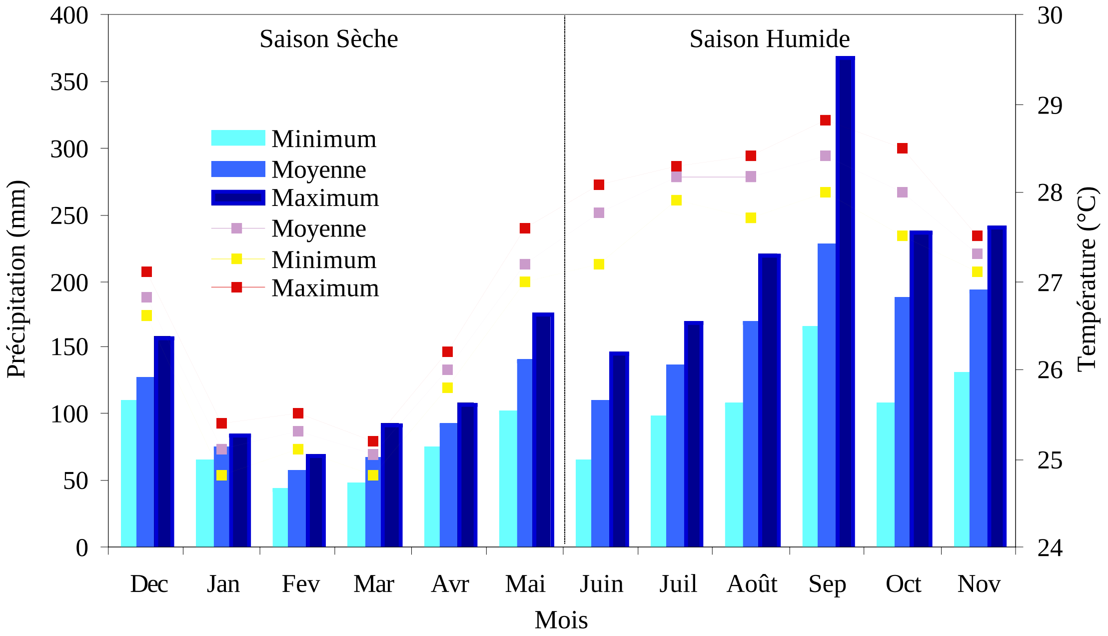


Figure 2.2 Précipitation (histogrammes) et température de l’air (courbes) mensuelles moyennes mesurées sur les îles guadeloupéennes (données de Météo France).

2.1.2 – Morphologie du Lagon

Le lagon du Grand Cul-de-sac Marin (GCSM) est une baie située du côté nord entre les deux îles formant la Guadeloupe (Figure 2.1) ; il occupe une superficie d'environ 11 000 ha (30 km est-ouest et 10 km maximum nord-sud) délimité par la barrière récifale.

La topographie du lagon a été dessinée par les anciennes vallées fluviales d'origine Pléistocène et leur réseau hydrographique. Elles ont été creusées lors de l'émersion du lagon au cours des dernières glaciations puis ennoyées par la remontée du niveau de la mer (Guilcher & Marec 1978) ce qui a conduit à une nouvelle croissance de la barrière récifale (Bouchon & Laborel 1990). La morphologie du lagon se caractérise par i) la **barrière récifale** dont le platier, peu développé, permet les échanges d'eau entre la pleine mer et le lagon, ii) un ensemble de **haut-fonds** internes avec des formations coralliennes (cayes), et iii) un **système de chenaux** qui se ramifient à partir de quatre passes s'ouvrant dans la barrière récifale et permettant la communication entre le lagon et la Mer des Caraïbes. Ces passes sont la passe à Colas, la plus profonde (–35 m), la passe à Fajou (–15 m), la passe à Caret (–20 m), et la passe de la Grande Coulée (–15 à –20 m). Cette dernière draine la plus grande partie des eaux de décharge du lagon (Castaing et al. 1984). Le prolongement des passes à l'intérieur du lagon forme une zone de grands fonds (entre –15 et –30 m) dont le rôle est capital dans l'hydrodynamique du secteur nord du lagon (Figure 2.3). Des baies, des anses et des micro-lagunes sont réparties tout autour du lagon avec des caractéristiques qui leur sont propres conditionnant l'hydrodynamique et la sédimentation dans ces régions (Assor & Julius 1987).

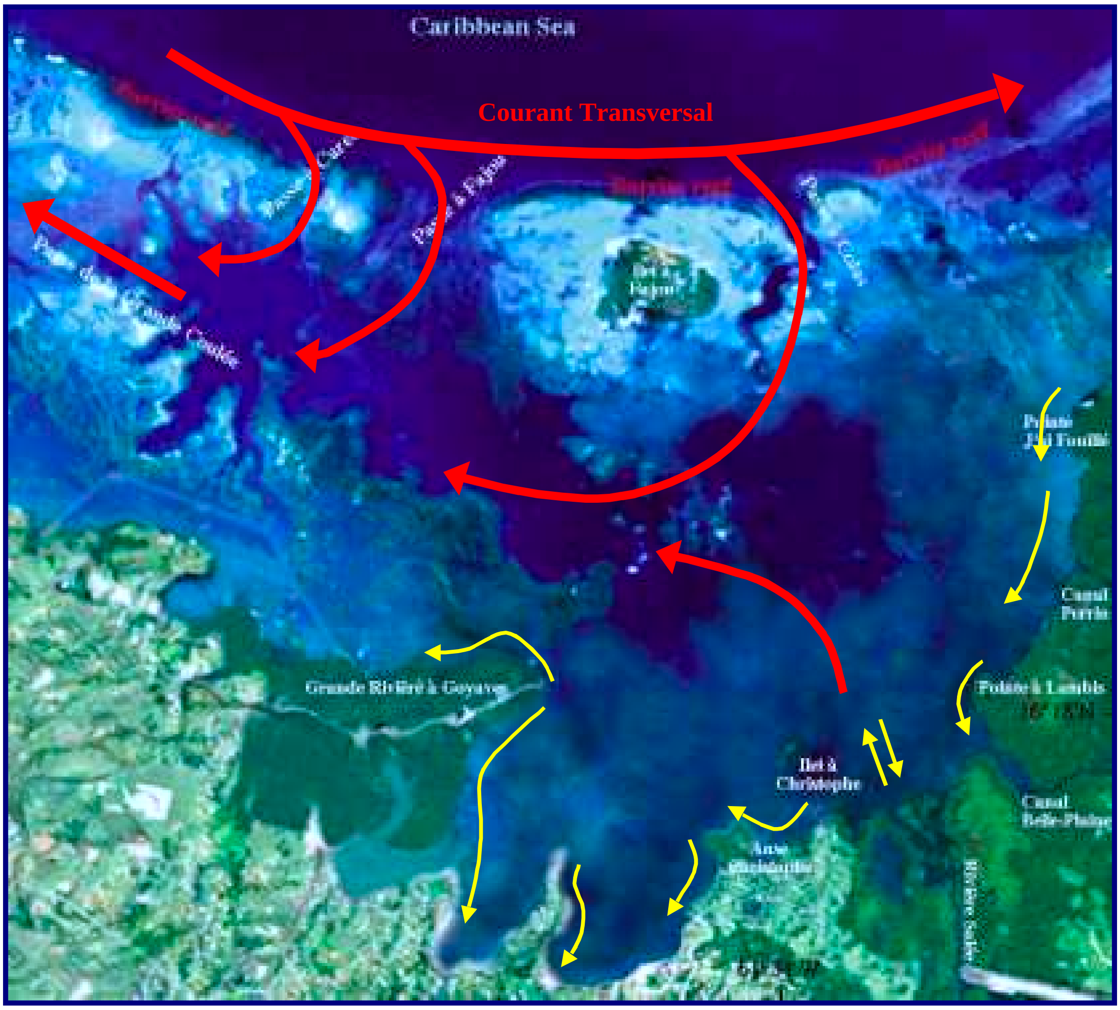


Figure 2.3 Hydrodynamique dans le lagon du Grand Cul-de-Sac Marin. La circulation générale des masses d'eaux est indiquée en rouge, les flèches jaunes indiquant les courants de la dérive littorale (la double-flèche matérialise le courant de marée).

2.1.3 – Hydrodynamique

L'hydrodynamique du lagon du GCSM dépend du courant transversal, des courants de surface, du vent, de la marée, de la morphologie du lagon et de la sinuosité du rivage (Assor & Julius 1987). Les vents dominants sont de secteur est correspondant à la direction des alizés au large de la Guadeloupe. La similitude entre la direction des vents dominants et l'allongement du lagon génère des courants de surface de nord-est facilitant l'évacuation des eaux du lagon par la passe de la Grande Coulée à l'ouest du lagon. La marée a un caractère mixte (diurne ou semi-diurne selon les phases lunaires) dû à la rencontre entre l'onde de marée venant de l'Océan Atlantique et celle venant de la Mer des Caraïbes, avec un marnage ne dépassant pas 50 à 60 cm (Assor &

Julius 1987).

L'hydrodynamique du lagon (Figure 2.3) se caractérise par une circulation générale sous la dépendance d'un courant transversal (généré par le courant Nord Équatorial) provenant du nord-ouest et qui longue la barrière récifale sur sa marge nord (Castaing et al. 1984). Des ramifications de ce courant pénètrent dans le lagon par les différentes passes, principalement en profondeur lors des vives–eaux et en surface une partie des mortes–eaux, et forment un tourbillon anticyclonique. Les eaux du lagon sont évacuées par la passe de la Grande Coulée sous l'influence de la morphologie des fonds, des courants et des vents dominants. Le fond du lagon est caractérisé par une circulation très faible principalement induite par des courants de dérive littorale alors que le vent et la marée constituent les moteurs de la dynamique des lagunes marginales générant des micro-courants. L'hydrodynamique du lagon du GCSM génère une circulation complexe caractérisée par deux zones dynamiques distinctes : une zone septentrionale (partie nord du lagon) où l'action du tourbillon anticyclonique assure, avec les vagues et les courants de surface induits par les vents, un bon renouvellement des masses d'eau et une zone méridionale (partie sud du lagon) semi-abritée, moins renouvelée (Assor & Julius 1987).

Les apports d'eau douce d'origine insulaire proviennent principalement de la mangrove et de la Grande Rivière à Goyaves (bassin versant de 130 km^2). Son débit moyen est de 10 m^3/s avec un débit maximum pouvant atteindre 450 m^3/s; le débit d'étiage étant inférieur à 2,5 m^3/s (Morell & Hoepffner 1987). Son embouchure est sous l'influence de plusieurs systèmes de houle qui engendrent des courants de dérive littorale (Assor & Julius 1987). Dans des conditions météorologiques normales, l'eau de la Grande Rivière à Goyaves s'évacue vers le nord et vers le sud-ouest (Figure 2.3).

2.1.4 – Sédimentologie

L'hydrodynamique du lagon génère trois faciès sédimentaires disposés parallèlement à la barrière récifale : (1) des **sables bioclastiques** grossiers sur la marge sud de la barrière récifale, et moyens à fins autour des cayes, (2) des **vases**, à faible teneur en carbonates, localisées dans les domaines marginaux recevant les apports terrigènes des îles de Grande-Terre ou de Basse-Terre et (3) des **boues**, riches en carbonates, qui se retrouvent dans la partie centrale du lagon et qui représentent un faciès de transition surtout influencé par la partie nord du lagon (sables bioclastiques).

Ces trois faciès disposés parallèlement au récif-barrière témoignent de la décroissance du niveau d'énergie du nord vers le Sud et porte la marque d'une influence océanique graduelle. L'extension limitée du faciès terrigène qui est l'un des traits majeurs de la sédimentation dans le lagon montre une influence limitée du domaine insulaire. Les mesures physico-chimiques confirment l'existence d'une dynamique de faible niveau énergétique dans les parties méridionale et orientale du lagon. Elles permettent de cerner les zones directement sous influence côtière (forte teneur en silicium, température plus élevée) de celles sous influence océanique (concentration en magnésium excédentaire) (Assor & Julius 1987).

2.2 Les Différents Écosystèmes du Lagon du Grand Cul-de-Sac Marin

Les caractéristiques morphologiques, hydrodynamiques, physico-chimiques et sédimentaires du lagon du Grand Cul-de-Sac Marin conditionnent l'installation de différents écosystèmes marins. L'écosystème lagunaire du GCSM a la particularité d'être composé d'une mosaïque de cinq écosystèmes qui font de ce lagon un système particulièrement complexe et original. Ces écosystèmes sont i) le **récif-barrière**, ii) les **cayes**, iii) les **herbiers à phanérogames marines**, iv) les **grands fonds vaseux** et v) la **mangrove** dans les zones vaseuses intertidales. Ces milieux qui abritent de nombreux organismes benthiques et pélagiques sont distribués le long d'un gradient allant de la côte vers le large (Figure 2.4).

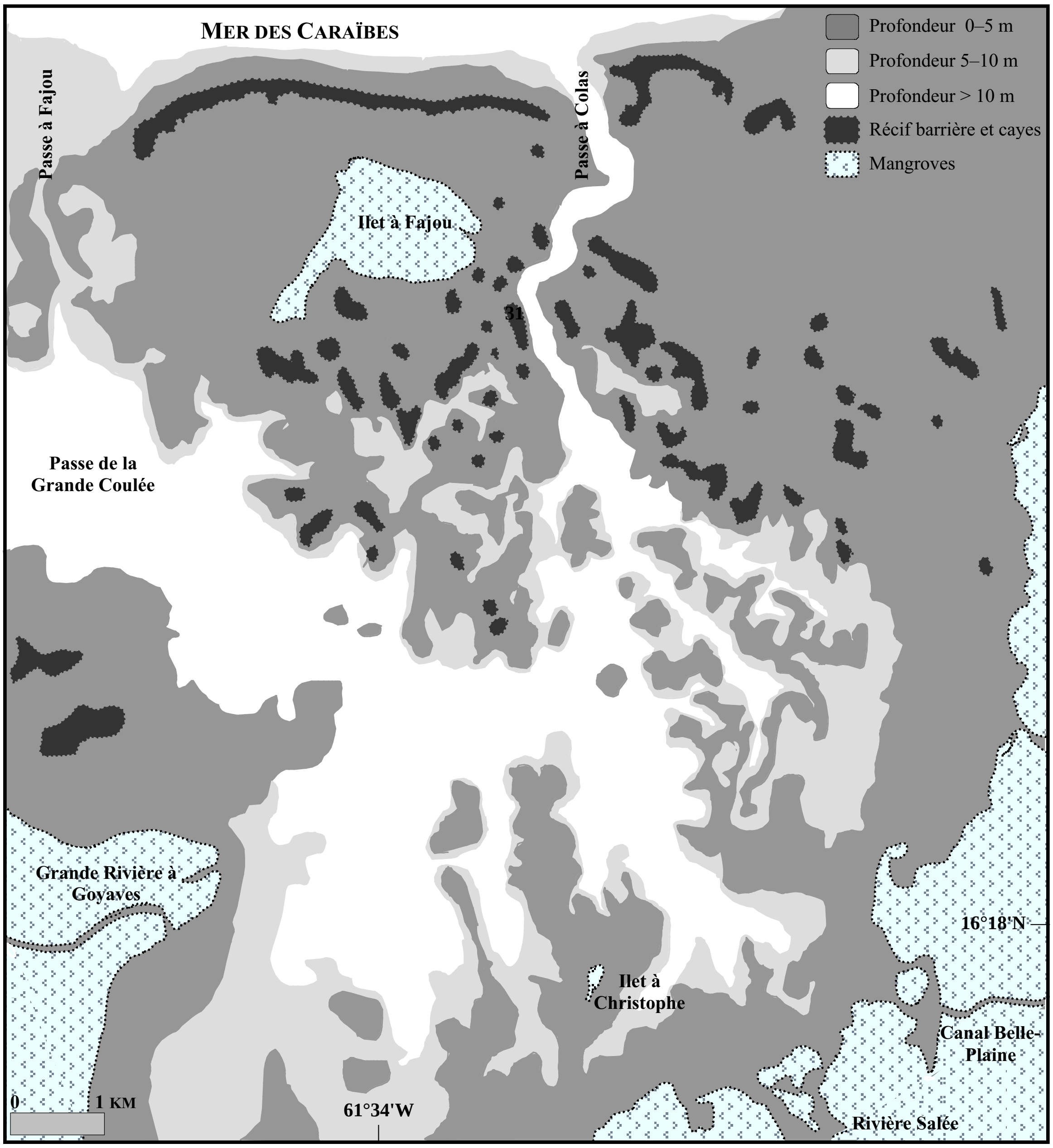


Figure 2.4 Distribution spatiale des différents écosystèmes rencontrés dans le lagon du Grand Cul-de-Sac Marin. La mangrove couvre une grande partie des zones littorales. Les herbiers à phanérogames marines colonisent les fonds de 0 à 10 m de profondeur et les fonds vaseux se localisent à des profondeurs supérieures à 10 m.

2.2.1 – Mangroves et Fonds Vaseux

La mangrove est une association d'arbres halophiles qui se développent dans les zones intertidales, vaseuses et peu oxygénées des régions tropicales et subtropicales (entre 25°N et 25°S). Les forêts de mangrove sur le pourtour du lagon du GCSM sont composées de diverses espèces de Palétuviers (*Rhizophora mangle*, *Avicennia germinans* et *Laguncularia racemosa*). Les racines aériennes des arbres forment une masse entortillée qui piège les sédiments (accumulation des détritus terrigènes) et qui rend l'accès à ces forêts très difficile. La mangrove est essentiellement sous l'influence des marées, du régime des pluies et de l'intensité de l'évapo-transpiration. Elle est soumise à un rythme saisonnier de circulation des eaux avec une période d'inondation quasi-permanente de juin à décembre et une période d'assèchement continu de janvier à mai (Imbert & Rollet 1989). La présence de la mangrove sur les pourtours littoraux lui confère un rôle de filtre pour les eaux et les matières organiques drainées vers le lagon.

Les mangroves abritent une communauté riche et diversifiée incluant poissons, mollusques, bivalves, crustacés, organismes microscopiques (algues et plancton) et elles ont un rôle essentiel de nursery pour l'ichtyofaune (Louis & Guyard 1982, Louis et al. 1985). La forte densité d'organismes marins rencontrés dans les mangroves serait expliquée en grande partie par la disponibilité de la nourriture, la réduction de la prédation et les microhabitats formés par l'entrelacement des racines de Palétuviers (Daniel & Robertson 1990).

Les fonds vaseux dans le lagon du GCSM se situent principalement en eaux profondes (> 10 m) dans lesquelles on retrouve 19 espèces de poissons pélagiques (Aliaume 1990). Ces fonds sont des zones d'élimination de matière et d'énergie provenant des apports terrigènes, des herbiers et de la mangrove.

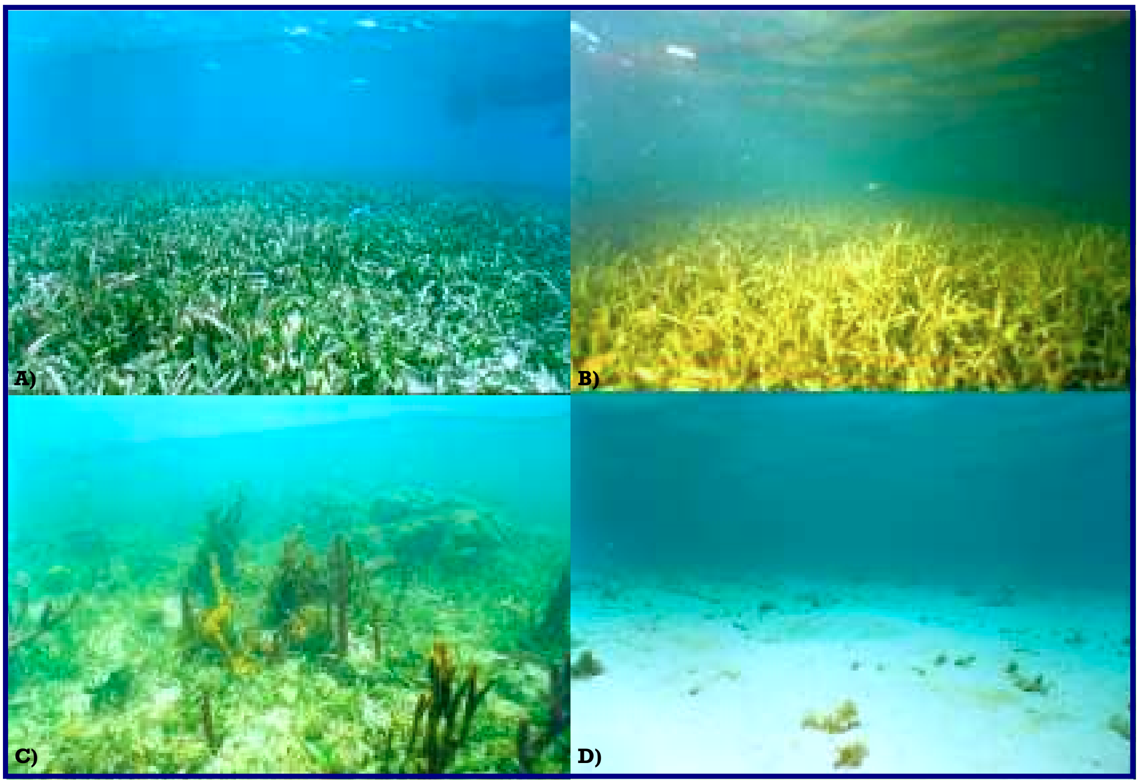
2.2.2 – Herbiers à Phanérogames Marines

Les herbiers communément rencontrés dans les lagons tropicaux côtiers sont composés par des espèces possédant des petites racines capables de coloniser des sédiments instables et oxydés comme l'espèce *Syringodium sp.* et par des espèces formant de véritables prairies sous-marines grâce à leurs rhizomes comme l'espèce *Thalassia sp.* (Photos 2.1, A). Les herbiers sont généralement localisés dans des zones peu profondes où l'action des vagues et des marées n'est pas excessive. Leur présence modifie les caractéristiques physiques, chimiques et biologiques de l’environnement (Cole & Syms 1999, Koch & Gust 1999, Turner et al. 1999) par leur aptitude à atténuer les vagues, à diminuer la vitesse des courants et à augmenter la luminosité grâce à l’accrétion des sédiments. Les herbiers sont bien connus pour supporter une forte abondance d’organismes, une forte diversité de ces organismes et une forte productivité des invertébrés grâce à la disponibilité de la nourriture et la possibilité de refuge contre les prédateurs (Edgar 1999). Les herbiers colonisent de grandes surfaces sur lesquelles les algues croissent et fournissent de la nourriture pour les organismes brouteurs et constituent un lieu de frai pour de nombreuses espèces de poissons.

Les herbiers montrent des expansions et des fragmentations naturelles dues à leur croissance saisonnière, leur mortalité et aux évènements météorologiques (tempêtes). L’hydrodynamique générée par le vent, les courants de marée et la profondeur de l’eau sont des facteurs importants qui influencent leur distribution spatiale (Turner et al. 1999). Les herbiers subissent également les activités de broutage de prédateurs épibenthiques (crabes et raies) et d’herbivores (oursins) ainsi que les impacts anthropiques (dommages engendrés par les hélices des bateaux ou par les dragues) qui altèrent leur structure spatiale (Eggleston et al. 1998).

Dans le lagon du GCSM, les herbiers à *Thalassia testudinum*, plus rarement à *Syringodium filiforme*, colonisent les fonds entre 0 et 8 m de profondeur. À l’arrière de la barrière récifale, *T. testudinum* construit de grandes prairies sous-marines sur les fonds sableux (Photos 2.1, A) à l’abri de l’action des vagues et loin de l’influence des eaux turbides de la mangrove. Dans ces endroits, leur limite bathymétrique se situe entre –5 et –8 m. Dans les baies abritées proche du littoral, les herbiers sur fonds vaseux (Photos 2.1, B) se situent en bordure de la mangrove, soit immédiatement après le bourrelet de Palétuviers (*Rhizophora sp.*), soit après une dépression de 3 à 10 m de large. Sur les cayes, les herbiers à *T. testudinum* peuvent être associés à des espèces coralliennes (Photos 2.1, C) comme *Porites divaricata*, *P. furcata*, *Solenastrea bournoni*, *Oculina diffusa* et *Millepora alcicornis* (Bouchon & Laborel 1990). La phanérogame marine *S.*

filiforme est moins présente dans le lagon. Elle colonise des sédiments plus grossiers situés en mer ouverte (entre –10 et –20 m) bien qu'elle puisse se rencontrer en association avec *T. testudinum* (Bouchon et al. 1991). 118 espèces de poissons sont associés aux herbiers à *T. testudinum* dans le lagon du GCSM (Aliaume 1990, Baelde 1990, Aliaume et al. 1993, Bouchon-Navaro 1997, Bouchon-Navaro et al. 1997).



Photos 2.1 Herbiers à *Thalassia testudinum* sur fond sableux (A), sur fond vaseux (B) et mélangés avec des espèces coralliennes sur une caye (C) dans le lagon du Grand Cul-de-Sac Marin. D) Fond sableux proche de la barrière récifale à l'intérieur du lagon (Photos de M. Louis).

2.2.3 – Barrière Récifale et Cayes

Les récifs coralliens sont des formations complexes qui augmentent l'hétérogénéité de l'habitat créant des micro-habitats et des refuges contre les prédateurs (Photos 2.2). Les formations coralliennes sont le résultat d'une production biologique de carbonate de calcium fabriqué par des coraux constructeurs de récif (Scléractiniaires, Hydrocoralliaires, Octocoralliaires). Les algues calcaires, les mollusques, les bivalves, les échinodermes et les protozoaires contribuent également à l'édification des récifs (Sorokin 1993). Bien que les espèces coralliennes assurent la majeure partie de la croissance récifale, les algues calcaires ont un rôle important dans les zones subissant fortement l'action des vagues.

Photos 2.2 Formations coralliennes dans le lagon du Grand Cul-de-Sac Marin. A) Platier récifal interne de la barrière récifale. B) Pente externe de la barrière récifale (–5 m). C) Pente externe de la barrière récifale (–10 m). D) Caye colonisée par quelques espèces coralliennes à l'intérieur du lagon (Photos M. Louis).

Les récifs coralliens se développent dans les eaux marines tropicales et subtropicales (Figure 2.5) caractérisées par des eaux non turbide, une température supérieure à 18°C, un faible marnage (< 2 m) et une salinité supérieure à 27 psu (Longhurst & Pauly 1987). Plusieurs facteurs physiques et biologiques contrôlent la structure et la dynamique des communautés coralliennes (Sorokin 1993). La capacité des espèces coralliennes à coloniser les substrats durs, le broutage des coraux par les poissons et les échinodermes, la bioérosion générée par les organismes perforants (bivalves) et les maladies causées par des bactéries et des virus sont les principaux stress biologiques que subissent les espèces coralliennes (Sorokin 1993, Hughes 1994). Les stress physiques sont l'action des vagues, la resuspension des sédiments, les variations de salinité et de température et l'excès de lumière. Les vagues et les courants de marée sont les facteurs de stress les plus importants dans les zones turbulentes peu profondes alors que les stress biologiques dominent dans les zones calmes (Sorokin 1993). Bien que les formations récifales soient assujetties à un important forçage hydrodynamique qui est un agent d'érosion et de destruction, ce stress physique stimule de nombreux processus biologiques incluant la croissance des coraux, la redistribution des matières carbonatées et la productivité (Hughes 1994).

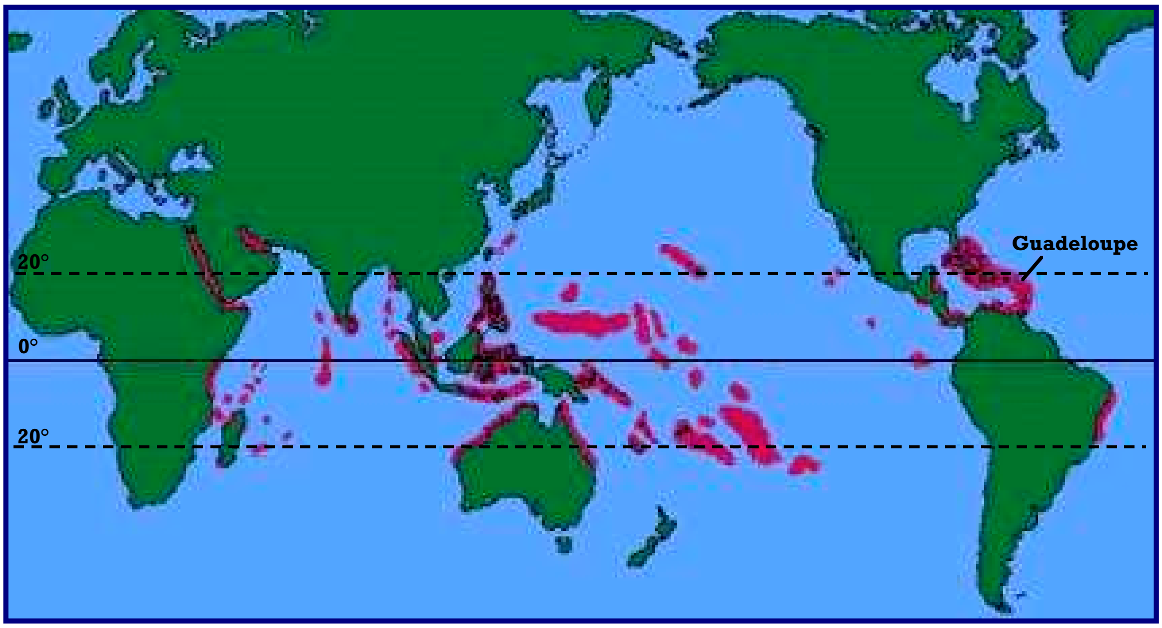


Figure 2.5 Distribution spatiale des récifs coralliens à travers les mers et les océans.

Les récifs coralliens dans le lagon du GCSM se sont développés sur les substrats durs (de 0 à 35 m de profondeur), hors d'atteinte des eaux insulaires. La barrière récifale n'est pas une construction récente, mais une formation datant du Pléistocène (Adey & Burke 1977, Guilcher & Marec 1978). La recolonisation par les coraux qui l'occupent actuellement ne date que d'environ 10 000 ans, ce qui explique l'apparence de la dalle corallienne Pléistocène à certains endroits et le faible encroûtement corallien récent qui ne dépassent pas 2 à 3 m d'épaisseur (Bouchon & Laborel 1990). L'édifice corallien ne présentant pas de platier très développé, les échanges d'eau entre la pleine mer et le lagon peuvent s'effectuer à travers et au-dessus du récif-barrière, les passes jouant un rôle moins important que sur les récifs Indo-Pacifique (Bouchon & Laborel 1990). 50 espèces de coraux (4 Hydrocoralliaires et 46 Scléractiniaires) ainsi que 161 espèces de poissons récifaux ont été inventoriés sur le récif-barrière (Bouchon & Laborel 1990; Bouchon-Navaro 1997; Bouchon-Navaro et al. 1997).

Cinq structures coralliennes, dont quatre formant la barrière récifale proprement-dite, peuvent être décrites dans le lagon du GCSM (Bouchon & Laborel 1990). On rencontre de l'intérieur vers l'extérieur du lagon : i) les **haut-fonds** ou **cayes**, à l'intérieur du lagon (Photos 2.2, D), colonisés par des formes coralliennes branchues (*Porites furcata, Acropora cervicornis*), ii) la **pente interne récifale** composée par des colonies coralliennes isolées (*Diploria sp*.) et des formes massives (têtes de corail), iii) le **platier récifal** (Photos 2.2, A) très peu développé et composé principalement de *Porites asteroides* et *Acropora palmata*, iv) le **front récifal** correspondant à la zone de déferlement de la houle et caractérisé par *Acropora palmata*, *Siderastrea radians*, *Favia fragum* et *Millepora Complanata,* et v) la **pente externe** (Photos 2.2, B et C) où trois zones se distinguent. La zone de 0 à –10 m caractérisée par des conditions environnementales contraignantes pour les coraux (grande agitation de l'eau, influence dévastatrice des cyclones, éclairement important) ne présente qu'un petit nombre d'espèces bien adaptées (*Acropora palmata*, *Millepora complanata*). Le développement maximum des peuplements coralliens se situe entre –10 et –25 m. Le peuplement s'appauvrit à partir de –25 m où la dalle rocheuse disparaît sous l'épandage de sable détritique.

2.3 Conclusion

Mangroves, herbiers à phanérogames marines et formations coralliennes constituent les écosystèmes marins les plus productifs des côtes guadeloupéennes. L'écosystème du lagon du GCSM est déjà bien connu grâce aux travaux antérieurs sur l'hydrodynamique du lagon (Castaing et al. 1984, Assor & Julius 1987), la physico-chimie des masses d'eau (Assor & Julius

1987, Baelde et al. 1987), les sédiments (Assor et al. 1983, Assor & Julius 1987), la mangrove (Imbert 1985, Imbert & Rollet 1989), les herbiers à phanérogames marines (Louis & Guyard 1982, Aliaume 1990, Bouchon et al. 1991, Aliaume et al. 1993), la barrière récifale (Baelde et al. 1987, Bouchon & Laborel 1990, Bouchon et al. 1991), l’ichtyofaune (Lasserre & Toffard 1977, Galzin et al. 1982, Louis & Guyard 1982, Louis et al. 1985, Baelde et al. 1987, Baelde 1990, Aliaume 1990, Bouchon et al. 1991, Aliaume et al. 1993), le phytoplancton (Ricard & Delesalle 1979, Delesalle 1981), les bactéries (Papa 1978, Bernard 1980), et l’étendue des perturbations anthropiques dans cet écosystème (Bernard 1995, Bernard et al. 1996).

La communauté zooplanctonique du lagon du GCSM reste peu connue; les seules données proviennent d’une étude indirecte sur les poissons des herbiers (Aliaume 1990, Aliaume et al. 1993). Aliaume (1990) précise que le zooplancton prélevé dans les herbiers à *T. testudinum* est constitué de 92 % de copépodes (adultes, copépodites et nauplii confondus) et de 3–4 % de larves de cirripèdes et de gastéropodes ; les autres groupes zooplanctoniques (isopodes, décapodes, cladocères) étant très faiblement représentés. L’étude de la communauté zooplanctonique du lagon du GCSM a été réalisée pendant la saison sèche (février-avril). Cette période a été choisie pour sa stabilité météorologique qui confère à l’écosystème une certaine stabilité temporelle.

CHAPITRE 3

IMPLICATIONS DE L'HETEROGENEITE ET DE L'ÉCHELLE DANS LA VARIABILITE SPATIALE DU ZOOPLANCTON

3.1 Résumé de l'Article en Français

Deux thèmes fondamentaux et interconnectés en écologie sont le développement et le maintien des patrons spatiaux et temporels et les conséquences de ces patrons dans la dynamique des populations et des écosystèmes. Comme toutes les entités écologiques, les organismes zooplanctoniques montrent une variabilité non-aléatoire à différentes échelles spatiales et temporelles et de nombreuses études ont mis en évidence les processus physiques et biologiques qui génèrent et maintiennent leurs patrons spatiaux. Puisque les patrons de la variabilité spatiale du zooplancton et les processus sous-jacents sont des phénomènes échelle-dépendants, la variabilité du zooplancton doit être étudiée en utilisant une approche multiéchelle. De nombreuses études ont déterminé les corrélations entre les patrons du zooplancton et les facteurs environnementaux à une échelle ou à plusieurs échelles spatiales, mais peu d'études ont quantifié les processus échelle-dépendants et ont déterminé les relations spatiales entre la complexité environnementale et la structure spatiale des communautés zooplanctoniques sur un continuum spatial. Dans cet article, nous relatons les études théoriques, empiriques et statistiques actuelles sur les rôles de l'hétérogénéité et de l'échelle spatiales dans l'étude du zooplancton. Notre objectif est de définir l'hétérogénéité et l'échelle spatiales dans le contexte de l'écologie du zooplancton et d'argumenter l'utilisation de l'approche multiéchelle dans ce contexte.

3.2 Article 1 : Implications of Heterogeneity and Scale in Zooplankton Spatial Variability (soumis à *Oikos*)

Abstract – Two fundamental and interconnected themes in ecology are the development and maintenance of spatial and temporal patterns, and the consequences of these patterns for the dynamics of populations and ecosystems. Like all ecological entities, zooplankton exhibits patchiness over a broad range of spatial and temporal scales and many investigations have highlighted the biological and physical mechanisms that generate and maintain such patterns. Because patterns of zooplankton spatial variability and generating processes are scale-dependent, the zooplankton patchiness must be investigated using the multiscale approach. Many studies have determined correlations between environmental and zooplankton patterns at one or more scales, but few have quantified scale-dependent processes and determined scaling rules linking environmental complexity to spatial structure in zooplankton communities over a scale continuum. In this paper, we review the current theoretical, empirical and statistical research on the roles of heterogeneity and scales in the study of zooplankton. Our aim is to define heterogeneity and scale in the context of zooplankton ecology, and to promote arguments supporting the multiscale spatial approach in this context.

Introduction

All ecosystems are heterogeneous in space and time, and most processes in natural environments—physical forcing, population and community dynamics—are sources of heterogeneity (Roughgarden et al. 1989, Kolasa and Pickett 1991, Peterson and Parker 1998 for reference books). Ecological heterogeneity is fundamental to both structure and dynamics of ecosystems (Levin 1992, Pinel-Alloul 1995). Ecosystems are assumed to organize themselves along a continuum of scales of space, time, and function. The resulting dynamic behaviour of ecosystems is characterized by high spatio-temporal 'variability'. Spatio-temporal variability is also encountered in populations and communities for which the individuals are distributed neither uniformly nor at random in nature but, rather, are aggregated in patches, or form gradients or other kinds of spatial structures (Legendre and Fortin 1989, Dutilleul and Legendre 1993). Patches (Wiens 1976, Roughgarden 1977), density gradients (Moore and Sander 1976, Hassett and Boehlert 1999), aggregations (Pinel-Alloul 1995), swarms (Haury and Yamazaki 1995, Leising and Yen 1997), and schools (Leising and Yen 1997), all refer to distribution patterns. These heterogeneous structures are particularly well developed in marine environments (Steele 1978, Hamner and Carleton 1979, Haury and Wiebe 1982, Mackas et al. 1985, Lewis and Boers 1991, Currie et al. 1998, Swartzman et al. 1999, Turner et al. 1999, Franks and Jaffe 2001).

The investigation of the spatial and temporal patterns of ecological entities—individuals, species, populations or communities—is now a current topic of research (Thrush 1991, Legendre et al. 1997, Piontkovski et al. 1995a, Currie et al. 1998, Roman et al. 2001), because spatial variability is recognized to be an important ecological feature of ecosystems (Legendre 1993). Concomitant with these investigations is the notion that the patterns of spatial variation may depend on the scale of observation (Levin 1992, Legendre et al. 1997, Dungan et al. 2002). Indeed, patterns and processes are scale-dependent phenomena (Wiens 1989, Schneider 1994): new emerging ecological properties may appear at different observation scales (Mackas et al. 1980, Wiens 1989, Allen and Hoekstra 1991). These statements depend both on the community members, which experience the environment over a unique range of scales (Denman and Platt 1975, Mackas and Boyd 1979, Legendre et al. 1986, Levin 1992), and on the physical and biological processes which vary with scale (Haury et al. 1978, Legendre and Demers 1984, Pinel-Alloul 1995). Both properties reinforce the recognition that there is no single correct scale at which to view a community or an ecosystem (Wiens 1989, Levin 1992), and when scale differences are not considered, quantitative and interpretational errors occur (Ricklefs 1987, Allen and Hoekstra 1991). Thus, the perception and investigation of ecological variability —the non-random variability of populations, communities or ecosystems—led to a new concept: that of 'scale'. For that reason, Levin (1992) wrote "the problem of pattern and scale is the central problem in ecology, unifying population biology and ecosystems science, and marrying basic and applied ecology". The scale is an intrinsic component of ecological heterogeneity (Dutilleul 1998a). Thus, in addition to recognizing heterogeneity, it is essential to refer it to a spatial scale.

Consequently, a central issue in ecology is spatio-temporal scaling of community structures and dynamics (Wiens 1989, Levin 1992). The goal of spatial ecology is to determine how space and spatial scales influence population and community structures and dynamics. In aquatic ecology, the interest in scale effects has been increasing (Ricklefs 1990, Rose and Leggett 1990, Dower et al. 1997, Claustre et al. 1999, Guichard et al. 2001), and patterns and processes have been investigated over a range of spatial and temporal scales (Haury and Yamazaki 1995, Solow and Steele 1995, Dunstan and Jonhson 1998, Attayde and Bozelli 1999, Blanchard and Bourget 1999, Murdock and Aronson 1999, Petersen et al. 1999, Huntley et al. 2000, Huskin et al. 2001). The multiscale approach is used to identify and characterize the scales of spatial dependency (Piontkovski and Williams 1995, Seuront and Lagadeuc 1997, 2001, Seuront et al. 1999, Lovejoy et al. 2001), which are critical: i) to appreciate the nature and magnitude of the sources of variability, ii) to understand the underlying biological and physical processes, and iii) to design sampling strategies. Since phytoplankton respond directly to variations in the physical environments (Legendre and Demers 1984), it is not surprising that spatial ecology first focussed on this trophic level. This explains the large number of studies published to date on the spatial organization of phytoplankton. Such a multiscale approach is not as obvious for higher trophic levels such as zooplankton, where the proximal determinants of biological responses include other living organisms, resulting in a smaller number of published papers. Like all ecological entities, zooplankton exhibits patchiness over a broad range of spatial and temporal scales (Haury et al. 1978, Mackas et al. 1985, Legendre et al. 1986, Pinel-Alloul 1995, Piontkovski and Williams 1995). The size of theses patches may vary from a few centimetres (micro-patches) to thousands of kilometres (biogeographic structures). According to Longhurst (1981), patchiness of zooplankton is a necessary condition for survival in the aquatic environment and it is probably the most fundamental reason why the mechanisms controlling zooplankton heterogeneity are being studied. Many investigations have highlighted the biological and physical mechanisms that generate and maintain such patterns (Hamner and Carleton 1979, Legendre and Demers 1984, Mackas et al. 1985, Davis et al. 1991, Pinel-Alloul 1995, Piontkovski et al. 1995b, Noda et al. 1998, Folt and Burns 1999, Huntley et al. 2000, Roman et al. 2001). All physical and biological processes operate at some preferential spatial and temporal scales (Haury et al. 1978, Mackas et al. 1985, Legendre et al. 1986, Barry and Dayton 1991, Pinel-Alloul 1995), so that they generate multiscale spatial and temporal variability in zooplankton communities (Haury et al. 1978, Piontkovski and William 1995, Pascual et al. 1995, Marguerit et al. 1998, Avois-Jacquet et al. submitted a). This explains that there is a close correspondence between the temporal and spatial scales of the physical and biological processes and aspects of the biological heterogeneity associated with them (Denman and Powell 1984). Because zooplankton patterns and environmental processes—physical and biological—are scale-dependent phenomena, considering the spatial scale is a requirement both to examine zooplankton patchiness and to understand the controlling mechanisms. Not only zooplankton patchiness leads to deal with scale, but the multiscale variability of zooplankton also leads to adopt a multiscale approach.

Many studies have determined correlations between environmental and zooplankton patterns at one or several scales, but few have quantified scale-dependent processes and determined scaling rules linking environmental complexity to spatial structure in zooplankton communities over a scale continuum. In this paper, we review the current theoretical, empirical and statistical advances on the roles of heterogeneity and scale in zooplankton studies. Our aim is to define heterogeneity and scale in the context of zooplankton ecology, and to promote arguments about the importance of the multiscale approach in this context.

Heterogeneity

Heterogeneity and Variability

‘Heterogeneity’, which is opposed to uniformity, classically refers to patterns and processes composed of parts of different kinds (Shachak and Brand 1991). While heterogeneity (in an ecological sense) has been viewed for a long time as a filter of noise that imposes interference or constraints (Steele 1976), it is now recognized to be an important concept in ecology (Kolasa and Rollo 1991, Dutilleul and Legendre 1993). Kolasa and Rollo (1991) differentiate ‘measured heterogeneity’, which is a product of the observer's arbitrary perspective, from ‘functional heterogeneity’, that which the ecological entity (i.e. individuals, species, populations, or communities) actually perceives, relates to, and responds to. This distinction depends on the prior knowledge of the organisms involved and on the resolution of the study. The heterogeneity perceived by a single individual of a species (having a specific age and size) depends on the temporal and spatial scale at which the individuals operate, which depends in turn on their movements relative to the environment (Kolasa and Rollo 1991). For example, when species differ in their mobility and capacity for habitat selection, the less mobile species, which are confined to a single patch, experience the heterogeneity of resources at coarse grain. Mobile species, in contrast, may experience different degrees of resource heterogeneity at finer grain (Naeem and Colwell 1991). The distribution of resources in the environment thus appears different to each species. Consequently, the perceived heterogeneity of an ecological entity differs from that of another. Thus, measured heterogeneity may converge to functional heterogeneity if the scale of the study addresses relevant aspects of environmental heterogeneity for the ecological entity (Kolasa and Rollo 1991). In marine environments, macrozooplankton typically show more intense and finer-scale variation in their concentration than do the smaller and less mobile micro- and mesozooplankton with respect to phytoplankton patchiness (Mackas et al. 1985).

‘Heterogeneity’ differs from ‘variability’, which indicates changes in values of a qualitative or quantitative descriptor (Shachak and Brand 1991). It is noteworthy that heterogeneity and variability are linked by common processes even if they are differently related to them. For instance, environmental heterogeneity controls non-uniformity in resource distribution (e.g. phytoplankton distribution), whereas zooplankton variability in abundance and biomass is the result of the ecological processes initiated by resource distribution. In other words, the variability of an ecological entity may be considered as its response to environmental heterogeneity. All ecological entities exhibit variability over a broad range of scales, and this variability is fundamental to population dynamics, community organization and stability, and element cycling (Levin 1992). In aquatic environments, patchiness is generally used to describe variability at horizontal scales between approximately 10 m and 100 km and at vertical scales between approximately 0.1 and 50 m (Mackas et al. 1985). Such variability is encountered in zooplankton communities in which the overwhelming majority of species shows over-dispersed or aggregated dispersal patterns (Haury et al. 1978, Piontkovski and William 1995, Currie et al. 1998), with significant non-random variability in horizontal and vertical positions (Haury and Wiebe 1982, Omori and Hamner 1982). Zooplankton exhibits variability in biomass and abundance (Piontkovski et al. 1995a, Stockwell and Sprules 1995, Pakhomov et al. 2000, Rollwagen-Bollens and Landry 2000, Landry et al. 2001) as well as in species number and composition (Haury and Wiebe 1982, Mackas et al. 1985, Webber et al. 1996, Alvarez-Cadena et al. 1998, Harvey et al. 2001). Moreover, zooplankton patchiness is a species- and size-specific property (Pinel-Alloul 1995). Piontkovski and Williams (1995) reported that the spatio-temporal variability of biomass of organisms increases in higher trophic levels, from phytoplankton through microzooplankton to macrozooplankton, i.e., with the increase in size of the organisms. These authors concluded that the lower energy flow of higher trophic level is accompanied by increased fluctuations in time and space. Organisms, acting as predators, should be more sensitive to spatio-temporal variability of the abundance and biomass of their prey over these trophic levels.

Summary —Examining the functional heterogeneity of an ecological entity (individuals, species, populations, or communities) requires to identify the environmental heterogeneity produced by biological and physical processes on which this entity depends. In this context, variability may be considered as the response of an ecological entity to environmental heterogeneity.

Spatial and temporal heterogeneity

Space and time are conventionally used to classifying types of heterogeneity in ecology but 'temporal heterogeneity' is not equivalent to 'spatial heterogeneity' (Kolasa and Rollo 1991). The time axis is directional and one-dimensional, whereas the spatial axis is non-directional and may be one-, two-, or three-dimensional. These differences explain that all nearest neighbours may influence the value observed at a given location, whereas future observations will never influence past observations (Dutilleul 1998a). Differences in temporal heterogeneity between locations will induce spatial heterogeneity, but consistent spatial heterogeneity between locations over time does not necessary imply temporal heterogeneity at each site (Kolasa and Rollo 1991). Therefore, temporal heterogeneity is not equivalent to spatial heterogeneity, but its role is also very important. For example, zooplankton temporal heterogeneity has an important role in predator-prey relationships (Lampert 1989, Neill 1990).

'Spatial heterogeneity' can be defined as the complexity that results from interactions between the spatial distribution of environmental constraints and the differential responses of organisms to these constraints (Milne 1991). Ecologists recognized that spatial heterogeneity is a major factor regulating the structure and dynamics of ecological entities (Levin 1992, Pinel-Alloul 1995). For example, high spatial heterogeneity interferes with competition in increasing habitat diversity, which also increases species diversity (Williams 1988), reduces the impact of predation, and increases population stability (Neill 1990). Habitat spatial heterogeneity has a central role in prey-predator interactions. Indeed, macrophyte beds patchiness seems to play an important role in limiting fish predation pressure on pelagic zooplankton (Bertolo et al. 1999). Phytoplankton spatial heterogeneity influences swarm formation, swimming behaviour and grazing of marine krill and copepods (Tiselius 1992). Phytoplankton spatial heterogeneity also has an important role in zooplankton individual fitness. Zooplankton response to only the most intense vertical patterns of phytoplankton availability seems to be an energetically efficient strategy (Fiedler 1983).

Zooplankton spatial heterogeneity is of great ecological significance since the distribution patterns of abundance, biomass and species, as well as the individual behaviour of zooplankters, strongly influence prey-predator interactions (Bollens and Frost 1991, Tiselius 1992, Folt et al. 1993, Ribes et al. 1996). For example, the location of mysid juveniles (*Hemimysis speluncola*) closest to a cave entrance, while the population spawners are found away from the cave entrance, results in protection of the population from predation (Ribes et al. 1996). The presence of juveniles in the area closest to the entrance and hence most accessible to predators is a means of increasing the protection of the population spawning potential: the activity of predators which enter the cave by chance is confined to juvenile individuals. A swarm, which is a major form of zooplankton spatial heterogeneity (Hamner and Carleton 1979, Haury and Yamazaki 1995, Leising and Yen 1997), serves several adaptive functions including food exploitation and mating encounters, but protection from predators appears to be one of the most important. Copepods in swarms align and flee from moving objects as do fish, visually confusing the predator (Hamner and Carleton 1979). This is reinforced by water coloration that decreases visibility (Emery 1968). Swarming behaviour may reduce the predation rate on egg-bearing females which represent large, high-contrast targets to planktivorous fish (Buskey 1998). Zooplankton patchiness influences their own reproductive activity. Indeed, swarming enhances copepod mating encounters and success, bringing together adult males and females in high concentrations

(Ribes et al. 1996, Buskey 1998). For example, *Dioithona oculata*, a cyclopoid copepod, exhibits a diel behavioural pattern that allows them to synchronize their mating and reproductive behaviour to the daily pattern of swarm formation and dispersal (Ambler et al. 1991). Swarming may also result from an attempt to maintain a favourable position into the species' ecological niche. Swarming permits copepods to cluster in local eddies, thereby restricting their dispersion by currents (Hamner and Carleton 1979) and reducing the energy required to maintain a favourable position in food patches. This has been shown for *Acartia tonsa* that does not store energy reserves (i.e. lipids) and thus has adapted to maintain itself in food patches by decreasing motility and swimming horizontally (Tiselius 1992).

Finally, plankton spatial heterogeneity is size-specific. In marine environments, heterogeneity of the spatial distribution increases with the size of organisms, from phytoplankton through mesozooplankton to macrozooplankton (Piontkovski et al. 1995a). Larger freshwater zooplankters, however, seem to be less heterogeneously distributed than small zooplankters (Pinel-Alloul et al. 1988). These authors suggested that greater spatial aggregation might allow small zooplankters to avoid predators and locate mates, whereas reduced spatial heterogeneity in large species may decrease competition.

Summary — Spatial and temporal heterogeneity play a central role in the structure and dynamics of zooplankton communities. Most zooplankters are distributed in swarms or aggregates. Understanding the spatial heterogeneity of zooplankton has profound effect on our understanding of populations, their interactions with others species, and the consequences on community properties and functions.

Environmental heterogeneity

'Environmental heterogeneity' refers to the non-uniform, spatial and temporal distribution of biotic and abiotic conditions that influence species or species interactions (Addiccott et al. 1987). Resource heterogeneity and habitat heterogeneity are two forms of environmental heterogeneity, which is omnipresent in nature and is known to affect many ecological processes and phenomena, including population dynamics, life histories, dispersal, behaviour, patterns of natural selection, predation, species diversity, and species interactions (González and Tessier 1997, Boström and Mattila 1999, Eggleston et al. 1998, 1999, García-Charton and Pérez-Ruzafa 1999, Steiner 2001).

Because species differ in terms of diet, metabolic rate, consumption rate, efficiency of conversion of resources to new individuals, and the scale at which they encounter the environment (Ricklefs 1987), the heterogeneity of resources has different consequences for the growth and development of copepods (Roff et al. 1995, Hopcroft et al. 1998) and for the distribution and abundance of species (Mackas et al. 1980, Rollwagen-Bollens and Landry 2000). Algal heterogeneity can have substantial effects on zooplankton-algae dynamics, trophic structure, and the strength of predator control (Steiner 2001). Patchiness in the distribution of resources is also fundamental to the way organisms exploit the environment. At different food concentrations, copepods change swimming speed, turning angle, or hopping rate, and actively locate and remain within food patches over a few millimeters (Tiselius 1992).

Pelagic and benthic marine habitats can be viewed as mosaics of patches of different environmental quality produced by spatial and temporal variation in the physical and biological constraints encountered by populations. Habitat heterogeneity may refer to the definition of ‘environmental heterogeneity’ given by Addiccott et al. (1987). These authors defined ‘environmental heterogeneity’ as a ‘patterning‘ which is produced by combinations of two qualitatively different kinds: i) the ‘division’ (i.e. the separation of patches by regions of less suitable environmental conditions), and ii) the ‘heterogeneity’ (i.e. the existence of two or more qualitatively different types of patches). Thus, habitat may be undivided and homogeneous, divided and homogeneous, heterogeneous but not divided, or both divided and heterogeneous (Fig. 1). Kolasa and Rollo (1991) noted, however, that ‘habitat complexity’ may be an important component of heterogeneity for some ecological entities, but does not constitute a class of heterogeneity on its own. Nevertheless, like resource heterogeneity, habitat heterogeneity may influence community structure by modifying the diversity (Eggleston et al. 1999), biomass (Rios-Jara 1998, Avois-Jacquet et al. submitted a), distribution and abundance of organisms (Mackas et al. 1993, Eggleston et al. 1998, García-Charton and Pérez-Ruzafa 1999, Avois-Jacquet et al. submitted b). For example, substratum heterogeneity enhances densities of organisms on the bottom (Rios-Jara and Gonzalez 2000). Most harpacticoids remain at the bottom, where they are very diversified and constitute distinct communities associated with the types of sediment to which they are adapted (Villiers and Bodiou 1996). The variation in the quality of the substratum can contribute to heterogeneous species distributions by modifying physiological processes linked to settlement, growth and reproduction, and by mediating biological interactions that can control recruitment and survivorship (Barry and Dayton 1991). Indeed, habitat patterning is known to affect many ecological processes including predation intensity (González and Tessier 1997), predation avoidance (Alvarez-Cadena et al. 1998), and larval dispersal and recruitment (Eggleston et al. 1998). For example, recruitment of fish to temperate zone seagrass beds shows strong responses to habitat structure at local scale such as individual beds, while recruitment of temperate reef fish shows correlation with habitat structure over a broad range of scales (Jenkins et al. 1998).

Finally, hierarchical patchiness (O'Neill 1989) is a common feature of natural habitats and environments. One of the properties of nested patchiness is 'threshold heterogeneity' consisting of two levels of resolution (Kolasa and Rollo 1991). First, 'lower threshold heterogeneity' is the grain of resolution at which a species or other ecological entity stops changing its features (those of interest to ecologists are, for example, distribution or energy transfer). At this level of resolution, the world becomes functionally homogeneous for that entity. Second, the 'upper threshold heterogeneity' is determined by the interaction between the extent of the ecological entity and habitat heterogeneity. When the size of a patch perceived to be homogeneous exceeds the extent of the distribution of the ecological entity (e.g. population or species), the habitat becomes virtually homogeneous for the entity. Note that for a single species, several thresholds may be identified depending on the organizational level (e.g. age group, size, or local population). Thus, for any ecological entity, there is an upper and a lower limit of resolution at which the entity stops responding to environmental heterogeneity.

Summary — Resource heterogeneity and habitat patterning, which are two forms of environmental heterogeneity, are common features of natural environments, affecting the structure and dynamics of ecological entities. Since each ecological entity has a specific threshold heterogeneity, entities perceive, relate to, and respond to resource heterogeneity and habitat patterning differently.

All roads lead to scale

What is scale?

Scale is a key concept for the description of spatial patterns and sampling designs; it includes several properties characterizing aspects of the spatial variability. A scale cannot be assigned to a process or variable that is uniform in space or time (Powell 1989). Patterns, processes, and events can be characterized and distinguished from others by their scale. The scale may vary according to the variable (which may be spatially patterned) or process considered (Wiens 1989, Dutilleul 1998a). For example, tropical oceanic zooplankton in the area off Puerto Rico displays well-developed fine-scale patchiness (1–1000 m), but no detectable patchiness over scales from 1 to 100 km (Yoshioka et al. 1985). These authors reported that environmental processes, including eddies and meanders operating in this region, have little effect on the patchiness of zooplankton abundance over coarse (1–10 km) and mesoscale (10–100 km). These environmental processes operate at scales either smaller than 1 km or larger than 100 km. Scale also has an important influence on the focus of the topic under study (Sparrow 1999). For example, grazing or predation is not performed by populations, but by individuals, and interactions between prey and predator are discrete events over short distances and times. So these interactions must be studied at the scale of individuals (Tiselius 1992). At the scale of organisms, the focus may be on morphological, physiological, or behavioural responses to the heterogeneity of the available resources, and to the heterogeneity of threats from competitors, predators, and parasites. At the population and ecosystem scales, the focus may be on how persistence of the population is determined by environmental heterogeneity. Thus an increase in the spatial scale of a study results in studying new interactions and relationships, because the type of organization varies with scale. A change in scale often necessitates consideration of new levels of organization. A level is not a scale, but a level of organization can have one or several characteristic scales (O'Neill and King 1998). An association between scale and level is formed because each level is associated with a range of scales.

Scale is not a property of nature alone (i.e. ecological scale), but is something associated with both observation and analysis (i.e. observation scale) (Dungan et al. 2002). The observer imposes a perceptual bias, a filter through which the system is viewed. In some cases, the scale of the observations may be chosen deliberately to elucidate key features of a natural system, but more often the scale is imposed on us by our capabilities of perception, or by technological or logistic constraints. The ‘observation scale’ (Fig. 2) in sampling designs and analysis of patterns is a concept that can be divided into three components (Wiens 1989, Allen and Hoekstra 1991, Legendre and Legendre 1998, Dungan et al. 2002): i) ‘grain size’, i.e. the size of the elementary sample), ii) ‘sampling interval’, i.e. the distance between neighbouring samples, and iii) ‘extent’, i.e. the total length or area included in the study. Grain size relates to the level of resolution. It determines the lowest level of organization that can be ascertained. In contrast to grain size, extent determines the largest entities that can be detected in the data (Legendre and Legendre 1998); it is the span of the measurements in a study (Allen and Hoekstra 1991).

The ‘observation scale’ affects our view of the heterogeneity of a system. If the system is observed at an inappropriate scale, we may not detect the actual dynamics and patterns but may instead identify patterns and processes that are artifacts of scale (Legendre and Demers 1984, Wiens 1989). For example, assemblages that seem unstable at short spatial scales may be stable when viewed at broader spatial scales, as suggested for coral reef fish. Likewise, assemblages may appear stable over short time periods but unstable when examined over longer time periods (Sale 1999). Thus the perception of any ecological pattern and process depends on the chosen observation scale (Platt and Denman 1975, Levin 1992, Schneider 1994, Legendre et al. 1997, Dungan et al. 2002). Using a single, inadequate, observation scale can lead to incorrect conclusions about ecological heterogeneity, phenomena, processes and interactions (Allen and Hoekstra 1991, Horne and Schneider 1995). Experimental results, in particular, cannot be directly extrapolated to broader scales without misinterpretation (Ricklefs 1987). Different physical and biological processes prevail at different scale. As a consequence, fine-scale experiments or local observations provide limited insights into regional or global phenomena. One solution is to incorporate spatial scale explicitly into the experimental and sampling design of field studies (Hughes et al. 1999, Petersen et al. 1999).

To identify the ecological patterns and processes in a system, the observation scale must detect the functional heterogeneity of the ecological entity under consideration; the scale of observation must converge to the ecological scale of the entity. By analogy to the ‘observation scale’, the ‘ecological scale’ of an entity (Fig. 2) may be defined by its ‘grain’ (i.e. the lowest patch size where an ecological entity responds to environmental heterogeneity) and ‘extent’ (i.e. the largest area possibly experienced by the ecological entity). With reference to ‘threshold heterogeneity’ (Kolasa and Rollo 1991), the ‘grain’ corresponds to the ‘lower threshold heterogeneity’ and the ‘extent’ to the ‘upper threshold heterogeneity’ bounding the ecological scale of the ecological entity, i.e., the scale at which it operates. The ‘grain’ of environmental heterogeneity must be smaller than the ‘extent’ of the organism or population to have an effect on environmental heterogeneity (Fig. 2). If the grain is larger than the extent, then heterogeneity either tends to be interpreted as an 'environmental gradient' (Sparrow 1999), or it remains undetectable by the entity.

So to identify ecological patterns and processes, it is necessary that i) the sampling grain be larger than the entity involved (e.g. an individual organisms) and the same as, or preferably smaller than, the structures resulting from a unit process (e.g. a patch), ii) the sampling interval be smaller than the average distance between the structures resulting from a unit process, and iii) the sampling extent be the same as the total area covered by the entity or by the process under study (Legendre and Legendre 1998, Dungan et al. 2002). No structure can be detected which is smaller than the grain or larger than the extent of the study.

Summary — A scale is assigned to a pattern or process, which varies in space or time. Since grain size and extent define the observation scale, the lower threshold heterogeneity (grain) and the upper threshold heterogeneity (extent) characterize the ecological scale at which an ecological entity operates. Our view of any system depends on the scale of observation. Thus the choice of a working scale may strongly affect our perspective, influencing the interpretation of patterns and processes. The observation scale must allow us to detect, perceive, and describe the functional heterogeneity of ecological systems.

Spatial versus temporal scale

The 'temporal scale' of a phenomenon is the period over which one must wait before observing a significant change in some quantity of interest (Powell 1989). Temporal scale is much like spatial scale, except that time involves only one dimension and is one-directional. Since each physical and biological property in an aquatic environment varies only within a range of temporal and spatial scales (Legendre and Demers 1984), our ability to predict ecological phenomena depends on the relationships between these scales of variability (Wiens 1989). The spatial variability of an ecological entity or process which is identified at fine spatial scale occurs over short time scales, whereas the broadest-scale processes vary over thousands or millions of years. For example, copepod swarms encountered at fine spatial scale (0.1–1 km) persist during a few weeks, whereas the biogeographic structures of zooplankton (a few thousand kilometres) occur over thousands of years (Table 1). The time scale of important processes also increases with increased spatial scales, because processes operate at slower rates, time lags increase, and indirect effects become increasingly important. For example, changes in the community structure of zooplankton observed on a broad temporal scale (Table 1) may result from changes in population growth rates that occurred at the scale of a few months. Moreover, the dynamics of different ecological phenomena in different systems follow different trajectories in space and time (Wiens 1989). For example, a water mass with a surface area of 1 m^2 may be exposed to copepod grazing during a few hours, whereas the temporal scale of ciliate efficiency may be hours to days.

Summary — Spatial and temporal scales are interdependent. Both of them influence our perception of ecological patterns and processes.

Importance of spatial scale

Because the environment is a spatially structured and dynamic system, ecological patterns and generating processes are dependent across space and time (Table 1). Since all physical and biological processes as well as the resulting patterns take place in preferential spatial and temporal scales (Legendre et al. 1986), considering scale is necessary to understand the structure and dynamics of any ecological system. One of the major objectives of ecological research is to understand the creation and disappearance of spatial variability as a function of spatial scales (Mackas et al. 1985).

The importance of spatial scale has been shown in many cases. For example, Hughes et al. (1999) reported the role of spatial scales in coral species recruitment on the Great Barrier Reef. Recruitment rate variation is greater at scales of 250–500 km and 0.5–3 km than at intermediate scales of 10–15 km. Cole and Syms (1999) showed that the scales of mortality patterns may suggest the scales at which the process responsible for mortality operates. He noted that mortality factors change with scale. In spatial population dynamics, a topic of central importance is the spatial scale of population synchrony, which results from the interaction of temporal fluctuations in population density between two localities, which in turn influence regional population dynamics and the risk of regional or global extinction (Lande et al. 1999). To appreciate the significance of biological processes for zooplankton patchiness, one must understand the way in which their influence on aggregation relative to physical processes varies with spatial scales (Folt and Burns 1999).

Summary — Because patterns and processes are scale-dependent phenomena, considering the spatial scale is fundamental to examine ecological patchiness and understand its controlling mechanisms.

Why is the multi-scale approach important?

The properties of communities and ecosystems lead to describe their structure and dynamics across scales (Legendre and Demers 1984, Addicott et al. 1987, Wiens 1989, Levin 1992, Schneider 1994, Legendre et al. 1997, Seuront et al. 1999). These properties are the following: i) community members may experience the environment over a given range of scales (Denman and Platt 1975, Mackas and Boyd 1979, Legendre et al. 1986, Levin 1992), ii) biological and physical processes change with scale (Haury et al. 1978, Legendre and Demers 1984, Pinel-Alloul 1995), iii) biological interactions with the environment occur over several scales (O'Neill 1989), and iv) new properties may appear at different scales (Allen and Hoekstra 1991). Not only do the physical and biological properties change with scale, but phenomena that are positively correlated over one scale may change to negative correlation at another scale (Mackas et al. 1980, Wiens 1989, Allen and Hoekstra 1991). For example, at fine spatial scale, predator and prey dynamics may appear to be negatively correlated, but at broad scale, the correlation is positive, since they both respond to a set of background environmental conditions (Fiedler 1983, Rose and Leggett 1990). Changes in correlation structure often imply a change in scale (Allen and Hoektra 1991). Thus there is no single correct scale at which one may describe population or community structure and dynamics (Wiens 1989, Levin 1992). In marine systems, various studies have characterized the spectrum of variability for zooplankton (e.g. Mackas and Boyd 1979, Mackas et al. 1985, Solow and Steele 1995). Over broad spatial scales (from hundred to thousands of kilometres), it has clearly been established that physical processes, which are generated mainly by climatic and hydrodynamic regimes, are the dominant mechanisms generating and maintaining zooplankton spatial patterns (Haury et al. 1978, Denman and Powell 1984, Legendre and Demers 1984, Mackas et al. 1985, Pinel-Alloul 1995). Over meso- (10–100 km) and fine scales (from few cm to 10 km) that are of main interest for the understanding of biological processes, the dominant mechanisms controlling zooplankton spatial variability are not so clear. Patchiness in zooplankton biomass or species composition seems to be related to local hydrodynamic features such as coastal fronts, internal waves or tides, turbulence (Legendre and Demers 1984, Mackas et al. 1985, Davis et al. 1991, Petersen et al. 1998) associated with bottom topography (Denman and Powell 1984, Genin et al. 1988, Ribes et al. 1996), and biological processes associated with the underlying individual behaviour, including diel vertical migration, predator avoidance, food searching and feeding, and mating behaviour (Bollens and Frost 1991, Folt et al. 1993, Yen et al. 1998, Folt and Burns 1999). The spatial scales of variability for zooplankton community composition and zooplankton biomass (as well as phytoplankton community composition and biomass) differ for each quantity (Mackas et al. 1985, Powell 1989). A large amount of zooplankton biomass variability can occur within the confines of a more-or-less uniform community patch. This implies that the dominant processes generating variability across spatial scales differ between community structure and biomass. For instance, Salas-de-Leon et al. (1998) showed that zooplankton biomass is affected by river inputs through nutrient run-off and upwelling, whereas the spatial variability of zooplankton community structure is controlled by the general hydrodynamics of the bay, which occurs over a broader spatial scale.

The idea of considering spatial variability of planktonic communities as a multiscale process has been introduced into marine biology nearly 30 years ago by Platt and Denman (1975). It was developed and elaborated further (Haury et al. 1978) to the level of a concept that can now be regarded as the ‘multiscale spatial and temporal variability of marine ecosystems’. Most physical and biological processes in marine environments create zooplankton space-time patchiness over a continuum of scales (Mackas et al. 1985, Steele 1989); the forces generated by these processes cascading from broad to fine scales (Mackas et al. 1985). Mackas et al. (1985) noticed that the variability in the ocean occurs through a hierarchical spectrum of time and space scales. They called this phenomenon the ‘turbulent cascade’. These authors established that fractionation of the kinetic energy from broad-scale oceanic gyres and energy derived from baroclinic instabilities (gradients in potential energy) lead to the formation of several types of scale features. Although this energy originated from global-scale processes, it is fractionated in a turbulent cascade of energy to finer and finer scales until it is ultimately dissipated through molecular processes. As a corollary, patterns of zooplankton patchiness have been observed at different spatial scales characterising the multiscale patchiness of zooplankton (Pascual et al. 1995, Marguerit et al. 1998, Seuront and Lagadeuc 2001, Avois-Jacquet et al. submitted a,b); the size patch varied from a few centimetres (micro-scale: 1 cm–1 m) to thousands of kilometres (mega-scale: 1000–10000 km).

It is important to understand and anticipate the implications of moving from one scale to another. Perhaps the most obvious effect of scale change is the level of discernable detail that is present. Shifts of scale, for an ecological entity, may lead from perceived homogeneity to heterogeneity, and vice versa; the information contained at one level of resolution may look like noise at another level (Dutilleul and Legendre 1993). Allen and Hoekstra (1991) also showed how increasing the extent leads to averaging variation, whereas increasing the grain size transforms a variable into a constant (it is the case for temperature or salinity). The number of variables useful for modelling and other analyses also changes with scale, generally becoming smaller at coarser scales. Since the number of important variables generally decreases towards broader scales, scale changes may also dramatically change the model structure. This switch occurs in models because some variables change greatly with a change of spatial scale, whereas others do not. Thus, conclusions appropriate for a scale of an environmental or population pattern may be inappropriately transferred to other scales, so that when scale differences are not considered, quantitative and interpretational errors may occur (Ricklefs 1987, Allen and Hoekstra 1991).

A key to understanding heterogeneity is to conduct studies across a continuum of scales. Bellehumeur et al. (1997) showed that an ecological phenomenon spread out in space and time does not have discrete spatial scales, but a continuum of spatio-temporal structures whose perception depends on the size of the sampling units, an assumption which greatly agrees with the multiscale approach. Consequently, ecological processes seem to be better described by a continuum of scales rather than a hierarchy of overlapped scales (O'Neill 1989, Allen and Hoekstra 1991). The multiscale approach enables the extrapolation of ecosystem characteristics across scales and can be used to understand heterogeneity and its ecological consequences, for example, understand how variability at one scale may lead to the emergence of ecological phenomena at another scale.

Summary — Because ecological entities may experience the environment over a unique range of scales and that new properties may appear at different scales, there is no single correct scale at which to describe communities or ecosystems. Multiscale perception becomes a requirement to better understand the structure and dynamics of communities or ecosystems.

Multiscale analysis

In statistical analysis, a spatial structure may appear in a variable y because the process that has produced the values of y is spatial and has generated autocorrelation in the data (e.g. salinity gradient generated by the river-water flows); or it may be caused by dependence of y upon one or several causal variables x which are spatially structured (e.g. zooplankton patchiness controlled by the phytoplankton dispersion); or both (Legendre and Legendre 1998). Horne and Schneider (1995) have reviewed the statistical analyses of spatial variance at single scales and at several scales. The power of methods of spatial statistics, including fractal analysis, nested quadrat analysis, correlograms and spectral analysis, is in their capability to describe how patterns change across scales. Most of the methods of spatial analysis investigated and compared by Dale et al. (2002) can be used in that way.

The need for multiscale analysis in investigations of spatial variability of planktonic communities is now recognized for many reasons, which have been reviewed above. A multiscale approach enables the extrapolation of population and ecosystem characteristics across scales. It is used to identify and characterize the scales of spatial dependency that are critical i) to appreciate the nature and magnitude of sources of variability, ii) to understand the underlying biological and physical processes, and iii) to design sampling strategies. Three statistical methods are widely used as multiscale analysis tools by oceanographers and limnologists: 'spectral analysis' (Platt and Denman 1975, Mackas and Boyd 1979), 'multifractal analysis' (Pascual et al. 1995, Seuront and Lagadeuc 1997), and 'universal multifractal analysis (Marguerit et al. 1998, Seuront et al. 1999, Lovejoy et al. 2001). However, these analyses cannot be conducted without taking into account a number of theoretical and practical considerations (See Horne and Schneider 1995, Dutilleul 1998b, Seuront et al. 1999 for extensive reviews).

Spectral analysis is a form of analysis of variance in which the total variance of a process is partitioned into contributions arising from processes with different spatial scales or time scales in the case of spatially or temporally recorded data, respectively. A power spectrum separates and measures the amount of variability occurring at different wave numbers or frequency bands (Platt and Denman 1975). Spectral analysis, being only a second-order statistic, characterizes the variability very poorly by implicitly assuming 'quasi-Gaussian' statistics, which are not relevant for intermittent fields (Seuront et al. 1999). Continuous processes are well described by sine and cosine waves but the non-Gaussian character of point processes, such as mobile organism counts, limits the use of spectral models. Moreover, the partitioning of variance among frequencies by spectral analysis is sensitive to low means and to the presence of zeros in count data. Spectral analysis does not adequately reflect non-linear relationships between variables (Horne and Schneider 1995).

Multifractal analysis (Pascual et al. 1995, Seuront et al. 1996, Seuront and Lagadeuc 1997) can be regarded as a statistical generalisation of the fractal theory (i.e. based on the geometric form—fractal geometry—which exhibits structure at all scales; Mandelbrot 1983), leading to the consideration of multifractal fields as a hierarchy of sets, each with its own fractal dimension. Multifractal fields are described by scaling relationships that require a family of different exponents, rather than the single exponent of traditional fractal patterns, which then characterise variability in a very limited way (Seuront and Lagadeuc 1997). Recently, 'universal multifractals' (Marguerit et al. 1998, Seuront et al. 1999, Lovejoy et al. 2001) appeared to be a potential powerful tool in analysing multiscale space-time variability of any intermittent processes (e.g. turbulence). The use of universal multifractals provides three fundamental parameters characterizing the structure of the whole variability of an intermittent process and can be regarded as a way to delineate the relative contributions of the biological and physical processes to the patterns observed. However, like spectral analysis, multifractal analysis requires the continuous and simultaneous recording of the variables involved (e.g. temperature, *in vivo* fluorescence); biological data do not always provide long temporal or spatial series and often violate other assumptions, such as regular sampling intervals and stationarity of means.

Moreover, the degree to which these methods can reveal spatial pattern is sensitive to sampling scale (Wiens 1989, Dutilleul 1998b).

Recently, a new form of multiscale analysis has been used to determine the multiscale spatial variability in zooplankton structure (Avois-Jacquet et al. submitted a, b). The method called 'Principal Coordinates of Neighbour Matrices' (PCNM: Borcard and Legendre, 2002) is based on the close neighbourhood relationships among sampling sites; it can be used to detect and quantify spatial patterns over a wide range of scales. One major advantage of this method is that the components of the spatial model obtained are orthogonal, and can thus be either examined separately or combined at will into independent sub-models that can be interpreted with the help of environmental information. When such knowledge is not available, the sub-models may help generate hypotheses about the underlying processes that have generated the structures (Borcard and Legendre 2002). Another advantage is that continuous recording of all variables is not necessary. The method can be used with irregularly spaced data, although the interpretation is then complicated by the fact that the individual principal coordinates often bear structures belonging to several scales. However, the degree to which this method can reveal spatial patterns is also sensitive to the sampling scale, in the sense that it is limited by the 'observation window' bounded by sampling interval at one end and extent of the sampled area at the other.

New sampling technologies

New technological aids to study zooplankton patchiness help resolve some problems linked to the choice of sampling scale (i.e. grain and extent) which influences the spatial analyses and, consequently, the identification of the ecological patterns and processes. The increasing awareness of the fact that time and space scales involved in sampling zooplankton (Steele 1978, Mackas and Boyd 1979, Haury and Wiebe 1982, Fiedler 1983) must be appropriate to the biological processes being investigated, has highlighted the deficiencies of standard plankton sampling gears, i.e. nets and pumps (Omori and Hamner 1982), especially when high-frequency sampling is required. During the last two decades, three advanced sampling techniques have been developed. They resolve some problems linked to spatial scales (e.g. limitation of the size of sampling grain and/or sampling extent). These technologies are i) the particle sizing/counting instruments, ii) the optical sensors, and iii) the multiple-frequency acoustic sensors. Although each of these techniques presents limitations (see Williamson et al. 1992, Pinel-Alloul 1995, Folt and Burns 1999 for extensive reviews), these new sampling methods permit to acquire continuous in situ data and/or rapidly cover large surface areas with high-resolution sampling. The particle sizing/counting instruments, including optical plankton counters (OPC; Herman 1992) and dual light sheet sensor (DLS; see in Sutton et al. 2001) are among the few oceanographic instruments that can collect biological information over broad scale without compromising high-resolution data at the fine scales. Although they do not allow the identification of species, they permit determination of the size and abundance distributions of zooplankton in considerably less time than conventional methods do. Currie et al. (1998) used the OPC with time/spatial-series, from which neighbour relationships can quickly and easily be quantified. This methodology allows determination of zooplankton spatial distributions from the km scale down to that of millimetres. Optical sensors that have the capability of imaging particles are the video plankton recorder (VPR; Davis et al. 1992), the in situ video camera (Tiselius 1998), and the shadow image particle profile evaluation recorder (SIPPER; see in Sutton et al. 2001). These video recorders produce interesting results for fine-scale vertical and horizontal plankton patchiness. Optical techniques can be augmented by multiple-frequency acoustic sensors that provide general information on spatial distributions of zooplankton and fish by size class (Sameoto et al. 1993, Greene et al. 1998, Swartzman et al. 1999, Coyle 2000). They permit to identify, for example, the relationships between zooplankton and fish spatial patterns.

Another problem in acquisition of biological data in marine systems is that the procedures differ for different groups of pelagic organisms (from phytoplankton through microzooplankton to fish, which have different scales of spatial-dependency), each group requiring special sampling methods. Physical and biological data are also obtained for different space and time scales. Physical data acquisition is generally rapid with continuous in situ recording, while biological data are generally acquired after laborious and time-consuming examination procedures, particularly in planktology. The use of a multisensor high-resolution sampler including particle sizing/counting instruments, optical sensors, fluorometre, conductivity, temperature and depth (CTD) sensor units, nets, and water bottles (Sutton et al. 2001) allow high-resolution analyses of ecosystem variables for the study of broad and fine-scale patchiness of organisms, as well as the factors that may influence these patterns.

Conclusion

The three foundation of ecological science are: ideas and theory, evidence, and means of disproof. This paper discussed heterogeneity and scale as a framework to generate theories and hypotheses about zooplankton patterns and processes; new means of gathering information have been mentioned; and multiscale analysis seems to be an appropriate approach for supporting or disproving hypotheses about spatial patterns and processes.

To address patterns of zooplankton spatial patchiness and their generating processes, ecologists need to find ways to quantify patterns of variability in space and time, to understand how patterns change with scale, and to understand the causes and consequences of spatial patterns. In this perspective, the multiscale approach may help identify and characterize the scales of spatial dependency. Recognizing changes in patterns with scale and understanding the ecological processes that effect these changes are of considerable importance for practical and theoretical reasons. It is evident that identifying and understanding scale-dependent changes in patterns and processes is a prerequisite for predicting the consequences of changes in ecological systems induced by natural disturbances and human alterations of the environment. There are many mechanisms driving population dynamics. Understanding what drives the dynamics of a population requires investigating all possible mechanisms, each at its appropriate scale. Even if a few of the possible mechanisms operate at broad spatial scale, and others at fine scale, a systematic investigation of all possible mechanisms remains impossible. Thus, rather than trying to determine the correct scale of a zooplanktonic entity (individual, species, population, community), marine ecologists should try to find out how zooplankton structure and dynamics change across scales.

The multiscale spatial relationships between zooplankton variability and environmental heterogeneity are still far less clear, particularly in marine coastal ecosystems, and are much more complex than for phytoplankton variability. We still lack an overall perspective on such questions as: i) how do zooplankton patterns vary with spatial scales? ii) how do resource heterogeneity and habitat patterning affect zooplankton spatial variability? iii) what is the relative importance of zooplankton behaviour and hydrodynamic processes generating the multiscale spatial variability of zooplankton? and finally, iv) under what conditions are environmental heterogeneity and zooplankton spatial variability positively or negatively related to each other? The new sampling techniques and a multiscale approach may help identify the multiscale spatial patchiness of zooplankton individuals, populations or communities, and characterize the scales of spatial dependency in order to understand the underlying biological and physical processes and assess the role of zooplankton spatial variability on the structure and dynamics of ecosystems.

Acknowledgements – It is a pleasure to acknowledge support of the Société de Secours des Amis des Sciences (Académie des Sciences, France) granted to C.A.-J.

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Table 1 Correspondence between spatial and temporal scales for physical and biological processes, in aquatic systems. Not all possible processes occurring at these scales are mentioned. From Haury et al. (1978), Legendre and Demers (1984), Mackas et al. (1985), Barry and Dayton (1991), and Pinel-Alloul (1995).

Spatial Scale	Temporal Scale	Physical processes	Biological Processes
Broad scale 100–1000 km	From decades to 10^4 years	Oceanic currents Oceanic fronts El Niño events Eddies Upwelling	Primary production patterns Differential growth Competition Community shifts
Mesoscale 10–100 km	From months to years	Oceanic fronts Island effects Upwelling Eddies	Population growth Migration behaviour Patchiness Phytoplankton patterns
Fine scale ≈ cm–10 km	From minutes to weeks	Oceanic fronts Oceanic currents Tidal fronts Internal waves Langmuir circulation Turbulent mixing	Micro-patches Swarming Migration behaviour Swimming behaviour Physiological adaptation Phytoplankton patterns Prey-predator interactions

Figure Legends

Figure 1 Illustration of 'habitat patterning' encountered in coastal reef lagoons with sea-grass beds (wavy lines) and reef patches (in black). The habitat may be A) homogeneous but divided, B) heterogeneous but not divided, or C) heterogeneous and divided.

Figure 2 Components of the sampling scale (i.e. the scale of the observation, in bold), and of the scale of an ecological entity (e.g. a type of community, in italics). The patches represent the grain size of environmental heterogeneity at which the ecological entity responds.

Figure 1

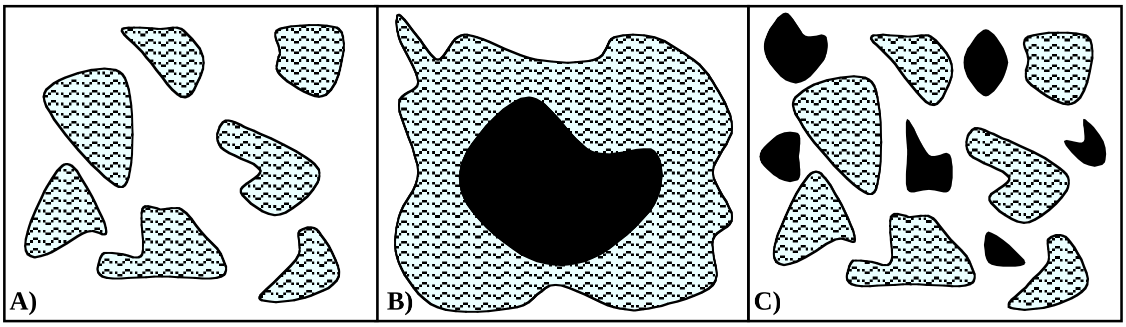
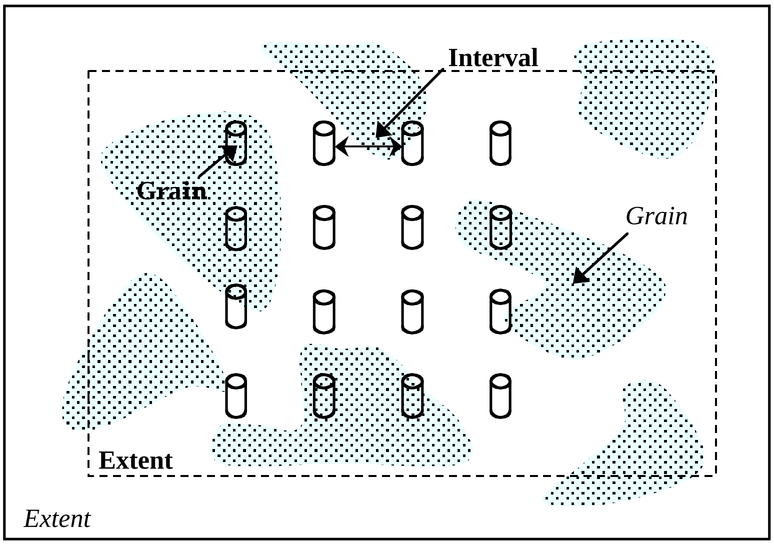


Figure 2



CHAPITRE 4

ZOOPLANCTON TROPICAL COTIER : PATRONS ET PROCESSUS A TRAVERS LES ÉCHELLES SPATIALES

4.1 Résumé de l'Article en Français

Les études sur la distribution spatiale de l'abondance, de la biomasse et des espèces zooplanctoniques associées aux eaux tropicales côtières se sont restreintes à un petit nombre de stations qui ne permet pas d'établir clairement les patrons spatiaux du zooplancton. Bien que plusieurs processus physiques et biologiques ont été évoqués pour leur rôle dans la création et le maintien des patrons spatiaux du zooplancton tropical côtier, les échelles de dépendance spatiale de ces processus et leurs effets sur la variabilité spatiale du zooplancton n'ont jamais été étudiés. Dans cet article, nous rapportons les études actuelles sur la variabilité spatiale du zooplancton et sur les processus impliqués, dans les environnements marins côtiers. Notre objectif est de souligner l'importance de l'échelle et de l'approche multiéchelle pour l'étude de la variabilité spatiale du zooplancton et de promouvoir de telles études pour comprendre la dynamique du zooplancton, son interaction avec les autres organismes planctoniques et nectoniques et par conséquent, les implications dans la structure et le fonctionnement des écosystèmes tropicaux côtiers.

4.2 Article 2 : Coastal Tropical Zooplankton : Patterns and Processes over Spatial Scales (soumis à *Coral Reefs*)

Abstract – Previous studies on the abundance/biomass and species distributions of coastal tropical zooplankton have been done at a few stations, making them unsuitable to study spatial patterns. Whereas several physical and biological processes have been found to generate and

maintain the spatial patterns of coastal tropical zooplankton, the scales of spatial dependency of these processes and their effects on zooplankton spatial variability have not been investigated. In this paper, we review current research on zooplankton spatial structure and the invoked generating processes in marine coastal environments. Our aim is to highlight the importance of scale, and of a multiscale approach for the study of zooplankton spatial variability, and promote arguments supporting this type of study to understand community dynamics and the interaction of zooplankton with other planktonic and nektonic compartments — and, as a result, the implications for the structure and function of coastal tropical ecosystems.

Introduction

Marine zooplankton is one of the most abundant and widely distributed forms of life on earth. Like all ecological entities, zooplankton exhibit spatial patterns — the non-random spatial variability of populations or communities — over a broad range of spatial and temporal scales (Haury et al. 1978; Mackas et al. 1985; Legendre et al. 1986; Pinel-Alloul 1995; Currie et al. 1998). According to Longhurst (1981), zooplankton patchiness is a necessary condition for life in the aquatic environment and it is probably the most fundamental reason why the mechanisms controlling zooplankton spatial structures are being studied. Several investigations have highlighted environmental processes that generate and maintain the spatial patterns of marine zooplankton. These processes are of two types: i) physical processes mainly generated by climatic and hydrodynamic regimes, associated with bottom topography (Haury et al. 1978; Denman and Powell 1984; Davis et al. 1991; Piontkovski et al. 1995b; Leising and Yen 1997; Noda et al. 1998; Huntley et al. 2000; Roman et al. 2001), and ii) biological processes (Hamner and Carleton 1979; Haury and Wiebe 1982; Mackas et al. 1985; Tiselius 1992; Ribes et al. 1996; Buskey 1998; Folt and Burns 1999; Rollwagen-Bollens and Landry 2000; Bullard and Hay 2002). All physical and biological processes take place at preferential spatial and temporal scales (Haury et al. 1978; Legendre et al. 1986), generating multiscale spatial and temporal variability of zooplankton (Haury et al. 1978). The scales of patterns and processes depend on both the organisms themselves, which experience the environment over a unique range on scales (Denman and Platt 1975; Legendre et al. 1986; Levin 1992), and the physical and biological processes which vary with scale (Haury et al. 1978; Legendre and Demers 1984; Pinel-Alloul 1995). Because zooplankton patterns and environmental processes are ‘scale-dependent’ phenomena, considering the spatial scale is a requirement to examine zooplankton spatial variability and understand its controlling mechanisms. Zooplankton spatial patterns lead researchers to focus on scale and the multiscale variability of zooplankton leads to adopt a multiscale approach.

Recently, some investigations on zooplankton variability have adopted a multiscale approach; these studies have focussed on temperate and tropical oceanic areas (Pascual et al. 1995; Piontkovski and Williams 1995; Seuront and Lagadeuc 2001). Although zooplankton inhabiting coastal tropical waters has been the topic of numerous investigations, the emphasis has been placed on growth rates and production of copepods (Le Borgne et al. 1989; Chisholm and Roff 1990; McKinnon and Thorrold 1993; Hopcroft et al. 1998a, b), diel vertical migrations (Alldregde and King 1980; Robichaux et al. 1981; Ohlhorst 1982; Walters and Bell 1986, 1994), seasonal or annual variability (Moore and Sander 1979, Youngbluth 1980; Lewis and Boers 1991; Zaballa and Gaudy 1996; Rios-Jara 1998), and species composition (Emery 1968; Hamner and Carleton 1979; Alvarez-Cadena et al. 1996, 1998). These investigations studied zooplankton communities of different coastal tropical habitats such as coral reefs (Emery 1968; Moore and Sander 1976; Hamner and Carleton 1979; Ohlhorst 1982; Lewis and Boers 1991; Leichter et al. 1998; Suárez-Morales and Gasca 2000), seagrass beds (Youngbluth 1980; Walters and Bell 1986, 1994; Connolly 1997; Rios-Jara 1998; Bullard and Hay 2002), and mangroves (Youngbluth 1980; Ambler et al. 1991). They highlighted the critical role of zooplankton for the nutrition of many invertebrates and reef fish (Emery 1968; Hamner and Carleton 1979; Alldredge and King 1980; Robichaux et al. 1981; Noda et al. 1998), coral species (Hamner et al.

1988), carnivorous zooplankters (Moore and Sander 1979), and as a vehicle for energy transfer and recycling of material on reef flats (Roman et al. 1990) and within lagoons (reviewed by Bishop and Greenwood 1994). It is likely that zooplankton is the main source of prey for reef inhabitants in tropical coral reefs, rather than phytoplankton (Hamner et al. 1988; Erez 1990; Sebens 1997), although substantial feeding on ultra- and picophytoplankton has been observed by soft-coral species (Yahel et al. 1998 and references therein). Due to their abundance and distribution in oceanic and coastal waters, zooplankton species are important indicators of water masses (Webber et al. 1992, 1996). Copepod production in coastal tropical waters is equivalent to that of temperate coastal waters (Chisholm and Roff 1990), and some recent studies have also shown the importance of nauplii and copepodites in terms of abundance and production (Hopcroft et al. 1998a, b). Even if biomass in tropical systems is lower than in temperate waters, these differences are offset by higher growth rates in tropical areas (Hopcroft and Roff 1998, Hopcroft et al. 1998a). Not only do nauplii have a central role in secondary production in tropical systems, but also they may be critical intermediaries between the classical (= grazing) food web and the microbial loop (Roff et al. 1995).

Ecologists recognize the important implications of spatial structures of coastal tropical zooplankton to understand zooplankton dynamics and their interactions with other planktonic and nektonic compartments through reproduction (Hamner and Carleton 1979; Haury and Wiebe 1982), population dynamics (Alldredge and King 1980; Robichaux et al. 1981; Fiedler 1983; Noda et al. 1998), prey-predator interactions (Emery 1968; Youngbluth 1980; Hamner and Carleton 1979; Ribes et al. 1996), coral reef dynamics (Le Borgne et al. 1989; Sorokin 1993). Sampling strategies at the population and community levels should also depend on the anticipated spatial structures (Hamner and Carleton 1979; Omori and Hamner 1982; Yoshioka et al. 1985). Most previous studies on the spatial distribution of zooplankton abundance, biomass, and species (Champalbert 1993; Alvarez-Cadena and Segura-Puertas 1997; Carleton and Doherty 1998; Rios-Jara 1998; Suárez-Morales and Gasca 2000) have been done at a few stations only, making them unable to clearly establish the spatial structuring of zooplankton. High variation observed in the data suggest, however, strong spatial variability of zooplankton communities in coastal tropical waters that forces researchers to adopt high-resolution sampling in order to efficiently establish the multiscale spatial structuring of coastal tropical zooplankton.

Zooplankton associated with coastal tropical environments displays ecological features that diverge from associations in temperate areas and surrounding waters. Temperate regions are characterized by extreme seasonal fluctuations of temperature and phytoplankton concentrations, either or both of which may control the rate of secondary production. In tropical areas, seasons are difficult to predict and are usually less pronounced, compared to temperate zones (Webber and Roff 1995). The seasonal variations in sea temperature are slight, and the annual fluctuations are generally related to the rather variable pattern of annual rainfall (e.g. Yoshioka et al. 1985), especially in coastal tropical regions (e.g. Chisholm and Roff 1990). The strong variations in rainfall define two periods referred to as the dry and wet seasons, they influence coastal water flood in aquatic systems as well as surface layer salinity (Yoshioka et al. 1985; Webber et al. 1992). Tropical oceanic waters are generally considered to be a fairly stable environment, only characterized by small seasonal changes in physical and chemical variables, where low seasonal amplitudes of variation of biomass and production are recorded (Hopcroft and Roff 1990; Champbell et al. 1997). In contrast, coastal tropical plankton may show great ecological fluctuations caused by the impact of seasonal variation in meteorological events, including wind-induced currents and rainfall patterns (Youngbluth 1980; Yoshioka et al. 1985; Chisholm and Roff 1990; Hopcroft and Roff 1990; Rios-Jara 1998). Both coastal and oceanic influences, regulated by meteorological events, contribute to affect the stability of phytoplankton (Hopcroft and Roff 1990) and zooplankton communities (Webber et al. 1992, 1996; Rios-Jara 1998). Like the coastal and oceanic influences (Webber et al. 1992, 1996; McKinnon and Thorrold 1993; Rios-Jara 1998), the behaviour of coastal tropical zooplankton (Emery 1968; Alldredge and King 1980), zooplankton swarming behaviour involved in feeding, predation, reproduction (Emery

1968; Hamner and Carleton 1979; Ambler et al. 1981; Le Borgne et al. 1989; Lewis and Boers 1991; Alvarez-Cadena et al. 1998), island mass effect (Moore and Sander 1979; Alvarez-Cadena et al. 1998; Hassett and Boehlert 1999), and habitat heterogeneity (Hamner and Carleton 1979; Omori and Hamner 1982; Conolly 1997; Alvarez-Cadena et al. 1998; Rios-Jara and Gonzalez 2000) are susceptible to explain species associations and organism distribution of zooplankton. These phenomena occurring in the coastal tropical ecosystems lead to assume that zooplankton communities present in such ecosystems are not spatially controlled by the same physical and biological processes as in temperate and tropical oceans. Thus the environmental mechanisms controlling the spatial structure of zooplankton cannot be simply extrapolated from temperate and tropical oceanic areas to coastal tropical regions.

Coastal tropical reef lagoons are both of fundamental and practical interests. They constitute a physical, chemical and biological interface between the marine and coastal systems, and they are very vulnerable to natural disturbances and human activities. Reefs occupy less than 0.2% of the world's ocean, but they provide 25% of the fishery catch in developing countries (Sale 1999). Reef environments generate substantial and growing incomes through tourism and they protect coastal environments from storms and marine erosion. These important economic and ethical values all require that these ecosystems be managed. This is particularly true when considering that coral reefs are more and more degraded and strongly affected by natural disturbances (i.e. hurricanes and diseases), and human activities including over-fishing, construction, pollution, and perhaps global warming (Hughes 1994; Sale 1999). One of the main consequences of these disturbances is a drastic and dramatic shift from systems dominated by coral species to systems dominated by macroalgae (Hughes 1994). The relationship between disturbance and species diversity, and many recent studies of physical disturbance in reef ecosystems (see in Hughes 1994), all recognize the fundamental importance of temporal and spatial environmental variability. Sea grasses provide another example of the impacts of natural disturbances and human activities. They often are the dominant subtidal vegetation in nearshore coastal marine environments and support large standing crops and high species diversity of organisms (e.g. Eggleston et al. 1998). Seagrass beds exhibit natural expansion, fragmentation and contraction due to seasonal growth, die-off, feeding activities of epibenthic predators and herbivores, and storm events, but also anthropogenic impacts (e.g. damage by boat propellers and dredging; Eggleston et al. 1998). These phenomena cause spatial and temporal changes not only to the distribution of seagrass beds but also, and as a consequence, in the distribution of species within and around seagrass meadows (Walters and Bell 1994; Connolly 1997). If there is pressing need to monitor coastal tropical ecosystems to assess the spatial and temporal scales of any potential damage (i.e. natural disturbances and human activities) that may occur in these important ecological, social, and economical areas, the study of the multiscale spatial structure of coastal tropical zooplankton is fundamental to understand the population dynamics of the various species and their interactions with other planktonic and nektonic compartments, which have implications on the structure and function of coastal tropical ecosystems. Such investigations may aid to determine, for example, the extent of water quality deterioration (bottom-up effect) or over-fishing impact (top-down effect).

Whereas several physical and biological processes have been suggested to explain the generation and maintenance of spatial patterns of coastal tropical zooplankton, the scales of spatial dependency of zooplankton spatial patterns and its controlling mechanisms have not been investigated. In this paper, we review current research on zooplankton spatial structures and generating processes in coastal ecosystems. Our aim is to highlight the role of scale, and of the multiscale approach, in the study of zooplankton spatial patterns, and to promote arguments supporting such studies for the conservation and management of coastal tropical ecosystems.

Spatial patterns of coastal tropical zooplankton

Patches, density gradients, aggregations, swarms and schools, all refer to spatial patterns.

Patches – 'Patchiness' is generally used to describe aggregation at horizontal scales between approximately 10 m and 100 km and at vertical scales between 0.1 and 50 m (Mackas et al. 1985). Such variability is encountered in coastal tropical zooplankton communities for biomass and abundance (Youngbluth 1980; Yoshioka et al. 1985; Piontkovski et al. 1995a; Rios-Jara 1998) as well as species composition (Moore and Sander 1976, 1979; Webber et al. 1996; Alvarez-Cadena et al. 1998).

Gradients – Most studies have shown a decreasing gradient in tropical zooplankton biomass/abundance and an increasing gradient in species number from the coasts to the open ocean (Moore and Sander 1976, 1979; Youngbluth 1980; Alvarez-Cadena et al. 1998; Hassett and Boehlert 1999; Avois-Jacquet et al. submitted a, b). Moore and Sander (1976) described these gradients as the result of the 'island mass effect' that corresponds to local enhancement of productivity due to interactions between islands and the surrounding ocean waters. Gradients of abundance/biomass and richness are of great interest because important ecological processes are responsible for this pattern. Various mechanisms have been proposed to explain this phenomenon, including tidal-induced mixing, internal waves (Leichter et al. 1998), wind-induced current (Alvarez-Cadena et al. 1998), benthic interactions (Dandonneau and Charpy 1985), zooplankton behaviour such as diel vertical migrations (Hassett and Boehlert 1999), and phytoplankton distribution (Moore and Sander 1979; Webber et al. 1992; Rios-Jara 1998; Avois-Jacquet et al. submitted a, b). Zooplankton variability in coastal tropical waters is generally associated with changes in phytoplankton standing stocks (Rios-Jara 1998) and with the combined effects of regional climate (Yoshioka et al. 1985; Rios-Jara 1998) and local patterns of water movements (Youngbluth 1980; Webber et al. 1996). Fluctuations in zooplankton abundance and biomass are closely related to the rainfall pattern, which is a proxy for nutrients inputs from land drainage and the consequent increase in phytoplankton productivity (Hopcroft and Roff 1990; Webber et al. 1992). Wind direction and intensity associated with shallow waters may also explain the decreasing gradient of zooplankton biomass and abundance (Avois-Jacquet et al. submitted a, b). It may be responsible for an accumulation of organisms towards the coast and circulation of oceanic fauna within the lagoon (Alvarez-Cadena et al. 1998). This assumes, however, that zooplankters are either passive drifters or have limited mobility; this is the case for meroplankton which is more influenced by currents than holoplankton (Youngbluth 1980; Rios-Jara 1998) and small mesozooplankton (Avois-Jacquet et al. submitted a, b). In coastal reef lagoons, grazing and predation over the reef barrier may accentuate the zooplankton and phytoplankton decreasing gradients from the coast to the open sea. In coral reefs, zooplankton is a major prey for reef fish (Emery 1968; Hamner and Carleton 1979; Alldredge and King 1980; Robichaux et al. 1981; Noda et al. 1998), coral species (Hamner et al. 1988), and coral reef inhabitants (Erez 1990; Sebens 1997); a phytoplankton-depleted layer is commonly found above the reef slope. Several members of the coral-reef community are known to feed on particles within the size range of phytoplankton: bivalves, gastropods, sponges, and soft corals (Pile et al. 1996; Yahel et al. 1998). Moreover, carnivorous zooplankton like siphonophors, chaetognaths, amphipods, euphausids, and copepods are more abundant offshore than inshore (Moore and Sander 1979).

Swarms – Swarming (Haury and Yamazaki 1995; Leising and Yen 1997) is another type of spatial patterning encountered in coastal tropical zooplankton. Swarming appears to be widespread among tropical copepods (Emery 1968; Hamner and Carleton 1979; Le Borgne et al. 1989; Ambler et al. 1991; McKinnon 1991), which compose up to 75 % of the total zooplankton abundance (Moore and Sander 1979) and constitute the dominant group of metazoan secondary producers (Chisholm and Roff 1990; Hopcroft et al. 1998b). Swarms have been observed to range in size from a few cubic meters to more than 60 m^3 (e.g. *Acartia spinata*, *Oithona oculata*) in the coral reef spur and groove formations, inside coral caves, or near coral heads (Emery 1968; Hamner and Carleton 1979). Swarming is one example of complex behavioural adaptations that have evolved in resident plankton species to survive within the reef ecosystems (Hamner and Carleton 1979). It provides compelling evidence for biologically driven and maintained patchiness (Folt and Burns 1999). Swarms are formed and maintained as the result of individual behaviour such as predator avoidance, which is the most common adaptive explanation for the swarming of copepods, food exploitation, and social interactions including mating encounters. Subdividing the population into swarms is an evolutionary response by demersal organisms with a highly patchy distribution preferential protection from predation (Hamner and Carleton 1979). Because they are always located slightly above the bottom, swarms are not available to benthic filtering feeders;, protection against predators is reinforced by water coloration, which decreases visibility. Swarming behaviour may also reduce the rate of predation on egg-bearing females which represent large, high-contrast targets to planktivorous fish (Buskey 1998). These forms of behaviour are usually accompanied by a tendency to aggregate in more compact swarms during daytime (at dawn) and to disperse at dusk, which also results in reduction of predation (Hamner and Carleton 1979; Omori and Hamner 1982; Ribes et al. 1996). Swarming enhances copepod mating encounter and success, bringing together adult males and females in high concentrations (Buskey 1998). For example, *Dioithona oculata*, which commonly forms swarms in mangroves and coral reefs, exhibits a diel behavioural pattern that allows individuals to synchronize their mating and reproductive behaviour to the daily pattern of swarm formation and dispersal (Ambler et al. 1991). Swarming may also result from an attempt to maintain a favourable position into the ecological niche: swarming permits copepods to cluster in local eddies, thereby restricting dispersion by currents and reducing the energy required to maintain a favourable position in food patches. Swarms of *A. tonsa*, *A. spinata*, and *Oithona nana* were observed in tropical seagrass beds, in which copepods were able to maintain their positions in waves and against currents (Emery 1968). *Acartia tonsa* does not store energy reserves (i.e. lipids) and thus has adapted to maintain itself in food patches by decreasing its motility and swimming horizontally (Tiselius 1992). Zooplankters capable of maintaining themselves within their habitat form a ‘stationary community’ (i.e. resident) which shows a tendency towards epibenthic behaviour (Emery 1968; Hamner and Carleton 1979). Swarming behaviour is important to understand the generation and maintenance of spatial variability, and it must be viewed as a biological mechanism to be studied in order to understand zooplankton patchiness.

In coastal tropical waters, strong spatial patterning of zooplankton is therefore expected, but remains to be unambiguously demonstrated. One problem in the investigation of the spatial variability of zooplankton is linked to the characteristics of species. These characteristics are directly linked to their life cycle, origin, and behaviour in response to the environment. For example, on exposed coastlines, the resistance to wave forces is a strong selective force determining the morphology as well as some of the life history characteristics of coastal species (Barry and Dayton 1991). The complexity of zooplankton communities is reflected in the diversity of definitions used by authors to identify types of zooplankton in coastal tropical environments. The differences concern the definitions of 'meroplankton', 'demersal plankton' and 'epibenthic plankton'. Some authors have used the term 'meroplankton' to characterize the organisms living one part of their diurnal cycle in or on the substratum (Robichaux et al. 1981). This definition refers to the 'demersal plankton' of other authors (Alldredge and King 1980; Ohlhorst 1982). For Robichaux et al. (1981), 'demersal' is equivalent to 'epibenthic', namely organisms going occasionally into the water column. For these authors, the distinction between 'meroplankton' and 'demersal' is based on the frequency and regularity with which the organisms enter the water column and become available to fixed and pelagic predators and suspensivores. For others, the 'epibenthic' species (i.e. organisms living near the bottom) may be demersal by conducting nycthemeral migrations (Emery 1968; Alldredge and King 1980; Ohlhorst 1982, Sorokin 1993). For Emery (1968), zooplankton can be characterized according to its origin and orientation behaviour; there is a 'behavioural continuum' from planktonic to epibenthic, and an 'origin continuum' from oceanic to endemic. For example, the transient holoplankton (i.e. non-localized) is highest in the water column, whereas the epibenthic holoplankton is lowest, very local (i.e. resident or endemic), and forming swarms partly tied to local topography. From the concepts of behavioural and origin continuum, two main groups of organisms can be distinguished: ‘planktonic-oceanic’ and ‘epibenthic-endemic’.

The flexibility of these definitions is directly linked to the environment in which zooplankters live. Shallow depths often characterize the coastal reef lagoons and the movements of water induced by wind and/or tide produce remarkable currents, especially in shallows, which are very efficient in mixing as well as transporting water and plankton (Sorokin 1993). As a result, it becomes difficult to make a clear distinction between the ‘epibenthic’ and ‘planktonic’ (*sensu stricto*) organisms, and between migrant and non-migrant species. This difficulty is also linked to the sampling techniques. Numerous studies have experienced difficulties and led to qualitative and quantitative errors due to the sampling methods used in lagoons and coral reefs (Hamner and Carleton 1979; Robichaux et al. 1981; Omori and Hamner 1982; Walters and Bell 1986). Nets cannot be towed from boats close to the coral without entanglement and tears, and this is a poor tool for discrete local sampling. Some techniques are efficient in these types of environment, including suction devices and plankton traps (Emery 1968; Robichaux et al. 1981; Walters and Bell 1986, 1994), although they were originally developed to study benthic and epibenthic communities. Plankton pumps may bring about some problems when collecting of zooplankton: (e.g. damage or destruction of organisms, differential avoidance of the pump intake by plankton (Taggart and Leggett 1984), but they present several advantages (Miller and Judkins 1981; Taggart and Leggett 1984; Rahkola et al. 1994), including sampling at biologically relevant time and space scales. The greatest advantage in lagoon and barrier reef ecosystems is that the plankton pump may be used in all types of habitats (i.e. shallows, seagrass beds, barrier reef and cays), which is preferable for data comparison and interpretation. However, the increasing awareness that time and space scales involved in sampling zooplankton (Steele 1978; Haury and Wiebe 1982; Fiedler 1983) must be appropriate to the biological processes being investigated has highlighted the deficiencies of standard plankton sampling gears, i.e., nets and pumps (Omori and Hamner 1982), especially when high-frequency sampling of discrete water masses is required. During the last two decades, three advanced sampling techniques have been developed, which solve some problems linked to spatial scales (e.g. limitation of the size of sampling grain and/or of the sampling extent). These techniques are: i) particle sizing/counting instruments, including the optical plankton counter (OPC; Herman 1992) and the dual light sheet sensor (DLS; see in Sutton et al. 2001); ii) optical sensors, including the video plankton recorder (VPR; Davis et al. 1992a), the in situ video camera (Tiselius 1998), and the shadow image particle profile evaluation recorder (SIPPER; see in Sutton et al. 2001); and iii) multiple-frequency acoustic sensors (Sameoto et al. 1993; Greene et al. 1998; Swartzman et al. 1999; Coyle 2000). Although each of these techniques has limitations (see in Williamson et al. 1992; Pinel-Alloul 1995; Folt and Burns 1999), they permit to acquire continuous in situ data, and/or to rapidly cover large surface areas without compromising high-resolution data at small spatial scales. However, these high-technology methods are difficult to apply or are inapplicable at the moment in coastal tropical environments, due to shallow areas and topography (e.g. barrier reef). More efforts must be made to develop new sampling techniques adapted to coastal tropical waters, that will help identify the spatial patterns of zooplankton in different habitats and will advance our understanding of the physical and biological processes responsible for the spatial patterns observed in zooplankton.

Physical processes producing spatial patterns in zooplankton

Patterns of marine zooplankton patchiness are mostly linked to physical processes generated mainly by climatic and hydrodynamic regimes, including tidal and regional wind forces (Haury et al. 1978; Denman and Powell 1984; Legendre and Demers 1984; Mackas et al. 1985; Davis et al. 1991; Piontkovski et al. 1995b; Leising and Yen 1997; Noda et al. 1998; Huntley et al. 2000; Roman et al. 2001), associated with the bottom topography (Genin et al. 1988; Blanchard and Bourget 1999; Guichard et al. 2001). In coastal reef lagoons, the cross-shelf transport—the exchange of water between the coastal and offshore environments—plays a major role in structuring zooplankton communities. The relationships between coastal reef lagoons and ocean are a function of climatic, hydrological and geomorphological factors. Water residence time in a lagoon depends on the amplitude of tides, the characteristics of currents, and lagoon morphology (Sorokin 1993). The dominant winds, which influence local hydrodynamics in various ways depending upon their direction, orientation and speed, modify water flow in the surface layer of the lagoon (Renon 1978). The barrier reef morphology plays an important role in the speed of oceanic water flow entering the lagoon (Sorokin 1993). Water exchange between the lagoon and surrounding water masses proceeds via surface hydrodynamics; ground water reaches the lagoon through the porous reef walls. Consequently the physical and chemical characteristics of oceanic water are modified when crossing the reef ecosystem (Renon 1978). Oceanic currents, local tidal- and wind-driven surface currents cause a permanent flow of plankton over and through the barrier reef and constitute one of the most important processes driving trophodynamics in reef ecosystems (Le Borgne et al. 1989; Sorokin 1993). Internal tidal bores, generated by breaking internal waves, have been identified as another mechanism of cross-shelf transport of cool, sub-surface water to several habitats, including the outer slopes of coral reefs (Leichter et al. 1998). The arrival of internal bores on the reef slope may affect the supplies of food particles to suspension feeders, dissolved nutrients to corals and benthic algae, and planktonic organisms to benthos. By transporting and redistributing organic matter and plankton inside the reef system and the lagoon, oceanic currents provide an energetic interconnection between different biotopes and different sites of the coastal reef lagoon (Sorokin 1993).

Like atolls, reef lagoons may be defined as systems composed by a ‘reef ecosystem’ and a ‘lagoonal ecosystem’, the whole functioning in a field of energy flux coming from the neighbouring oceanic ecosystem (Michel et al. 1971). In coastal reef lagoons, however, Renon (1978) showed the existence of a lagoonal differentiation generated by oceanic and coastal influences. Since coastal contributions represent a vector of energy for the planktonic communities in coastal reef lagoons, this ecosystem obtains a portion of its energy from the reef and oceanic ecosystems, and another portion from the coastal ecosystem. Their respective contributions depend on the importance of the oceanic and coastal influences, which may vary accordingly to rainfall, lagoon and barrier-reef morphologies, wind, tide, and currents. In response to environmental features, zooplankton populations display differences between areas influenced by fresh water input and those influenced by the open sea (Moore and Sander 1979; Webber et al. 1992, 1996). Hence, in coastal tropical waters, changes in part of or in the whole zooplankton community are likely to occur in response to changes in any part of the system.

Zooplankton patterns have been reported as being closely related to bottom topography and the type and structure of habitat with which they are associated. Irregular bottom topography associated with water flow is an important agent generating zooplankton patchiness (Denman and Powell 1984; Genin et al. 1988). Since the depth, the configuration of the coastline, and the topography of the bottom influence the direction and speed of water flow, they also cause local disturbances that affect the structure of zooplankton communities. For example, the configuration of the shoreline may induce regional zooplankton patchiness when water moves out of embayments (Genin et al. 1988). Most zooplankton species are intimately associated with their coastal tropical habitat (Alvarez-Cadena et al. 1998; Rios-Jara 1998; Suàrez-Morales and Gasca 2000), including coral reefs (barrier reefs, patch or platform reefs), cays (keys), seagrass beds, and mangroves in intertidal mud flats. The type and structure of habitat may influence community structure by modifying diversity (Eggleston et al. 1999), biomass (Rios-Jara 1998; Avois-Jacquet et al. submitted a), and distribution and abundance of organisms (Eggleston et al. 1998; García-Charton and Pérez-Ruzafa 1998; Avois-Jacquet et al. submitted b). Habitat is also known to affect many ecological processes, including predation intensity (González and Tessier 1997), predation avoidance (Alvarez-Cadena et al. 1998), and larval dispersal and recruitment (Eggleston et al. 1998; Jenkins et al. 1998). Coral reefs are complex formations with many convolutions that increase spatial heterogeneity, microhabitat variety, and refuges from predation (Sorokin 1993). Seagrass beds are well known to support enhanced species richness, abundance, and productivity of invertebrates compared to unvegetated habitats (Alvarez-Cadena et al. 1996; Conolly 1997 and references therein), because of the availability of food and refuges from predation (Edgar 1999). Planktivory by fish may be intense; it can affect zooplankton and larval abundance as water masses pass over reefs or through seagrass beds (Bullard & Hay 2002). The widespread incidence of defense and escape behaviour among resident reef and seagrass zooplankters suggests that planktivory may act as a significant selective force in these habitats (Bullard & Hay 2002). This may explain the differences in zooplankton biomass and abundance between the barrier reef and the seagrass beds (Avois-Jacquet et al. submitted b). It was also reported that swarm size, structure, and distribution are adapted to habitat topography (Hamner and Carleton 1979; Omori and Hamner 1982), whereas substratum heterogeneity enhances the density of organisms on the bottom (Rios-Jara and Gonzalez 2000). In reef lagoons, most harpacticoids remain on the bottom, where they are very diversified and constitute distinct communities associated with the types of sediment to which they are adapted (Villiers and Bodiou 1996). However, the nature of the substratum and the type of habitat may alter zooplankton swarming. Near patch reefs within lagoon, copepods may be found individually or in small swarms (Emery 1968). In these areas, often characterized by shallow waters, zooplankton is strongly affected by wind and tidal effects that are not favourable to the maintenance of aggregation.

Another physical factor considered as a primary stimulus for swarming behaviour is the occurrence of sharp spatial gradients in light intensity (Buskey et al. 1995; Leising and Yen 1997). This type of swarm induction has been observed above coral reefs that reflect light more than the surrounding water and over white substrates (Hamner and Carleton 1979), as well as beneath and between mangrove roots where *Dioithona oculata* uses light cues, such as shafts of light penetrating the mangrove canopy, as areas for swarm formation (Ambler et al. 1991). Light intensity and gradients of light intensity serve as proximal cues for swarm formation, which results from photoreception, including phototactic and klino-kinetic behaviour (Buskey et al.

1995), and photosensitivity (Hamner and Carleton 1979; Buskey et al. 1995). However, the effect of light on the formation and maintenance of patches appears to be better understood in combination with tides, predators, and endogenous rhythms (Buskey et al. 1995).

Turbulent mixing is one important process observed in aquatic environments. Although a considerable fraction of the energy present in waves and tides is dissipated in the coastal zone, which means that turbulent mixing is generally enhanced in nearshore ecosystems (Petersen et al. 1998), these effects have not been studied on coastal tropical zooplankton. Turbulence is increasingly mentioned as a key factor regulating zooplankton dynamics at the population and community levels of organization (Davis et al. 1991). Turbulence in the flow field, resulting from wind-induced currents and tidal advection, affects zooplankton behaviour (Saiz 1994; Kiørboe and Saiz 1995; Saiz and Kiørboe 1995; Caparroy et al. 1998; Visser et al. 2001) and has been associated with changes in zooplankton vertical/horizontal distributions (Haury et al. 1990; Hill 1991; Mackas et al. 1993; Incze et al. 2001). Turbulence creates and disturbs high-density patches of organisms, and transports plankton away from their sites of growth or production (Peters and Marrasé 2000). Investigations on copepods indicate a positive relationship between the degree of fine-scale turbulence and metabolic rate, and a negative relationship between turbulence and abundance/biomass (see review in Petersen et al. 1998). Since turbulence is ubiquitous and inherently variable, and organisms typically experience a wide range of degrees of turbulence in any habitat (Petersen et al. 1998; Incze et al. 2001), a better understanding of zooplankton responses to changing turbulence is needed in order to predict and interpret patterns and their biological consequences.

What are the most important biological processes inducing spatial patterns in zooplankton?

While physical processes alone are insufficient to explain most spatial patterns of zooplankton, biological processes are considered to contribute significantly to zooplankton patchiness.

Strutton et al. (1997) showed that broad-scale horizontal (100 km) chlorophyll patchiness was better explained by local primary production than passive aggregative processes. Wiafe and Frid (1996) reported that zooplankton community patches persisted for three hours during horizontal transfer despite periods of turbulent mixing; only 52% of the spatial variation in community structure was attributable to physical transport. The remaining variance was ascribed to behavioural processes (predation and food searching) capable of countering dissipative physical forces. Zooplankters were commonly referred to as ‘passive drifters’ (Castel and Veiga 1990) based on the widely held belief that they are unable to swim against water currents and thus are passively transported. However, evidence for considering the zooplankton as ‘active drifters’ has been provided by Davis et al. (1992b) with *in situ* video images that showed actively swimming zooplankton exhibiting 20-cm scale aggregated patches within a turbulent flow field.

New studies about fine-scale biological processes (Tiselius 1998) have altered our perception of the behavioural capacity and flexibility of zooplankton. They also grappled with the quantitative assessment of the relative contributions of biology and physics to patchiness (Lewis and Boers 1991; Pinel-Alloul 1995; Alvarez-Cadena et al 1998), and the extent to which biological processes counteract physical drivers (Folt and Burns 1999). Over scales from 1 to a few kilometres, biological processes (e.g. vertical migration) may combine with physical processes (e.g. currents) to create zooplankton patchiness (Hill 1991; Smith et al. 2001). Over finer scales (1 mm to 10 m), individual behaviour may be crucial and capable of overriding physical processes (Emery 1968; Hammer and Carleton 1979; Lewis and Boers 1991; Alvarez-Cadena et al. 1998). For example, swarming behaviour permits copepods to cluster in local eddies, thereby restricting their dispersion by currents.

Four biological processes associated with underlying individual behaviour, which are likely to be species-specific and differ among taxa and life stages (Ohlhorst 1982; Bollens and Frost

1991; Folt et al. 1993; Rios-Jara and Gonzalez 2000), are often cited for their potential responsibility for zooplankton patchiness:

• ‘Diel vertical migration’ (DVM) is one of the most widespread and powerful biological causes of patchiness (Folt and Burns 1999). Several physical or biological factors can alter DVM behaviour and patterns, including feeding, mating, dispersal, light intensity, tidal and diurnal periods, current velocity, and turbulence (Alldredge and King 1980; Ohlhorst 1982; Walters and Bell 1986, 1994; Incze et al. 2001). Even so, DVM in zooplankton is primarily a predator-avoidance behaviour (Bollens and Frost 1991).

• ‘Predator avoidance’ can create patchiness in prey spatial distributions directly by removing individuals. Indirectly, by eliciting avoidance or escape responses, predators can have even greater effects on zooplankton distributions, for instance by triggering DVM which, in turn, results in broad-scale aggregative patterns (Folt et al. 1993). Many reef and seagrass zooplankton species possess traits such as demersalism (Emery 1968; Robichaux et al. 1981; Lewis and Boers 1991; Walters & Bell 1994), schooling or swarming behaviour (Emery 1968; Hamner & Carleton 1979; Le Borgne et al. 1989; Ambler et al. 1991; McKinnon 1991), chemical defenses (Poulet & Ouellet 1982), or rheotactic abilities (hydromechanical signals; Visser 2001), which reduce their susceptibility to planktivorous fish.

• ‘Locating food patches’ is another mechanism explaining zooplankton patchiness. Aggregation in micropatches of food may be a strong driver of zooplankton patchiness (Hamner and Carleton 1979; McKinnon 1991; Franks and Jaffe 2001), and several processes may concentrate zooplankton in regions of high food density (Yen et al. 1998). Physical mechanisms may aggregate zooplankton with algae passively, particularly if the organisms are similar in shape, buoyancy or motility, and when physical processes overwhelm zooplankton locomotion. Aggregation may also result when individuals use similar behaviour to locate, or remain in, food patches. For example, the copepods *Acartia tonsa* were able to remain in food patches by a combination of decreased motility and horizontal swimming direction (Tiselius 1992). At the edge of the food patch, the copepods were able to detect a decrease in food concentration, and they responded by turning back into food patch. At different food concentrations, copepods change swimming speeds, turning angles or hopping rates, and actively locate and remain within food patches. However zooplankton behaviour with respect to food patches is often moderated or eliminated when predators are present. Tiselius (1992) showed that the presence of a predator reduces the amount of time the copepod *Acartia tonsa* remains in food patches. This might lead to the lack of correlation between spatial distributions of zooplankton and phytoplankton in the presence of predators (Folt and Burns 1999). While numerous laboratory experiments have been performed examining the behavioural response of herbivores to patchiness of phytoplankton (e.g. Tiselius 1992), little in situ work has been done.

- Finally, ‘mating behaviour’ is another powerful biological process for aggregation. For some zooplankton species, mating often depends entirely on chance encounters in patches generated by broad-scale physical processes and migrations (Folt and Burns 1999). On the other hand, other species including many copepods locate mates over small distances by mechanoreception, following fluid disturbances produced by species-specific mating behaviour, and by chemoreception (the most likely sensory modality to be used in mate recognition) using water-borne pheromone trails (Buskey 1998). One behavioural mechanism that increases encounter rates between male and female copepods is swarm formation. Swarming behaviour provides enhanced opportunities for mating; swarms clearly enhance the encounter portion of mating behaviour by bringing adults together and at high densities (see in Buskey 1998).

Neither the physical nor the biological forces alone can explain the complexity of zooplankton spatial heterogeneity. Individuals of any species encounter a profusion of environmental constraints, including those related strictly to physical features and those associated with biological entities or processes. The physical and biological mechanisms that cause zooplankton spatial patterns, whose relative importance should be estimated, refer to the ‘multiple driving forces hypothesis’ (Pinel-Alloul 1995). The importance of these processes may be viewed as corresponding to a gradation across scales, with physical effects predominating at broad spatial scales, while biological effects predominate at finer scales.

Relationships between patterns, processes and scales

Scales and patterns are ineluctably intertwined. The description of pattern is the description of variability, and the quantification of such variability requires the determination of scales. Patterns of zooplankton patchiness have been observed at different spatial scales (Haury et al. 1978; Mackas et al. 1985; Legendre et al. 1986; Pinel-Alloul 1995; Piontkovski and Williams 1995; Currie et al. 1998), patch size varying from a few centimetres (micro-scale: 1 cm–1 m) to thousands of kilometres (mega-scale: 1000–10000 km). However, the spatial scales of variability for zooplankton community composition and abundance/biomass (as well as phytoplankton community composition and biomass) differ (Mackas et al. 1985; Powell 1989). A large amount of variability in zooplankton biomass can occur within the confines of a fairly uniform community patch. This implies that the dominant patch generation processes differ across spatial scales for species composition versus abundance/biomass. Salas-de-Leon et al. (1998) showed that zooplankton biomass is affected by river inputs through nutrient run-off and upwelling, whereas the spatial variability of zooplankton community is controlled by the general hydrodynamics of the bay, which operates at broader spatial scale. Thus there is close correspondence between the temporal and spatial scales of the various physical and biological phenomena and aspects of the biological heterogeneity associated with them.

Meso- (10–100 km) and fine (from few cm to 10 km) scales are of interest when studying environmental processes and biological responses of coastal tropical zooplankters, but the relative contributions of physical and biological mechanisms controlling zooplankton patchiness are not clear. At mesoscale, even if zooplankton aggregation seems to be a response to phytoplankton biomass (Webber et al. 1992; Rios-Jara 1998; Avois-Jacquet et al. submitted a, b), it must be remembered that all scales and types of patchiness are strongly influenced by hydrodynamic processes (Mackas et al. 1985), through the creation of biological variability (e.g. by an active response of zooplankton to food availability) and turbulent redistribution of existing biological variability (zooplankton and phytoplankton are stirred and transported by the same turbulent advective/diffusive current fields). Turbulence can affect several fundamental processes in plankton, mostly related to the size distribution of the cells. Turbulent mixing may create and disturb patches of elevated food concentrations, hence affecting food availability for planktivorous predators (Kiørboe 1997), and transport plankton away from the sites of growth or production (Peters and Marrasé 2000). Fine-scale turbulence could play a significant role in the biology of copepods (Alcaraz 1997). Variation in fine-scale turbulence can produce effects, such as enhancing encounter rates between planktonic predators and their prey, by increasing velocity the difference between prey and predator (Rothschild and Olson 1988), eroding filtration currents (Kiørboe and Saiz 1995), affecting feeding rates in planktonic predators including copepods (Saiz et al. 1992; Saiz and Kiørboe 1995; Visser et al. 2001), changing feeding behaviour (Saiz and Kiørboe 1995), affecting production (Saiz et al. 1992), and altering metabolic rates (Alcaraz et al. 1994). The effect of fine-scale turbulence on prey encounter rates differs among predators and depends strongly on the feeding behaviour of the predator (e.g. cruising predator, ambush predator, suspension feeder; Kiørboe and Saiz 1995), the velocity difference due to mobility between predator and prey, and the spatial scale of the predator-prey interaction (Kiørboe 1997). Hydrodynamic processes and zooplankton behaviour have been given great importance in recent studies (Haury et al. 1990; Ribes et al. 1996; Petersen et al. 1998). In coastal zones, hydrodynamic processes such as turbulence (Haury et al. 1990) and individual behaviour, including feeding, predation, and reproduction (Haury and Wiebe 1982; Ribes et al. 1996; Bullard and Hay 2002) are the main sources of fine-scale heterogeneity in zooplankton communities. The assumption is that swarming behaviour may display adaptability to more or less vigorous physical conditions that may contribute to the formation and dispersal of aggregates.

Multiscale perception

Considering the spatial variability of planktonic communities as a multiscale process was introduced into marine biology nearly 30 years ago by Platt and Denman (1975). It was developed and elaborated further (Haury et al. 1978) to the level of a concept that can now be regarded as the paradigm of ‘multiscale spatial and temporal variability of marine ecosystems’. Most physical and biological processes in marine environments create zooplankton spatio-temporal structures over a continuum of scales (Mackas et al. 1985; Steele 1989). Patterns and processes are ‘scale-dependent’ phenomena: new ecological properties may appear at different scales (Allen and Hoekstra 1991). These statements depend on the fact that community members experience the environment over a unique range of scales (Denman and Platt 1975; Legendre et al. 1986; Levin 1992) and on the physical and biological processes that vary with scale (Haury et al. 1978; Legendre and Demers 1984; Pinel-Alloul 1995). Both properties reinforce the recognition that there is no single correct scale at which to view a community or an ecosystem (Wiens 1989; Levin 1992). When scale differences are not considered, quantitative and interpretational errors may ensue (Ricklefs 1987; Allen and Hoekstra 1991). Not only do the physical and biological properties change with scale, but the phenomena that are correlated positively over one scale may change to negative correlations at another scale (Wiens 1989; Allen and Hoekstra 1991). For example, at fine spatial scale, predator and prey dynamics may appear to be negatively correlated, but at broader scale, the correlation may be positive because the two dynamics respond to the same set of background environmental conditions (Fiedler 1983; Rose and Leggett 1990).

Lately, the interest in scale effects has been increasing (Rose and Leggett 1990; Dower et al. 1997; Claustre et al. 1999; Guichard et al. 2001), and patterns and processes have been investigated over a range of spatial and temporal scales (Haury and Yamazaki 1995; Solow and Steele 1995, Dunstan and Johnson 1998; Attayde and Bozelli 1999; Blanchard and Bourget 1999; Murdock and Aronson 1999; Huntley et al. 2000; Huskin et al. 2001). The multiscale approach (Piontkovski and Williams 1995; Legendre et al. 1997; Seuront and Lagadeuc 1997; Seuront et al. 1999; Avois-Jacquet et al. submitted a, b) is used to identify and characterize the scales of spatial dependency which are critical to i) appreciate the nature and magnitude of the sources of variability, ii) understand the underlying biological and physical processes, and iii) design scale-dependent sampling strategies. However, problems with measurement and interpretation of the spatial and temporal scales of patterns are still encountered. Not all methods are equally successful at detecting and characterizing spatial structures (see Dutilleul 1998; Seuront et al. 1999; Borcard and Legendre 2002).

To address patterns of zooplankton patchiness and their generating processes, ecologists need to find ways to quantify patterns of variability in space and time, to understand how patterns change with scale, and to comprehend the causes and consequences of patterns. In this perspective, the multiscale approach may help identify and characterize the scales of spatial dependency. Identifying the changes in pattern with scale and understanding the ecological processes that effect these changes are of considerable importance for practical and theoretical reasons. It is evident that identifying and understanding scale-dependent changes in pattern and process must be a prerequisite for predicting the consequences of changes in ecological systems induced by natural disturbances and human alterations of the environment. There is a multiplicity of mechanisms driving population dynamics. Understanding what drives the dynamics of a population would theoretically require investigating all possible mechanisms, each at its appropriate scale. Even if a few of the possible mechanisms operate at broad spatial scale, and others at fine scale, a systematic investigation of all possible mechanisms remains impossible. Thus, rather than trying to determine the correct scale, we must focus on understanding how zooplankton structure and dynamics change across scales.

Conclusion

Although multiscale spatial variability is a common characteristic of coastal tropical zooplankton, more effort must be made to characterize zooplankton spatial structures in coastal tropical ecosystems, especially at fine scales. Although we recognize the power of biological mechanisms at meso- and fine scales, we tried in this paper to highlight the significant role of physical processes (e.g. turbulence) at these scales, and we pointed out the importance of physical-biological coupling. We are presently limited by our rudimentary understanding of the behaviour of zooplankters and their spatial distribution in coastal tropical environments. We need to understand more about the biological and physical factors that affect their fine-scale distribution. This will in turn make it easier to understand the behaviour of organisms implicated in biological and physical processes responsible for their spatial organization.

To study the spatial distribution of zooplankton, future studies must use a multiscale approach capable of integrating habitat heterogeneity, the relationships between species and habitat, the coastal and oceanic influences, the hydrodynamics features highlighting turbulence as a result of the action of wind-induced currents and tidal advection, and the individual behaviour of zooplankton species, including swimming capacity and feeding behaviour. In the conservation and management of coastal tropical ecosystems, identifying the scales of spatial dependency of zooplankton is important for two reasons. First, the scale of the spatial patterns may indicate which disturbance agents are exerting the strongest effects on communities; secondly, in order to make predictions about the importance of disturbance on communities, it is necessary to ascertain the scale of the disturbance regime.

Acknowledgements – It is a pleasure to acknowledge the support of the Société de Secours des Amis des Sciences (Académie des Sciences, France) granted to C. A.-J.

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CHAPITRE 5

VARIABILITE SPATIALE MULTIECHELLE DE LA BIOMASSE DU ZOOPLANCTON ET FORÇAGE ENVIRONNEMENTAL

5.1 Résumé de l'Article en Français

La variabilité de la biomasse pour deux classes de taille de zooplancton (190–600 µm et > 600 µm) ainsi que plusieurs variables environnementales ont été examinées dans un lagon récifal côtier (Guadeloupe, Antilles Françaises) afin de déterminer les mécanismes qui contribuent à la création et au maintien de la variabilité spatiale multiéchelle de la communauté zooplanctonique. Une nouvelle méthode d'analyse multiéchelle, appelée PCNM, a été utilisée pour déterminer les patrons spatiaux du zooplancton sur un continuum d'échelles spatiales. L'analyse des facteurs physiques et biologiques qui sont impliqués dans ces patrons a été réalisée en utilisant l'analyse canonique et les tests partiels de Mantel.

L'analyse multiéchelle a montré que les patrons du zooplancton varient avec l'échelle spatiale (de l'échelle de l'habitat à l'échelle de l'écosystème lagunaire) et que les deux classes de taille de zooplancton possèdent des échelles de dépendance spatiale différentes bien qu'elles montrent les mêmes patrons spatiaux à certaines échelles. Les résultats de cette étude suggèrent que l'hydrodynamique locale, la distribution spatiale du phytoplancton et le comportement du zooplancton génèrent et maintiennent les patrons spatiaux du zooplancton. Il existe une relation spatiale multiéchelle entre la variabilité du zooplancton et les processus environnementaux, mais ces processus sont dépendants de l'échelle spatiale et change selon la taille des organismes (190–600 µm et > 600 µm). Ce travail permet de comprendre pourquoi la réponse de la communauté zooplanctonique au forçage environnemental, en termes de biomasse et d’abondance, change avec la taille des organismes et le long d’un continuum d’échelles spatiales.

5.2 Article 3 : Multiscale Spatial Variability of Zooplankton Biomass and Environmental Forcing in a Coastal Reef Lagoon (soumis à *Journal of Plankton Research*)

Abstract – The patchiness of zooplankton biomass for two size classes (190-600 µm and > 600 µm) as well as several environmental variables were examined in a coastal reef lagoon (Guadeloupe, French West Indies) in order to determine the mechanisms that contribute to the generation and maintenance of multiscale spatial variability in this community. A new form of multiscale analysis, called PCNM, was used to determine the spatial patterns of zooplankton over a continuum of scales. The analysis of physical and biological factors explaining these patterns was conducted using canonical analyses and partial Mantel tests.

Multiscale analysis showed that zooplankton patterns varied with spatial scale (from microhabitat to ecosystem scale) and that the two size classes of zooplankton had different scales of spatial dependency, but they showed common patterns at some spatial scales. Our findings suggest that local hydrodynamics, phytoplankton distribution, and zooplankton behavior generate and maintain the spatial patchiness of zooplankton. There is a multiscale spatial relationship between zooplankton variability and environmental processes, but the generating mechanisms are dependent on spatial scale and change from small to large zooplankton. This work helps explain why the response of a zooplankton community to environmental forcing, in terms of biomass, may change with the size of the organisms and along the continuum of scales.

Introduction

Spatial variability is now recognized as an ecological important feature of ecosystems (Levin, 1992). Concomitant with this attribute is the notion that the patterns of spatial variability depend on the scale of observation (Levin, 1992; Legendre *et al.*, 1997; Dutilleul, 1998). Patterns and processes are scale-dependent phenomena (Wiens, 1989); thus new ecological properties may appear at different observation scales (Wiens, 1989; Allen and Hoekstra, 1991). These statements depend both on the community members that experience the environment over a unique range of scales (Legendre *et al.*, 1986; Levin, 1992), and on the physical and biological processes that vary with scale (Legendre and Demers, 1984; Pinel-Alloul, 1995). These properties reinforce the recognition that there is not a single correct scale to view the entire community or ecosystem (Wiens, 1989; Levin, 1992) and that some quantitative and interpretational errors may occur when scale differences are not taken into consideration (Allen and Hoekstra, 1991). Patterns and scales are ineluctably intertwined so that the perception and investigation of ecological ‘patchiness’—the non-random spatial variability of populations, communities or ecosystems—lead to examine the scale of patterns and processes (Dungan *et al.*, 2002).

Like all ecological entities, zooplankton exhibits patchiness over a broad range of spatial and temporal scales (Haury *et al.*, 1978; Mackas *et al.*, 1985; Legendre *et al.*, 1986; Piontkovski and Williams, 1995). Many investigations have highlighted the biological and physical mechanisms that generate and maintain such patterns (Ribes *et al.*, 1996; Archambault *et al.*, 1998; Petersen *et al.*, 1998; Folt and Burns, 1999). All physical and biological processes operate at some preferential spatial and temporal scales (Legendre *et al.*, 1986) so that they generate multiscale spatial and temporal variability in zooplankton communities (Haury *et al.*, 1978; Mackas *et al.*, 1985). This explains that there is a close correspondence between the temporal and spatial scales of the various physical and biological processes and aspects of the biological heterogeneity associated with them (Denman and Powell, 1984). However, the data may not unambiguously establish if the responses of zooplankton to physical and biological variation were passive or active (Legendre and

Demers, 1984). On broad scales, phytoplankton and zooplankton have patchiness that is consistent with the local hydrodynamic features (i.e. passive response), while zooplankton shows more spatial variability than phytoplankton at finer scales; some other mechanisms such as the swimming behavior (i.e. active response) must be invoked to explain zooplankton patchiness (Levin, 1992). This trend continues as we consider higher trophic levels. Indeed, the swarms and schools formed by macrozooplankton typically show more intense and finer spatial aggregates that the smaller (and less mobile) micro- and mesozooplankton (Mackas *et al.*, 1985). The behavioral mechanisms (Bollens and Frost, 1991; Rios-Jara and Gonzalez, 2000) and physical processes (Petersen *et al.*, 1998; Tiselius, 1998; Yen *et al.*, 1998) affecting the patchiness of zooplankton are likely to be species- and size-specific. Thus, considering the spatial scale is a requirement when examining zooplankton patchiness in order to understand the controlling mechanisms. Such investigations must consider the species and size of zooplankton, and they require a multiscale approach. This approach (e.g. Piontkovski and Williams, 1995; Legendre *et al.*, 1997; Seuront and Lagadeuc, 1997; Lovejoy *et al.*, 2001) is used to identify and characterize the scales of spatial dependence, which are critical i) to appreciate the nature and magnitude of the sources of variability, ii) to understand the underlying biological and physical processes, and iii) to design appropriate sampling strategies.

Recent investigations on zooplankton patchiness have adopted a multiscale approach, but they have mainly focused on the temperate and tropical oceanic areas (e.g. Pascual *et al.*, 1995; Piontkovski and Williams, 1995; Ribes *et al.*, 1996; Marguerit *et al.*, 1998). Little emphasis has been placed on tropical coastal zooplankton patchiness. Our understanding of zooplankton communities inhabiting coastal reef lagoons is limited mainly to the distributions of species and their abundances over temporal scales (e.g. Lewis and Boers, 1991; Rios-Jara, 1998); most studies have only considered one or a few sites (e.g. Alvarez-Cadena and Sedura-Puertas, 1997; Suárez-Morales and Gasca, 2000) making them unsuitable to study the spatial patchiness of zooplankton. High variation observed in biomass, abundance and species composition suggests, however, strong spatial variability of zooplankton communities in tropical coastal waters (Lewis and Boers, 1991). It also suggests that zooplankton associated with this type of environment shows features that diverge from those of assemblages in temperate areas and surrounding waters (Yoshioka *et al.*, 1985; Piontkovski and Williams, 1995). Zooplankton swarming (Emery, 1968; Hamner and Carleton, 1979; Le Borgne *et al.*, 1989), 'island mass effect' (e.g. Alvarez-Cadena *et al.*, 1998; Hassett and Boehlert, 1999), 'habitat patterning' (Rios-Jara, 1998; Alvarez-Cadena *et al.*, 1998), tidal- and wind-induced currents (Alvarez-Cadena *et al.*, 1998; Suárez-Morales and Gasca, 2000) as well as continental/insular and oceanic influences (Webber *et al.*, 1996; Rios-Jara, 1998) are often cited for their potential responsibility in observed zooplankton variability in coastal reef ecosystems. However, the spatial scales of these physical and biological processes and their effects on zooplankton patchiness have not been investigated. To our knowledge, only one study has examined tropical oceanic zooplankton patchiness over several spatial scales (Yoshioka *et al.*, 1985). These authors indicated that tropical oceanic zooplankton in the area off Puerto Rico displayed a well-developed fine-scale patchiness (1–1000 m), but no detectable patchiness over scales from 1 to 100 km. Environmental processes (i.e., eddies and meanders) operating in this region have little effect on the variation of zooplankton abundance over coarse (1–10 km) and mesoscales (10–100 km). These environmental processes operate at scales either smaller than 1 km or larger than 100 km.

Zooplankton spatial heterogeneity is of great ecological significance since distribution patterns, abundance heterogeneity, and swarming behavior of zooplankters strongly influence reproduction (Hamner and Carleton, 1979; Haury and Wiebe, 1982), population dynamics (Noda *et al.*, 1998), prey-predator interactions (Hamner and Carleton, 1979; Tiselius, 1992; Folt and Burns, 1999), coral reef dynamics (Le Borgne *et al.*, 1989) and sampling strategies at the population and community levels (Omori and Hamner, 1982; Yoshioka *et al.*, 1985). It is now clearly recognized that zooplankton spatial heterogeneity has profound effects for the understanding and modeling of species population dynamics and their interactions with other planktonic and nektonic compartments (Legendre and Demers, 1984; Mackas *et al.*, 1985; Wiens, 1989; Levin, 1992; Pinel-Alloul, 1995). Consequently, spatial heterogeneity has important implications for the structure and function of the whole ecosystem. There is pressing need to monitor coastal reef lagoon ecosystems to assess the spatial and temporal scales of any potential damage (i.e. natural disturbances and human activities) that may occur (Hughes, 1994; Sale, 1999). The study of spatial heterogeneity of tropical coastal zooplankton communities is a central step to understand the mechanisms involved in the structure and dynamics of tropical coastal reef ecosystems. Such investigations may help determine, for example, the extent of water quality deterioration (bottom-up effect) or over-fishing impact (top-down effect).

In the present study, spatial variability of the zooplankton biomass has been investigated in a coastal reef lagoon along the Guadeloupe coast (Lesser Antilles, French West Indies). Two size classes of zooplankton have been considered, as well as several environmental factors. The aims of our study were: i) to describe the multiscale spatial variability of zooplankton biomass and ii) test hypotheses about the biological and physical processes that were possibly causing zooplankton patchiness. The primary questions were: i) how do the spatial patterns of zooplankton vary with spatial scale? ii) Is zooplankton patchiness changing with the size of the organisms? iii) Is there a multiscale spatial relationship between zooplankton variability and environmental processes? And iv) is the zooplankton response to environmental mechanisms depending on the size of the organisms?

Three statistical methods are widely used for multiscale analysis by oceanographers and limnologists: spectral analysis (e.g. Mackas and Boyd, 1979), multifractal analysis (e.g. Pascual *et al.*, 1995; Seuront and Lagadeuc, 1997), and universal multifractal analysis

(Marguerit *et al.*, 1998; Seuront *et al.*, 1999; Lovejoy *et al.*, 2001). These methods cannot, however, be conducted without taking into account a number of theoretical and practical considerations (see Horne and Schneider, 1995; Dutilleul, 1998; Seuront *et al.*, 1999 for an extensive review). They require continuous and simultaneous recording of the variables involved, while biological data do not always provide long temporal or spatial series and often violate other assumptions about regular sampling intervals and stationarity of the means. Moreover, the degree to which these methods can reveal spatial pattern is sensitive to the sampling scale, i.e. grain or extent (Wiens, 1989; Dutilleul, 1998). A new form of multiscale analysis was used here to determine the multiscale spatial variability in zooplankton biomass: the method of Principal Coordinates of Neighbour Matrices method (PCNM: Borcard and Legendre, 2002), based on the close neighborhood relationships among the sampling sites, will be used to detect and quantify the spatial patterns over a wide range of scales. Continuous recording of all variables is not necessary; and the method can be used with irregularly spaced data.

1. Materials and methods

1.1 Study site

The Grand Cul-de-Sac Marin (GCSM) is a shallow coastal reef lagoon (mean depth = 5 m, maximum depth = 30 m) located on the northern Guadeloupe coast in the eastern Caribbean Sea (61°34'W, 16°18'N). The morphology of the lagoon is characterized by i) a barrier coral reef with a reef flat allowing seawater exchanges between the open sea (Caribbean Sea) and the lagoon, ii) extensive shallow areas with cays, and iii) several passes and channels (Figure 1).

The hydrodynamics of the GCSM lagoon is characterized by a general circulation driven by a northwest current which follows the barrier reef on its northern fringe (Castaing *et al.*, 1984). Ramifications of this current enter the lagoon through the passes, mostly at depth during flood tide, but also on the surface during ebb tide. The dominant winds are easterlies and correspond to the trade wind direction off the Guadeloupe islands. This generates surface currents from the northeast, which carry water outside the lagoon through the Grande Coulée pass (Figure 1), especially during tide ebb. The general circulation shows the primordial role of the lagoon morphology (Castaing *et al.*, 1984). A great part of the flow exits the lagoon either by crossing the barrier reef or by following the lagoon passes and channels. The tide has a mixed character (i.e. diurnal or semi-diurnal) with an amplitude of 50 to 60 cm. GCSM hydrodynamics generates a complex circulation forming two distinct dynamic areas: a northern area (from the barrier reef to site 17, Figure 1) where the gyre action allows, with the support of waves and surface wind-induced currents, a renewal of the lagoon water, and a southern area (from the coastline to site 17) which is semi-sheltered and where water renewal is limited (Assor and Julius, 1987). The physics and chemistry of the GCSM lagoon confirm the existence of low energetic level dynamics in the southern and eastern portions of the lagoon (Assor and Julius, 1987).

The GCSM is shaped by a mosaic of five ecosystems: i) the barrier coral reef, ii) the cays (i.e. high bottoms located inside the lagoon), iii) the seagrass meadows dominated by the species *Thalassia testudinum*, iv) the deep muddy bottoms, and v) the mangroves located on the intertidal mud flats. These ecosystems are distributed along a physical and chemical gradient going from the southern coastline to the Caribbean Sea (Figure 1). The GCSM lagoon forms an interface between the marine and insular systems. It is highly vulnerable to natural disturbances like hurricanes, and human activities such as tourism, pollution and over-fishing (Bouchon *et al.*, 1991; Bernard, 1995).

1.2 Sampling design

The zooplankton community and environmental factors were sampled along a south-to-north transect, 8.6 km in length, corresponding to the largest dimension of the lagoon. Oriented from the southern coastline to the open sea (Caribbean Sea), the transect follows the main gradient of temperature, salinity and sedimentology (Figure 1).

Sampling, conducted during the dry season, was diurnal (from 08:00 to 16:00) to minimize possible effects due to the nycthemeral vertical migration of zooplankton. The width of the lagoon, the diurnal period and the allowable sampling effort were considered in the decision concerning the number of sampling sites. Samples were systematically collected in each habitat crossed by the transect. The habitats were: seagrass beds, barrier reef, bare mud, sandy bottoms, and cays. Two or three sites were selected for each type of habitat. Since zooplanktonic organisms tend to be found in deeper water layers during daytime (Emery, 1968; Alldredge and King, 1980), each site not exceeding 5 m in depth was sampled at one meter from the bottom. For the others sites, whose depth exceeded 5 m, the sample was collected one meter below the sea surface.

The choice of the sampling scale (grain size, extent and sampling interval) was constrained by technical and physical limitations. The extent of the observations (8.4 km) was imposed by the width of the lagoon, while the pumped volume of seawater defined the size of the sampling units (grain size: 2.5 m^3 and $2 \cdot 10^{-3}$ m^3 for zooplankton and phytoplankton, respectively). Due to the irregular distribution of the types of habitats in a corridor of about 500 m wide in the direction of the transect, the sampling route did not form a straight line and the distance between neighboring sites was not regular; the sampling interval varied from 100 to 500 m. The number of sampling sites (51) was determined by the total allowable sampling effort, taking into account the spatial distribution of the types of habitats. The 51 sites forming the transect (Figure 1) were sampled during two consecutive days; 24 sites were visited on 6 April (sites 1-24) and 27 more on 7 April 1998 (sites 25-51).

1.3 Zooplankton sampling and processing

The increasing awareness that time and space scales involved in sampling zooplankton must be related to the biological processes being investigated has highlighted the deficiencies of standard plankton sampling gears and standard sampling methods (Omori and Hamner, 1982), especially when high-frequency sampling of different water masses is planned. During the last two decades, three advanced technologies have been developed: high-frequency acoustic devices, optical plankton counters (OPC), and *in situ* video systems (see Williamson *et al.*, 1992; Pinel-Alloul, 1995; and Folt and Burns, 1999 for extensive reviews). These sampling methods allow researchers to rapidly cover large areas and collect zooplankton organisms at fine spatial scales, thus resolving problems such as temporal variation and/or limited size of the sampling units. However, these high-technology methods are not easily applicable on coral reefs due to shallow waters and the topography (e.g., cays and barrier reef).

Numerous studies have highlighted the difficulties as well as the qualitative and quantitative errors generated by conventional sampling techniques in lagoons and coral reefs (e.g. Hamner and Carleton, 1979; Omori and Hamner, 1982; Walters and Bell, 1986). Nets, for instance, cannot be towed from boats close to the coral without entanglement and tears; this is a poor technique for discrete local sampling. Some techniques including suction devices and plankton traps are efficient in this environment (Emery, 1968; Walters and Bell, 1986, 1994), even though they were first used in studies of benthic and epibenthic zooplankton communities. The plankton pumps may bring about some problems with the collection of zooplankton, including damage or destruction of organisms, and the differential avoidance of the pump intake by zooplankters (Taggart and Leggett, 1984).

A plankton pump was used in the present study for several reasons (Taggart and Leggett, 1984; Rahkola *et al.*, 1994). First, sampling at biologically relevant time and space scales was possible. Second, the necessary water volume could be pumped in a minimum amount of time. Third, all size classes could be sampled at the same place and time, down to the smallest size class, since the pumped water was filtered using a series of different mesh sizes. The biasing effects of using multiple nets at different times and/or locations were eliminated. Fourth, the same sampling technique could be used on all habitats of the lagoon. So, zooplankton samples obtained using the pump guaranteed comparability and facilitated the interpretation of the data.

We used a Monarch BSGF-8 self-priming centrifugal pump. A nominal flow rate of 0.5 $m^3 \cdot min^{-1}$ was delivered when coupled to 27 m (intake) and 3 m (discharge) lengths of suction hose. The end of the intake hose was fitted with a 0.5 m section of PVC tubing and ballasted by a load to keep the intake oriented perpendicular to the surface water. A 2 m long, 190 µm Nitex™ plankton net was fitted with a PVC disc joined to the end of the discharge hose and suspended to the outside of the boat during zooplankton sampling. The net floated freely above the water surface, avoiding abrasion (Taggart and Leggett, 1984) and eliminating the need for an on-broad collection system. The volume filtered was calculated through the time of pumping. Beforehand, the volume/time ratio had been calibrated at different depths and had not shown differences. Zooplankton samples were preserved upon collection by adding concentrated buffered (sodium carbonate) formaldehyde solution until a final concentration of 4% was obtained.

Zooplankton biomass was estimated by the ash-free dry mass (AFDM). Each sample was filtered through two sifters of 190 µm and 600 µm mesh size producing two zooplankton size classes: from 190 to 600 µm (small zooplankton), and 600 µm and higher (large zooplankton). Each fraction retained on the sifter was slightly washed with distilled water and filtered through a Whatman GF/A filter (manufacturer's nominal pore size of 24 µm). Beforehand, the filters were decontaminated by incineration at 500°C during 24-h. The 'wet' sample filters were dried at 40°C during 48 h. Dry mass was obtained using an automatic electronic scale (Cahn 26-Ventron™). The 'dry' sample filters were incinerated at 500°C during 24 h and weighted again to obtain the ash mass. Zooplankton biomass expressed in amount of organic carbon (milligrams of AFDM per m^3) was obtained by subtracting the ash weight from the dry mass.

1.4 Phytoplankton collection and processing

At each site, 2 L of seawater were collected to estimate phytoplankton biomass. Using the pump, the phytoplankton sample was obtained immediately after and at the same depth as the zooplankton sample. The bottles were stored in a dark icebox until return to the laboratory.

Concentrations of total chlorophyll *a* (i.e., chlorophyll *a* + phaeopigment) were measured by the acidification method (Parsons *et al.*, 1984) using a spectrophotometer (Jasco 7800/7850, Prati Eletronica) after filtering 2 L of seawater on a Whatman GF/F filter (manufacturer’s nominal pore size of 0.7 µm), 6 to 8 hours after collection of the water. The filters were immediately frozen (at –40°C) and stored for several weeks (at least 30 days: Parsons *et al.*, 1984) prior to extraction in 90% acetone for spectrophotometric determination of active chlorophyll *a* and phaeopigments (expressed as chlorophyll *a* equivalents; Conover *et al.*, 1986). The remaining methodology of pigment extraction followed that outlined in Parsons *et al.* (1984); their equations were adjusted for the correct acid ratio and compensation was made for the dilution of solvent by water retained in the filters.

1.5 Environmental variables

Ten physical and chemical factors were measured at each site. Seawater temperature, dissolved oxygen, turbidity and salinity were measured *in situ*, at the sampling depth, using a multiparametric probe (YSI 6000 Collector, YSI Model 610 DM, Bioblock Scientific). Maximum depth was measured with a hand probe, and water transparency with the assistance of a Secchi disk. Wind direction, swell height and cloud coverage were observed in the field and compared to the data from the meteorological center (Météo-France, Le Raizet, Guadeloupe), approximately 7 km southeast of the GCSM lagoon. Wind speed was obtained from the meteorological center.

Each site was described in terms of habitat features using the classification of Chauvaud *et al*. (1998). The qualitative and quantitative descriptors of the habitat were the nature of substrate (coral reef, mud or sand), the presence or absence of sea grass and coral and seagrass coverage. The habitat characteristics for each site are listed in Appendix A.

2. Statistical analyses

2.1 Multiscale spatial analysis

The 'Principal Coordinates of Neighbour Matrices' method (PCNM, Borcard and Legendre, 2002) was used to identify the multiscale spatial variability of zooplankton from the data, the sampling sites being irregularly spaced along the transect. This new method of multiscale analysis, which is based on the neighborhood relationships among the sampling sites, permits to detect and quantify spatial patterns over a wide range of scales. The spatial analysis was carried out for the zooplankton biomass data, considering the two size classes of zooplankton separately. It was repeated for the phytoplankton biomass data.

2.1 (a) Trend extraction

The first step of PCNM was to remove the spatial trend from the data in order to make them stationary (Figure 2, step 1). This preliminary step allowed to separately model the linear trend while retaining all the potential of the principal coordinates to model more complex spatial features (Borcard and Legendre, 2002). It consisted in fitting a spatial linear model to the whole data series of a given variable using the least-squares approach (Legendre and Legendre, 1998). The trend extraction obtained by regression on the latitudinal geographic coordinate of the sites was carried out for the two size classes of zooplankton, for phytoplankton biomass, and for the environmental variables.

After modeling and extracting the trend, the residuals (i.e., detrended data) of the zooplankton variables were used in PCNM analyses (Figure 2, step 2–5). Determining the trend of the zooplankton variables was equivalent to modeling the spatial pattern of zooplankton at the broader spatial scale, which is that of the lagoon.

2.1 (b) Principal coordinates of neighbour matrices (PCNM)

The PCNM method is described in Borcard and Legendre (2002); that paper also contains numerical simulations and tests on complex data. We will now describe the main steps of the method as it was used in the present paper (Figure 3).

Step 1 was the removal of the linear spatial trend from the dependent variable. Step 2: from the latitude coordinate of the sampling sites, a matrix of Euclidean distances among sites was computed, then truncated to retain only the distances between the closest pairs of sites (step 3). The longitude coordinate was not used because our hypothesis concerned a latitudinal gradient; in any case, the differences in longitude were small. The truncation threshold was fixed in order to retain only the immediate neighbors. The removed values were replaced by an arbitrary large value equal to 4 times the threshold. In step 4, the principal coordinates of the neighbor matrix were computed. Each principal coordinate represented a spatial variable that characterized a spatial scale. In step 5, the principal coordinates with positive eigenvalues were assembled into a “matrix of spatial variables”. The zooplankton residuals, after trend extraction, were regressed against these spatial variables to identify spatial patterns at different spatial scales (Figure 3, I).

The F statistic for the R^2 of the multiple regression, as well as the t statistics for the individual regression coefficients, were tested for significance using permutation of the residuals under a full model (ter Braak, 1990). The calculations were done using a program for multiple regression with permutation tests available from http://www.fas.umontreal.ca/biol/legendre/ (Legendre, 2001).

2.1 (c) Scalogram

The results of the PCNM analysis were summed up in a ‘scalogram’, which represents the amount of variance explained by the different spatial variables (principal coordinates) for a given response variable (e.g., biomass of the large zooplankton). The scalogram thus displays the variance spectrum (Figure 3, II). The abscissa represents the different spatial variables determined by the PCNM analysis. For data with a regular lag, the principal coordinates are ordered along a continuum of scales, from broad to fine scales. The ordinate axis represents the amount of variability explained by each spatial variable, namely the spatial variance. Each full symbol on the scalogram indicates that a significant amount of spatial variance has been detected at that specific scale; the significance was tested by the permutation method cited above. The variation explained by each given scale can be represented by a graph of fitted values (Figure 3, I). The abscissa is the geographic coordinate of the sampling sites while the ordinate represents the fitted values of the regression model for the given spatial variable (Figure 3, step 5). These graphs display regular waves in the case of data sampled with a regular lag. For irregularly-spaced data, the fitted shapes are irregular and the geographic variables are not perfectly ordered from broad to fine scale. We will see, however, that the spatial variables produced by PCNM in this study were fairly well ordered from broad to fine scale.

2.2 Environmental factors

2.2 (a) Biological and physical factors implicated in the zooplankton biomass variability

Multiple regression with a forward selection procedure (available in the redundancy analysis procedure of the program CANOCO™ version 3.10; ter Braak, 1990) was used to select the environmental variables that significantly explained each spatial pattern of zooplankton biomass for each size class (i.e., 190–600 µm and > 600 µm). There is a single response variable in this portion of the study; for a single response variable, redundancy analysis is simply a multiple linear regression. CANOCO was used here because it offers forward selection of the explanatory variables with permutation testing.

The environmental data were used first to explain the spatial pattern corresponding to the trend identified in the zooplankton data. Secondly, the residuals of the environmental variables (i.e., after detrending) were used to explain the zooplankton spatial patterns obtained from PCNM and found to be significant by regression modelling (Figure 2).

2.2 (b) Relationships between zooplankton, phytoplankton and space

The correlation between the zooplankton and phytoplankton biomass patterns could be either the result of an active response of zooplankton to phytoplankton food patches, or the result of a common spatial pattern created by some environmental processes (Mackas *et al.*, 1980; Legendre and Demers, 1984; Tiselius, 1992; Yen *et al.*, 1998; Folt and Burns, 1999). Consequently, if the phytoplankton biomass (estimated by total chlorophyll *a*) was identified as a biological factor implicated in zooplankton patchiness at a specific scale, causal modeling on resemblance matrices using partial Mantel correlations (Legendre and Troussellier, 1988; Legendre and Legendre, 1998) was applied to establish the nature of the relationships between zooplankton, phytoplankton, and space.

Calculations involved three Euclidian distance matrices computed for the zooplankton biomass variable, the total chlorophyll *a* variable and for the geographic distances among the 51 sampling sites using the *y* geographic coordinate. The Mantel statistics estimating the correlations between two matrices, and the partial Mantel statistics estimating the correlations between two matrices while controlling for the effect of the third matrix, were computed for each zooplankton size class separately. Mantel tests were one-tailed and the statistics were tested by permutation using The R Package (http://www.fas.umontreal.ca/biol/legendre/).

3. Results

3.1 Data description

During the study, water temperature varied from 26.6° to 29.6°C with an average of 27.9°C, and salinity from 36.4 to 37.4 psu with an average of 37.1 psu. Dissolved oxygen varied from 4.6 to 7.9 mg·L^{-1} (mean = 6.6 mg·L^{-1}) and turbidity from 0.9 to 2 NTU (mean = 1.4 NTU). These factors showed little variation with depth, which varied from 0.5 to 24 m with an average of 4.5 m. In the southern area of the lagoon (sites 1-23, Figure 1) where the cloud coverage was 5-20%, the wind speed varied from 3 to 11 m·s^{-1} and swell height from 0.2 to 0.8 m. The central part of the transect (sites 24–32) was characterized by easterly wind with wind speed between 5.5 and 11 m·s^{-1} and swell height averaging 0.5 m. The cloud coverage in this region was maximum (30–60%). In the northern part of the transect (sites 33–51), wind speed (from 1.5 to 3.5 m·s^{-1}) and swell height (from 0.2 to 0.4 m) were lowest with southeasterly winds and cloud coverage ranging from 4 to 45%.

The average concentration of total chlorophyll *a* (including phaeopigments) across the GCSM lagoon was 1.15 µg·L^{-1}. It formed a gradient going from 2.36 near the coats to 0.44 µg·L^{-1} at the barrier reef (Figure 4). For the 190–600 µm fraction, zooplankton biomass was 2.97 AFDM·m^{-3} on average (from 0.91 to 10.61 AFDM·m^{-3}); for the > 600 µm fraction, the mean was 1.77 mg AFDM·m^{-3} (from 0.43 to 6.90 AFDM·m^{-3}) (Figure 4). On average, the small fraction represented 63% and the large fraction accounted for 37% of the zooplankton.

3.2 Multiscale spatial variability of zooplankton

The trend extraction established the same model for the two size classes of zooplankton. A decreasing gradient of biomass from the coast to the barrier reef characterized the zooplankton spatial pattern at the broadest scale (i.e. the scale of the GCSM lagoon, 8.4 km). This broad-scale pattern represented 49.2% of the small zooplankton variability and only 12.4% of the large zooplankton variability although the total variance in the two zooplankton data series was 0.4178 and 0.4641, respectively (Table 1).

The PCNM analysis identified 28 spatial scales from the latitude coordinate of the sampling sites (Figure 5). At scales 6 and 9, both fractions of zooplankton exhibited the same pattern, but the spatial variability was higher for the large than for the small zooplankton (Table 1). Small organisms, however, showed spatial variability at more scales. Besides the trends, ten significant spatial patterns were detected on the scale continuum for small zooplankton and only four for large zooplankton; the total spatial variance (i.e. trend + scale patterns) represented 79% and 41.1% of the total variance, respectively. Spatial variability decreased from broad to fine scales for the large organisms but it was irregular for small zooplankton which showed high variance at broad (i.e., trend: 49.2%; Table 1) and fine scales (scales 12 to 24: 19.7%), but rather low over the mesoscales (scales 6 to 9: 10.1%). The patchiness of zooplankton was concentrated in the first 6 km of the transect (sampling sites 1 to 32), but the organisms presented less variability near the barrier reef (Figs. 6 and 7).

At mesoscale 4, variability was only found in the northern part of the lagoon for large zooplankton at 5.4 km from the coast (sampling sites 26 to 51). Two distinct patches shaped the spatial pattern; one patch of large zooplankters inhabiting the cays and another located around the barrier reef (Figure 6). From 0 to 5.4 km, large zooplankton exhibited two opposite responses at mesoscale 6 (sampling sites 1 to 25; Figure 6) with low biomass near the coast and high biomass in the middle of the lagoon. At finer scales (9 and 15), this fraction showed patchiness across the whole transect.

Although small zooplankton exhibited the same mesoscale pattern at scale 6 than the large zooplankton (Figure 7), the variability of small zooplankton was lower than that of large zooplankton (Table 1). Mesoscale 7 showed a patch of small zooplankton located in the central part of the lagoon with two regions of high biomass on the cays from 3.7 and 6.2 km of the coast (sites 19–22 and 30–32) and lower biomass on the seagrass beds (Figure 7). The organisms presented patchiness across the whole transect at mesoscales 8 and 9. Over fine scales (400–1000 m), the spatial variability of zooplankton biomass was high from the coast to the central part of the lagoon (from 0 to 6.2 km, sampling sites 1 to 32), especially over scales 16 and 23 (Table 1). Small organisms presented patchiness in the north of the lagoon at scale 14 (from 6.5 to 8.4 km of the coast, sampling sites 33 to 51), and across the whole transect at scale 18 (Figure 7).

3.3 Environmental factors explaining the zooplankton patterns

Table 2 reports the environmental variables that were found, by multiple regression, to significantly explain the spatial patterns what were identified in Table 1 to be of interest for zooplankton biomass. Partial standard regression coefficients are reported in Table 2 because they indicate the partial contribution of each environmental variable after controlling for the effect of the other variables in the model. The patchiness of both size classes of zooplankton was mostly linked to the variables describing the types of habitat (Bms to Reef in Table 2) across the scales, while the physical, chemical and biological factors (Depth to Phyto in Table 2) were implicated in the broad- and mesoscale patterns the zooplankton variability. Some environmental factors were retained at several spatial scales, a change of scale corresponding in many instances to a change of sign of the regression coefficient. For example, zooplankton biomass and wind speed appeared to be positively linked at large scale, but the relationship was negative at other scales (Table 2). A few factors always showed the same relationship (same sign) with the zooplankton patterns across the spatial scales like swell height.

At the broadest scale (i.e., the linear trend at the scale of the lagoon), the decreasing gradient of zooplankton biomass (large and small size classes) was mainly explained by phytoplankton biomass (*b* = 0.661, Table 2), which also decreased from the coast to the barrier reef (Figure 4). Three other selected explanatory factors were salinity, wind speed and dissolved oxygen. Salinity (*b* = –0.259) showed an increasing gradient from the coast to the barrier reef (Figure 4) and the two other factors were positively linked to zooplankton biomass at the scale of the trend. The responses of both zooplankton fractions at scale 6 were mostly linked to the presence of cays (b = 0.565) and seagrass beds (b = –0.458), followed by swell height (b = 0.324) and dissolved oxygen (b = 0.214). The cays presented higher biomasses of zooplankton, greater swell height and lower values of dissolved oxygen than the seagrass beds. At scale 9, deep muddy bottoms and seagrass beds were negatively linked to the biomass of both fractions of zooplankton (Table 2). Turbidity and swell height were positively linked to zooplankton biomass and they showed high values on the cays (Figure 4).

At mesoscale 4, large zooplankters inhabiting the cays covered solely with seagrass (b = 0.378) or coral (b = 0.142), and characterized by low values of dissolved oxygen (≤ 5 $mg \cdot L^{-1}$, b = –0.379), showed an inverse response to that of the cays inhabited by a combination of seagrass and coral (b = –0.275) where dissolved oxygen was rather high (≥ 6 $mg \cdot L^{-1}$, Figure 4). Around the barrier reef, high biomass values were linked to the inner reef flat (b = 0.252), but they were negatively correlated with depth (b = –0.426). The shallow muddy bottoms located near the coast and the seagrass beds on sandy bottom in the middle of the lagoon explained a portion of the spatial pattern of large zooplankton at fine scale 15. At that scale, phytoplankton was negatively linked to zooplankton (b = –0.238), whereas the relationship was positive at the broadest scale (b = 0.661). A great amount of the fine-scale variability of large zooplankton, however, remained unexplained.

At mesoscales 7 and 8, the response of small zooplankters was linked to the nature of the bottom and the coverage by seagrass and/or coral. Dissolved oxygen was another factor explaining these two patterns (Table 2). For example, high biomass was linked at scale 7 to the cays covered by mixed seagrass and coral. The biomass decreased from the seagrass beds on sandy bottom (26–50% coverage) to the cays covered only by seagrass, while dissolved oxygen increased (> 6 $mg \cdot L^{-1}$, Figure 4). Across the transect, the highest dissolved oxygen values were measured in the seagrass meadows (≥ 7 mg·L^{-1}) and the cays covered only by coral presented the lowest dissolved oxygen values (≤ 5 mg·L^{-1}). The fine-scale patterns of small zooplankton (scales 12-24) were only explained by the variables describing the types of habitat (Bms to Reef), although wind speed ($b = -0.266$) was selected as a significant factor for scale 12. At that scale, low biomass of zooplankton was linked to the presence of seagrass beds on muddy bottom ($b = -0.391$, wind speed ≈ 7 m·s^{-1}), whereas zooplankton biomass was positively linked to the presence of seagrass on sandy bottom ($b = 0.321$) where the wind speed decreased and to the bare muddy bottoms ($b = 0.446$, wind speed ≈ 3 m·s^{-1}). Although the selected environmental variables explained together 40% of the spatial variability of small zooplankton at scale 16, a great amount of the spatial variability of zooplankton detected at the other fine scales was not explained.

3.4 Zooplankton-phytoplankton relationships

The broad-scale trend of both zooplankton fractions was highly and positively linked to phytoplankton ($b = 0.661$), whereas large zooplankton and phytoplankton presented a negative relationship at scale 15 ($b = -0.238$, Table 2). The PCNM analysis showed that phytoplankton biomass displayed three significant spatial patterns over the scale continuum (Table 3). Like the zooplankton, the phytoplankton biomass at broad scale showed a decreasing gradient from the coast to the open sea, but its pattern was reversed at scale 9 (Figure 8), compared to the zooplankton pattern. No relationship between the zooplankton and phytoplankton patterns was found at scale 9, however (Table 2). Although the phytoplankton and large zooplankton were correlated at scale 15, the phytoplankton did not exhibit a significant pattern at that scale. Our findings thus suggest that the correlation between large zooplankton and phytoplankton was not the result of a common spatial patchiness at scale 15. Instead, the zooplankton and phytoplankton relationships detected at broad scale could be the result of either a common spatial pattern created by some environmental processes, or an active response of zooplankton to food.

The large zooplankton was negatively and significantly correlated with phytoplankton ($r^*_M = -0.143$, $p \leq 0.01$ after controlling for the effect of space, Figure 9a) as well as positively and significantly correlated with space ($r^*_M = 0.131$, $p \leq 0.05$ after controlling for the effect of phytoplankton). We possess no information allowing us to tell whether the relationship between the phytoplankton and large zooplankton is the result of a top-down (grazing) or bottom-up (food availability) process; so, the effect is represented by a double arrow in Figure 9a. On the other hand, although the simple Mantel tests (Figure 9b) indicated that the small zooplankton might be positively and significantly correlated with phytoplankton and space ($r_M = 0.393$ and 0.423, respectively), but not to the large zooplankton, the partial Mantel tests showed that the correlation between the small zooplankton and phytoplankton was not significant ($r^*_M = 0.087$ after controlling for the effect of space), whereas the small zooplankton remained significantly correlated with space ($r^*_M = 0.191$, $p \leq 0.01$ after controlling for the effect of phytoplankton). This indicates that the phytoplankton and small zooplankton have independent spatial patterns.

Like the two size classes of zooplankton, the broad-scale pattern of phytoplankton was positively linked to dissolved oxygen and wind speed, but negatively linked to salinity. However, the main factor that explained the phytoplankton gradient was turbidity (Table 3). At scale 9, phytoplankton biomass and turbidity were negatively linked, but the differences among seagrass beds explained a part of that patchiness. No environmental variable was selected to explain the fine-scale pattern of phytoplankton detected at scale 27 (Table 3).

4. Discussion

4.1 Multiscale spatial variability

In the GCSM lagoon, zooplankton and phytoplankton communities exhibited multiscale spatial variability from broad to small scales, but they differed strongly in the intensity and spectral composition of their patchiness. Zooplankton showed more intense and finer-scale variability in biomass than phytoplankton; this was also pointed out by others authors (Mackas and Boyd, 1979; Mackas *et al.*, 1985; Piontkovski *et al.*, 1995). In the trophic pelagic ecosystem, the spatio-temporal variability of biomass of organisms seems to increase for higher trophic levels, i.e., with increase in size of the organisms (Piontkovski and Williams, 1995). Our results show, however, that large zooplankton had smaller total spatial variability than small zooplankton and phytoplankton, although the total variability observed across the transect was higher for the large zooplankton (Tables 1 and 3). Most of this variability was not spatially structured (Table 1). This discrepancy may be imputed to the different responses of the organisms to environmental heterogeneity because the heterogeneity perceived by an ecological entity (i.e. individual, species, population or community) and at which the entity responds to, differs from that of another (Kolasa and Rollo, 1991; Dutilleul and Legendre, 1993). This type of heterogeneity, called ‘functional’, arises from the interactions between scales relevant to the ecological entity and its environment. Indeed, the heterogeneity perceived by an organism—an individual of a species characterized by specific age or size—depends on the temporal and spatial scales at which the individual operates, which depends on their movement relative to the environment (Kolasa and Rollo, 1991). Our findings support the hypothesis that zooplankton patchiness is size-specific (Piontkovski and William, 1995). We can assume that planktonic communities in the GCSM lagoon perceive and respond differently to the environmental heterogeneity and, consequently, have different scales of spatial dependence to the environment.

4.2 Broad-scale pattern

The broad-scale pattern of large and small zooplankton describing a decreasing gradient of biomass from the coast to the open sea is consistent with the findings of previous studies (e.g. Moore and Sander, 1976; Alvarez-Cadena *et al.*, 1998). Moore and Sander (1976) defined this gradient as the result of the ‘island mass effect’ that corresponds to local enhancement of productivity due to interactions between islands and the surrounding ocean waters. The relative importance of physical and biological processes in these patterns is still unclear, however; see Hassett and Boehlert, 1999 for an extensive review on the subject. In tropical waters, decreasing gradients from the coast to the open sea have also been observed for primary production, chlorophyll *a*, phosphorus and nitrogen concentration (e.g. Moore and Sander, 1979; Webber *et al.*, 1992), and several investigators found a positive correlation between phytoplankton and zooplankton (e.g. Moore and Sander, 1979; Webber *et al.*, 1992; Rios-Jara, 1998), also shown in our results, partly because of this gradient. The phytoplankton standing stock probably remains high during the dry season (Rios-Jara, 1998) due to autochthonous nutrient remineralization intensified by wind (Hopcroft and Roff, 1990). High zooplankton biomass near the coast may be attributed to a combination of the availability of high phytoplankton standing stock (Webber *et al.*, 1992; Rios-Jara, 1998) and the local patterns of water movements (Webber *et al.*, 1996). In the GCSM lagoon, the easterly winds prevailing during the dry season and the swell system close to the eastern and southern coasts (Assor and Julius, 1987) may help maintain high phytoplankton biomass near the coasts, which would then be available to the zooplankton. The standing stock of phytoplankton in this area may also be maintained by exporting organic nutrients and other growth enhancing substances from adjacent mangrove ecosystems controlled by tides and river discharges (Rivera-Monroy *et al.*, 1998 and references therein). As a consequence, the semi-sheltered system in the southern area of the lagoon, which is also associated with renewal of the water masses (Assor and Julius, 1987), may help explain the accumulation of plankton in this region.

Wind speed and the southerly winds present in the GCSM may generate currents which contribute to the formation of the biomass gradient by dispersing the coastal zooplankton from the coast to the open sea, as pointed out by Alvarez-Cadena *et al.* (1998). This requires, however, that zooplankton organisms either are passive drifters or have limited mobility, which depends on their swimming capacity and the hydrodynamic conditions. Indeed, hydrodynamic processes affecting a range of biological processes, mostly related to the taxa and the size of organisms (Petersen *et al.*, 1998), may aggregate zooplankton with algae passively, particularly if the organisms are similar in shape, buoyancy or locomotory ability, and when turbulence overwhelms zooplankton locomotion (Yen *et al.*, 1998). Assuming that small zooplankton is less mobile than large zooplankton, wind-induced currents might be implicated in the generation of the broad-scale patterns of small zooplankton in the GCSM lagoon. Indeed, small copepods in marine coastal waters aggregate in a food layer during calm conditions, but when winds are strong both copepods and algae are dispersed through the surface layer (Tiselius, 1998). The patterns of phytoplankton and salinity also support our assumption given that phytoplankton and salinity are passive tracers of hydrodynamic features (Geyer, 1997). The broad-scale pattern of large zooplankton, however, may be the result of the behavioral processes (i.e. food searching and grazing, as suggested by the negative correlation between large zooplankton and phytoplankton) capable of countering dissipative physical forces (Wiafe and Frid, 1996). Consequently, the small zooplankton and phytoplankton patterns are likely to be the result of the spatial redistribution of existing variability (i.e., zooplankton and phytoplankton are stirred and transported by the same turbulent current field), whereas the relationship between large zooplankton and phytoplankton may be the result of the creation of biological variance (i.e., an active response of zooplankton to the ‘resource heterogeneity’).

Zooplankton and phytoplankton depletion on the barrier reef may also be the result of grazing and predation. In coral reefs, a phytoplankton-depleted layer is commonly found above the reef slope where numerous members of the coral-reef community, like bivalves, gasteropods, sponges, and soft corals, are known to feed on particles within the size range of phytoplankton (Yahel *et al.*, 1998 and references therein). Zooplankton organisms are also a great source of preys on barrier reefs (Hamner *et al.*, 1988; Noda *et al.*, 1998). Moore and Sander (1979) noted that carnivorous zooplankters like siphonophors, chaetognaths, and euphausids, are more abundant offshore than inshore. However, the decline of phytoplankton biomass may also result in increased turbidity on the barrier reef. Cross-shelf transport generated by tidal currents (Le Borgne *et al.*, 1989) and by internal tidal bores (Leichter *et al.*, 1998) can affect turbidity by resuspension of organic and inorganic particles. So, variation in turbidity can have great effects on algal biomass. High concentrations of inorganic suspended solids may reduce chlorophyll concentration by decreasing light availability for photosynthesis (Attayde and Bozelli, 1999).

4.3 Mesoscale patterns

The spatial variability of large zooplankters detected in the northern region at mesoscale 4 (Figure 6) is mainly linked to habitat patterning, i.e. the division and heterogeneity of habitats (Addicott *et al.*, 1987). For example, high biomass of large zooplankters was associated with the presence of the inner reef flat, bare sand and cays, whereas the reef front, the outer slope of barrier reef and the *Thalassia* beds were characterized by low zooplankton biomass. Although abundance and biomass of zooplanktonic organisms are generally higher in seagrass beds than in unvegetated habitats (Connolly, 1997 and references therein), sharp spatial gradients in light intensity induce zooplankton swarming in unvegetated habitats. This type of swarm induction observed above patches of pale substrate, which reflect more light than the surrounding dark substrata (Hamner and Carleton, 1979), may explain the biomass difference between seagrass beds and bare sand. The effect of light on the formation and maintenance of patches appears, however, to be better understood in combination with tides, predators and endogenous rhythm processes (Buskey *et al.*, 1995). Considering the temporal variability generated by the sampling design, this mesoscale pattern may result from the nycthemeral migrations of organisms in seagrass beds (e.g. Walters and Bell, 1986, 1994) and on coral reefs (e.g. Robichaux *et al.*, 1981). However, nycthemeral data taken in seagrass meadows and on the barrier reef in the GCSM lagoon (unpublished data) did not corroborate this assumption. Habitat patterning is known to affect many ecological processes including predation intensity (González and Tessier, 1997), predation avoidance (Alvarez-Cadena *et al.*, 1998), and larval dispersal and recruitment (Egglestone *et al.*, 1998). In the GCSM lagoon, Baelde (1990) noticed that primarily coral-reef fish species (e.g., Apogonidae, Pomacentridae and Scorpaenidae) were apparently restricted to seagrass beds near the coral barrier reef (near Fajou Islet, Figure 1). It is also in seagrass beds that many juvenile coral-reef fish (e.g., Lutjanidae, Scaridae) were present at sizes at which they have taken up residence on the coral reefs. They utilize the coral reefs as shelter and the nearby seagrass beds as foraging ground. Emery (1968) also observed in *Thalassia* beds swarms of copepods, which were foraged by several species of fish (e.g. juveniles of *Haemulon aurolineatum*, species also present in the seagrass beds of the GCSM lagoon).

Over mesoscales, the organisms larger than 600 µm living from the coast to the middle of the lagoon showed distinct responses to hydrodynamic forcing, depending on the habitat. It is likely that large zooplankton inhabiting seagrass beds are not adapted to large hydrodynamic forcing, whereas large organisms living on the cays may maintain their position themselves. Seagrass meadows are generally located in shallow waters where wave and tidal actions are not excessive. These meadows alter both the physical and biological characteristics of their surrounding environment by the ability to attenuate waves and to decrease current velocities (Koch and Gust, 1999), and they influence the spatial structure of marine organisms (Turner *et al.*, 1999). Fine-scale hydrodynamics and the resulting turbulent mixing within seagrass beds, however, strongly depend on the hydrodynamic forces (waves and currents) acting upon the plants. Waves, which increase the exchange between the water column and water mass within the meadow (Koch and Gust, 1999), may affect zooplankton patterns in seagrass beds by horizontal (Haury *et al.*, 1990) or/and vertical dispersal (Incze *et al.*, 2001) of organisms.

On the contrary, the shallow cays are strongly exposed to wind, tidal and wave actions; copepods were found individually or in small swarms near the bottom on the cays (Emery, 1968). The morphology and some of the life history characteristics of coastal zooplankton species such as harpacticoid copepods (Villiers and Bodiou, 1996) are adapted to this environmental forcing. In the GCSM lagoon, large zooplankters on the cays seem to display adaptations to moderate to vigorous hydrodynamic conditions. Active behavioral swimming and passive hydrodynamic accumulation may combine to produce biomass peaks (Mackas *et al.*, 1985). Our findings corroborate this hypothesis that biomass accumulation of large organisms on the cays may result from the interaction between advection and swimming capacity.

Although aggregation of organisms by swimming in swarms, associated with hydrodynamic accumulation, may be important in the formation and maintenance of vertical patchiness (1–10 m) and of small horizontal swarms and schools of macrozooplankton, accumulation of organisms at a particular site (or probably more correctly, within a particular hydrodynamic feature) need not require swimming of the organisms into the patch (Mackas *et al.*, 1985). Like depth, the topography of the bottom influences the direction and speed of water flow and they cause local disturbances (Castaing *et al.*, 1984) that may affect the structure of zooplankton communities (Archambault *et al.*, 1998). Thus, irregular bottom topography in the middle of the GCSM lagoon associated with southerly winds and hydrodynamic forcing may induce zooplankton patchiness at mesoscale 9. Under the assumption that large zooplankters are more mobile than small zooplankton, swimming activity of large zooplankton associated with irregular bottom topography and hydrodynamic accumulation may explain the difference between the spatial variance of the two size classes of zooplankton at mesoscale 9 (Table 1). Thus, large zooplankton patchiness may result from aggregation/accumulation mechanisms, while small zooplankton patchiness is likely to be the result of accumulation processes.

Turbulent mixing may help explain the opposite patchiness of phytoplankton and zooplankton fractions detected at mesoscale 9, while no relationship between zooplankton and phytoplankton was identified. Turbidity and swell height implicated in these mesoscale patterns corroborate the assumption that increasing mixing has the potential to decrease primary production by increasing grazing pressure and turbidity due to sediment resuspension (Petersen *et al.*, 1998). The effects of broad- and small-scale mixing clearly depend, however, on complex interactions between organism physiology and behavior, nutrient dynamics, and the light environment (Petersen *et al.*, 1998 and references therein).

4.4 Fine-scale Patterns

Over fine- and mesoscales, habitat patterning influences zooplankton biomass whereas it had no influence on the community characteristics over broad scale. This is consistent with the findings of previous studies (e.g. Blanchard and Bourget, 1999). Although patchiness of small zooplankters may be the result of accumulation processes over fine scales (e.g., scale 12) and habitat patterning influences community structure by modifying biomass (Rios-Jara, 1998), diversity (Eggleston *et al.*, 1999), as well as the distribution and abundance of dominant organisms (Eggleston *et al.*, 1998), others processes must be invoked to explain the fine-scale patchiness of zooplankton. The negative relationship between large zooplankton and phytoplankton biomasses at fine-scale 15 may be partly the result of grazing. Biological processes including feeding (Tiselius, 1992; Yen *et al.*, 1998), predation (González and Tessier, 1997; Alvarez-Cadena *et al.*, 1998) and reproduction (Folt and Burns, 1999), have been evidenced to affect fine-scale patchiness of zooplankton. However, our results do not suggest biological processes explaining this observation. Further studies conducted at fine scales are needed to establish the relationships between fine-scale patchiness of zooplankton and environmental forcing.

Conclusion

Our results support the hypothesis that variability in zooplankton biomass depends upon i) spatial scales, ii) the size of the organisms, and iii) habitat patterning. Our findings suggest that zooplankton patchiness in the GCSM lagoon exists at three different spatial scales: broad (> 5 km), meso (1–5 km), and fine scales (400–1000 m), and that the spatial variability of zooplankton is inscribed in a scale continuum. Although they display different scales of spatial dependency, the large and small zooplankton show common patterns at some scales. Hydrodynamic forcing seems to affect the patchiness of small zooplankton across the scale continuum, while the behaviour of large zooplankton, including swimming activity and food searching, constitutes an important mechanism for the creation of patches. Zooplankton living on cays displays some adaptability to hydrodynamic forcing, which contributes more to the formation of aggregates than for organisms inhabiting seagrass beds.

It is clearly across the meso- and fine scales that the two size classes of zooplankton do not respond in the same way to environmental forcing; their responses are detected at different spatial scales. Wind forcing may explain the lesser spatial patchiness of small zooplankton over mesoscales: the increased intensity of transport of water masses, in the form of broad-scale currents, may lead to lower spatial variability of zooplankton biomass (Piontkovski and Williams, 1995). Different species associations have been described in the literature along coast-to-ocean gradients. The differences have been attributed to water masses (Webber *et al.*, 1996; Alvarez-Cadena *et al.*, 1998) and habitat characteristics (Alvarez-Cadena *et al.*, 1998; Rios-Jara, 1998; Suárez-Morales and Gasca, 2000). Fine-scale patchiness of zooplankton is regulated not only by physical, but also by biological processes (Tiselius, 1998; Folt and Burns, 1999) including feeding, predation, migration, and reproduction (associated with individual behavior). These mechanisms, which affect zooplankton patchiness, are likely to be species-specific (Bollens and Frost, 1991; Rios-Jara and Gonzalez, 2000). Thus, the identification of species associations may help establish the biological processes implicated in the fine-scale patterns of zooplankton.

Turbulent mixing, which is generally enhanced in near-shore ecosystems compared to lakes and the deep ocean, also affects a range of biological processes, mostly related to the size and of organisms and taxonomic composition of the assemblages (Petersen *et al.*, 1998). Small-scale turbulence occurs at scales similar to the size of zooplankton. The effects of mixing on individual organisms (i.e., growth, nutrient uptake, and feeding rates on particles: Peters and Marrasé, 2000) depend upon a number of factors including the intensity of turbulence, zooplankton size, means of motility, and mode of feeding (Petersen *et al.*, 1998). Zooplankton behavior and turbulence mechanisms may be important to understanding the generation and maintenance of small-scale patchiness. The swimming capacity of zooplankton organisms must be viewed as a biological mechanism, which must be considered in the study of zooplankton patchiness and included in mathematical models.

Acknowledgements – This study is part of a research on the multiscale spatial variability of zooplankton in the GCSM lagoon, which was submitted as part of the requirements for a Ph.D. degree at Université de Montréal (Canada) and Université Paris 6 (France). This work was supported by a doctoral fellowship from the Ministère de la Recherche et de l'Enseignement Supérieur and the Ministère des Affaires Étrangères of France granted to C. A.-J. Field work was financed by Ministère de la Recherche (France), Parc National de la Guadeloupe, and NSERC (Canada) grant number OGP7738 to P. Legendre.

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Appendix A: Habitat characteristics at each sampling site along the transect. d: distance from the coast (km); depth (m).

Site	d	Depth	Habitat	Site	d	Depth	Habitat
1	0.10	2.1	Bare mud (shallow bottom)	27	5.79	0.4	Cay — Corals
2	0.24	4.8	Bare mud (shallow bottom)	28	5.79	1.5	Cay — Sea-grasses
3	0.36	7.3	Bare mud (deep bottom)	29	5.98	1.4	Cay — Sea-grasses
4	0.61	1.3	Sea-grass beds on mud (76-100% coverage)	30	6.16	0.8	Cay — Corals
5	0.61	1.4	Sea-grass beds on mud (76-100% coverage)	31	6.16	2.0	Cay — Sea-grasses
6	0.70	1.2	Sea-grass beds on mud (76-100% coverage)	32	6.28	1.0	Cay — Corals
7	0.97	1.9	Sea-grass beds on mud (76-100% coverage)	33	6.55	3.1	Sea-grass beds on sand (51-75% coverage)
8	1.03	1.5	Sea-grass beds on mud (76-100% coverage)	34	6.70	1.7	Sea-grass beds on sand (51-75% coverage)
9	1.09	3.3	Sea-grass beds on muddy sand (76-100% coverage)	35	7.28	1.9	Bare sand
10	1.12	0.6	Cay — Corals	36	7.28	2.1	Bare sand
11	1.12	0.8	Cay — Corals	37	7.46	2.0	Sea-grass beds on sand (51-75% coverage)
12	1.15	1.7	Sea-grass beds on muddy sand (76-100% coverage)	38	7.46	2.1	Sea-grass beds on sand (51-75% coverage)
13	1.33	0.9	Cay — Corals	39	7.58	1.7	Sea-grass beds on sand (51-75% coverage)
14	1.40	1.8	Sea-grass beds on muddy sand (76-100% coverage)	40	7.58	1.9	Sea-grass beds on sand (51-75% coverage)
15	1.70	10.8	Bare mud (deep bottom)	41	7.70	2.0	Bare sand
16	2.34	15.5	Bare mud (deep bottom)	42	7.70	1.8	Bare sand
17	2.88	3.8	Sea-grass beds on muddy sand (0-25% coverage)	43	7.86	1.1	Inner reef flat
18	3.15	19.5	Bare mud (deep bottom)	44	7.86	1.4	Inner reef flat
19	3.70	1.7	Cay — Mixed sea-grasses and corals	45	7.86	1.4	Inner reef flat
20	3.76	0.9	Cay — Mixed sea-grasses and corals	46	8.07	2.6	Reef front
21	3.91	1.0	Cay — Mixed sea-grasses and corals	47	8.07	2.6	Reef front
22	4.13	1.7	Cay — Mixed sea-grasses and corals	48	8.25	9.8	Outer slope of barrier reef
23	4.25	10.3	Bare mud (deep bottom)	49	8.25	9.5	Outer slope of barrier reef
24	4.85	16.4	Bare mud (deep bottom)	50	8.40	21.8	Outer slope of barrier reef
25	5.16	6.2	Sea-grass beds on sand (26-50% coverage)	51	8.40	16.3	Outer slope of barrier reef
26	5.37	3.0	Sea-grass beds on sand (26-50% coverage)				

Table I: Spatial variance of zooplankton biomass detected at different scales for the two size classes of zooplankton, called 190–600 µm and > 600 µm. The scales that both size classes have in common are indicated in bold. %: percentage of the total variance explained by the trend, the spatial pattern at each significant scale, and the whole spatial model.

	> 600 µm		190–600 µm	
	Variance	%	Variance	%
TOTAL	0.4641		0.4178	
SPATIAL MODEL	0.1907	41.1^{**}	0.3301	79.0^{***}
Trend	**0.0577**	$\mathbf{12.4}^{**}$	**0.2052**	$\mathbf{49.2}^{***}$
Scale 4	0.0434	9.4^{**}		
Scale 6	**0.0521**	$\mathbf{11.2}^{**}$	**0.0262**	$\mathbf{6.3}^{***}$
Scale 7			0.0043	1.0^{*}
Scale 8			0.0085	2.0^{*}
Scale 9	**0.0249**	$\mathbf{5.4}^{**}$	**0.0032**	$\mathbf{0.8}^{*}$
Scale 12			0.0069	1.6^{*}
Scale 14			0.0072	1.7^{*}
Scale 15	0.0126	2.7^{*}		
Scale 16			0.0171	4.1^{**}
Scale 18			0.0079	1.9^{*}
Scale 23			0.0355	8.5^{***}
Scale 24			0.0081	1.9^{*}
RESIDUAL	0.2734		0.0877	

$^{***}p \leq 0.001$, $^{**}p \leq 0.01$, $^{*}p \leq 0.05$

Table II: Partial standard regression coefficients of the environmental variables, which significantly explained the spatial patterns of the large and small zooplankton at different scales. The common scales are marked in bold.

	Depth	Salinity	DO	NTU	Speed	Swell	Phyto	Bms	Bmd	Sm	Sms0	Sms76	Ss26	Ss51	Cs	Cc	Cm	Reef	Total
Trend		**–0.259**	**0.133**		**0.251**		**0.661**												**0.93** ***
Scale 4	–0.426		–0.379												0.378	0.142	–0.275	0.252	0.72 ***
Scale 6			**0.214**			**0.324**				**–0.458**							**0.565**		**0.67** ***
Scale 7			–0.527										–0.441	0.241	–0.247		0.186		0.46 ***
Scale 8			0.299						–0.191	0.311	–0.189				0.309	0.237	0.705		0.73 ***
Scale 9				**0.446**		**0.474**			**–0.409**				**–0.532**						**0.42** ***
Scale 12					–0.266			0.446		–0.391			0.321						0.64 ***
Scale 14														0.364					0.13 **
Scale 15							–0.238	0.318					0.276						0.24 **
Scale 16								–0.391	–0.274	–0.353	0.234		0.291						0.40 ***
Scale 18											0.268			–0.249					0.14 *
Scale 23												0.257							0.06 *
Scale 24													0.294						0.09 *

DO: dissolved oxygen, NTU: turbidity, Speed: wind speed, Swell: swell height, Bms: shallow bare muddy bottom, Bmd: deep bare muddy bottom, Sm: sea-grass beds on mud (76–100% coverage), Sms0 and 76: sea-grass beds on mud-sand (0–25% and 76–100% coverage), Ss26 and 51: sea-grass beds on sand (26–50% and 51-75% coverage), Cs: cay—sea-grass beds, Cc: cay—coral species, Cm: cay—mixed sea-grass beds and coral species. Reef flat: inner reef flat, Phyto: phytoplankton, Total: fraction of total variance explained by all selected environmental variables in the model. $^{***}p \leq 0.001$, $^{**}p \leq 0.01$, $^{*}p \leq 0.05$

Table III: Spatial variance of the phytoplankton biomass detected at different scales and partial standard regression coefficients of the environmental variables, which significantly explained the spatial patterns. %: percentage of the total variance explained by the trend, the spatial pattern at each significant scale, and the whole spatial model.

	Variance	%	Salinity	DO	NTU	Speed	Sms0	Ss26	Total
TOTAL	0.2047								
SPATIAL MODEL	0.1815	88.7^{***}							
Trend	0.1782	87.1^{***}	–0.479	0.304	–0.259	0.559			0.81^{***}
Scale 9	0.0013	0.6^{*}			–0.265		–0.266	0.411	0.29^{***}
Scale 27	0.0020	1.0^{*}							
RESIDUAL	0.0232								

DO: dissolved oxygen, NTU: turbidity, Speed: wind speed, Bm: bare muddy, Sms0: sea-grass beds on mud-sand (0–25% coverage), Ss26: sea-grass beds on sand (26–50%), Cm: cay—mixed sea-grass beds and coral species, Total: fraction of the total variance explained by all selected environmental variables in the model. $^{***}p \leq 0.001$, $^{**}p \leq 0.01$, $^{*}p \leq 0.05$

Figure Legends

Figure 1. Distribution of the habitats in the Grand Cul-de-Sac Marin (GCSM) lagoon. Location of the sampling sites along the South-North transect from the coast to the Caribbean Sea. Mangroves cover most of the shorelines, seagrass beds are found at 0-10 m depth, and muddy bottoms at depths higher than 10 m.

Figure 2. Summary of the method for detecting the zooplankton spatial patterns and for identifying the environmental factors affecting the spatial variability of zooplankton. Step 1: trend extraction for each zooplankton and environmental variable. Steps 2–5: PCNM analysis for the zooplankton residual values. Step 6: Multiple regression of the zooplankton spatial variables identified by PCNM against the detrended environmental variables.

Figure 3. Summary of the PCNM method (steps 2–5). This analysis produces the spatial patterns of zooplankton (I) and the scalogram (II).

Figure 4. Salinity, dissolved oxygen (DO), turbidity, wind speed, swell height, phytoplankton biomass (total chlorophyll *a*) and zooplankton biomass (190–600 µm and > 600 µm) observed along the transect.

Figure 5. Scalogram showing the variance spectrum for the two size classes of zooplankton (190–600 µm and > 600 µm) as well as for phytoplankton. Full symbols indicate a significant fraction of spatial variance detected at a given scale.

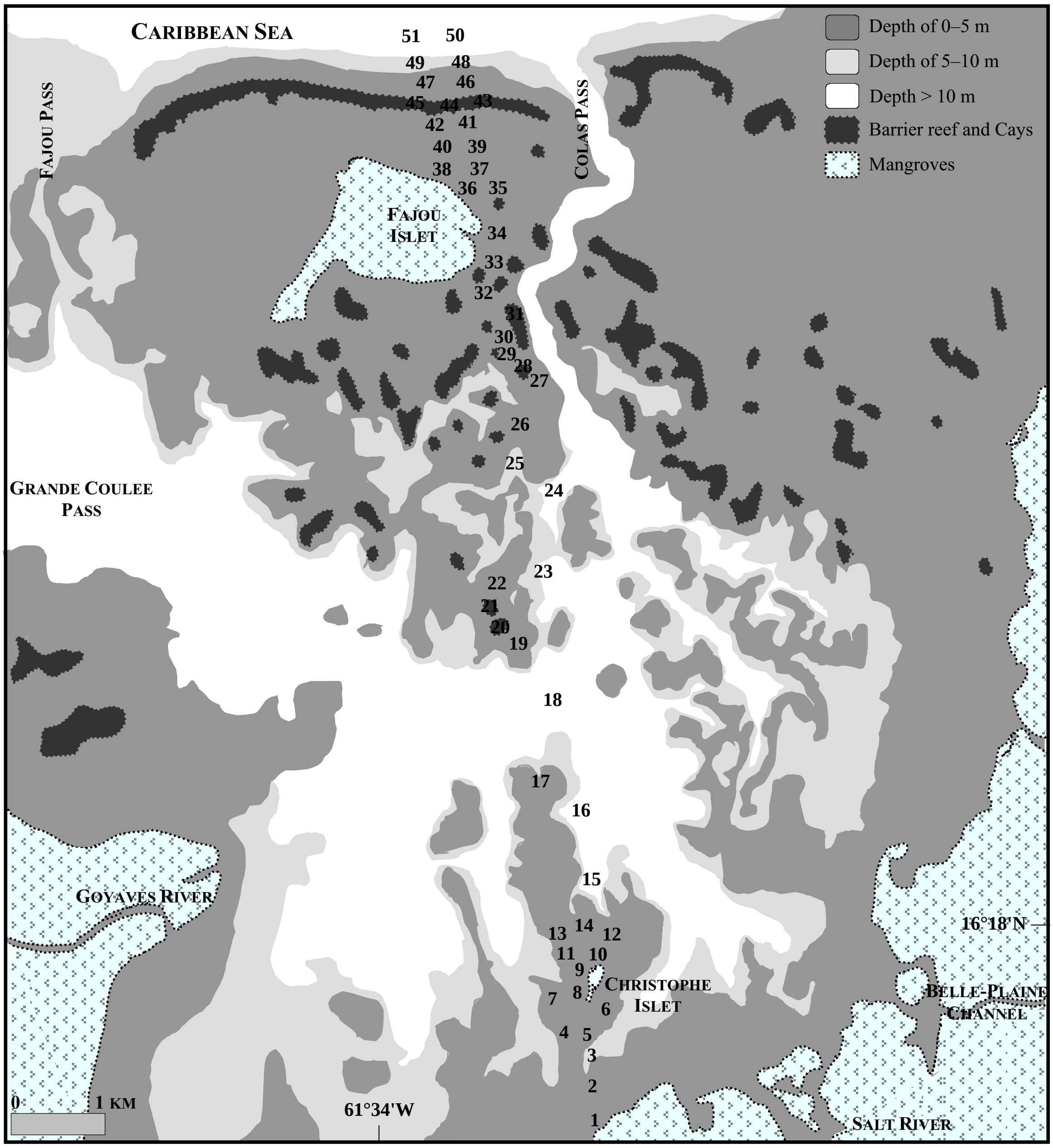
Figure 6. Significant spatial patterns of large zooplankton (> 600 µm) detected at the various scales and spatial model (sum of the 5 submodels). Abscissa: distance of the sampling sites from the coast. Ordinate: fitted values to the given spatial variable.

Figure 7. Significant spatial patterns of small zooplankton (190–600 µm) detected at the various scales and spatial model (sum of the 11 submodels). Abscissa: distance of the sampling sites from the coast. Ordinate: fitted values to the given spatial variable.

Figure 8. Significant spatial patterns of phytoplankton detected at the various scales. Abscissa: distance of the sampling sites from the coast. Ordinate: fitted values to the given spatial variable.

Figure 9. Mantel analysis of the relationships among matrices representing zooplankton variables (a: > 600 µm, b: 190–600 µm), phytoplankton, and space. In the tables, above the diagonals: simple Mantel statistics; below: partial Mantel statistics controlling for the effect of the third matrix. Significant statistics are coded as follows: $^{***}p \leq 0.001$, $^{**}p \leq 0.01$, $^{*}p \leq 0.05$, ns: not significant. Right: causal models supported by the results.

Figure 1


CARIBBEAN SEA
Depth of 0–5 m
Depth of 5–10 m
Depth > 10 m
Barrier reef and Cays
Mangroves
FAJOU PASS
COLAS PASS
FAJOU ISLET
GRANDE COULEE PASS
GOYAVES RIVER
CHRISTOPHE ISLET
BELLE-PLAINE CHANNEL
SALT RIVER
16°18'N
61°34'W
0
1 KM
51 50
49 48
47 46
45 44 43
42 41
40 39
38 37
36 35
34
33
32
31
30
29
28
27
26
25
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22
21
20
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6
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3
2
1

Figure 2

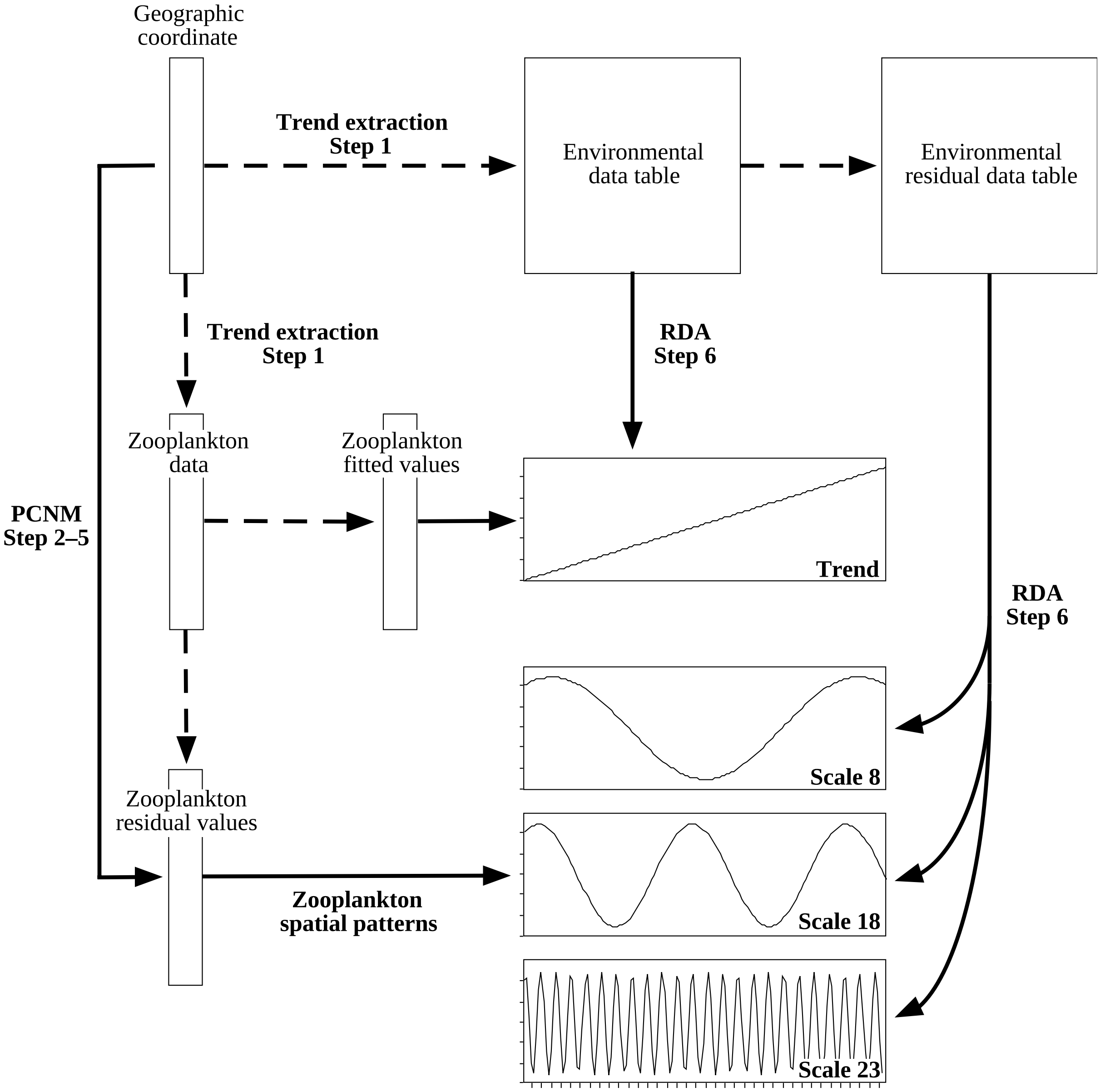

Geographic coordinate
Trend extraction Step 1
Environmental data table
Environmental residual data table
Trend extraction Step 1
RDA Step 6
Zooplankton data
Zooplankton fitted values
PCNM Step 2–5
Trend
RDA Step 6
Scale 8
Zooplankton residual values
Zooplankton spatial patterns
Scale 18
Scale 23

Figure 3

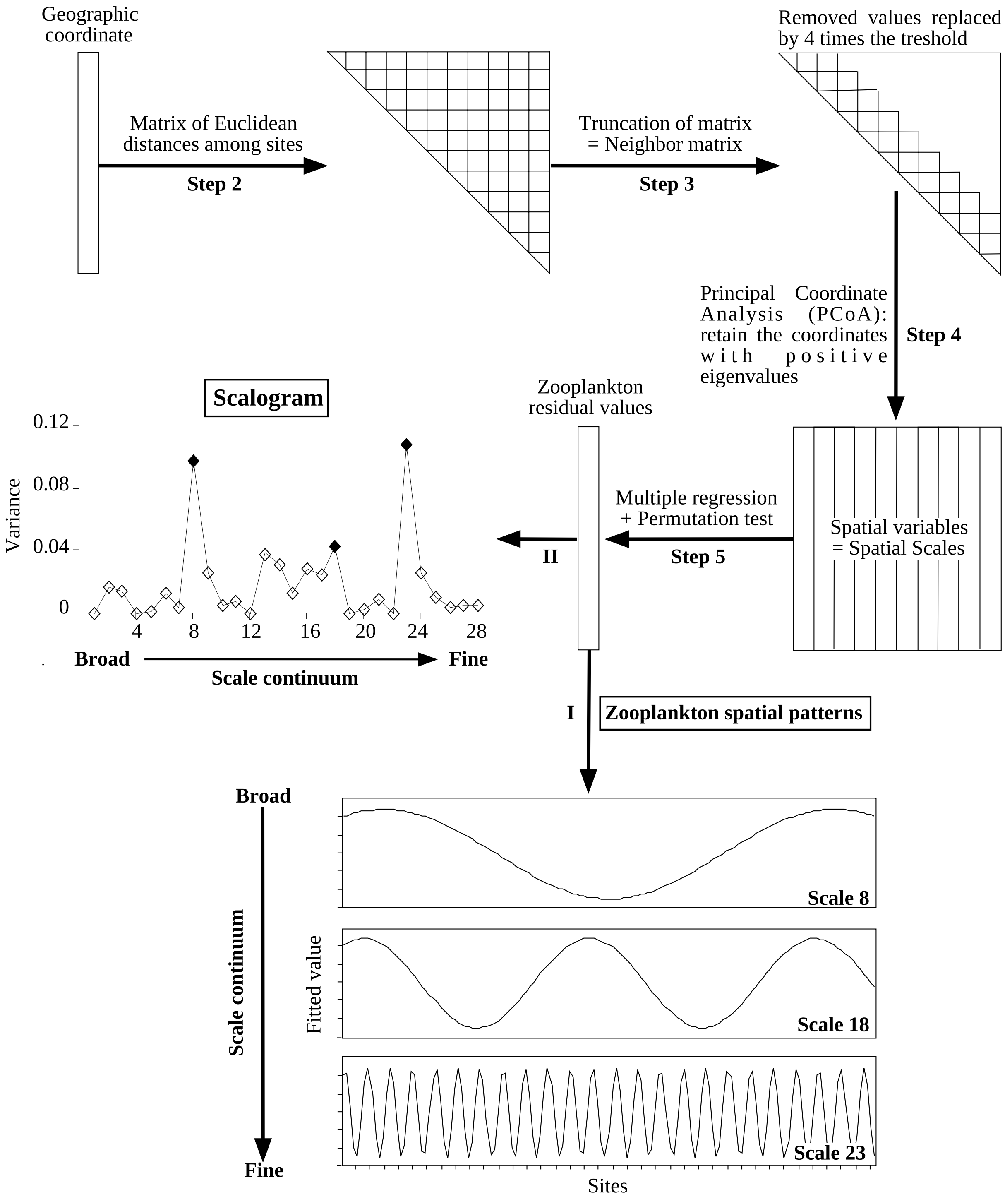
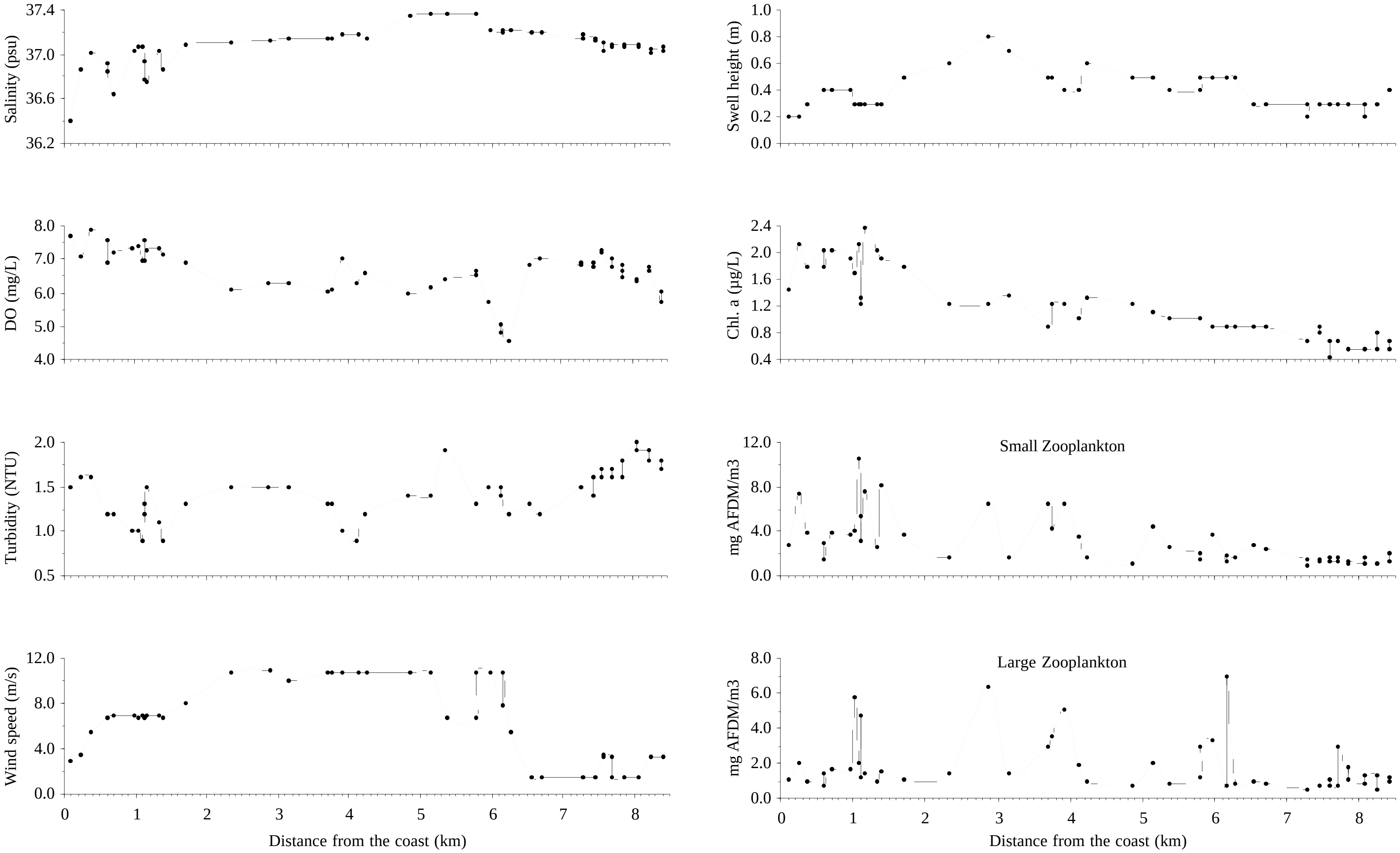

Geographic coordinate
Matrix of Euclidean distances among sites
Step 2
Truncation of matrix = Neighbor matrix
Step 3
Removed values replaced by 4 times the treshold
Principal Coordinate Analysis (PCoA): retain the coordinates with positive eigenvalues
Step 4
Zooplankton residual values
Multiple regression + Permutation test
Step 5
Spatial variables = Spatial Scales
II
Scalogram
Variance
0.12
0.08
0.04
0
4
8
12
16
20
24
28
Broad
Fine
Scale continuum
I
Zooplankton spatial patterns
Broad
Scale continuum
Fine
Fitted value
Scale 8
Scale 18
Scale 23
Sites

Figure 4



Salinity (psu)
37.4
37.0
36.6
36.2
Swell height (m)
1.0
0.8
0.6
0.4
0.2
0.0
DO (mg/L)
8.0
7.0
6.0
5.0
4.0
Chl. a (µg/L)
2.4
2.0
1.6
1.2
0.8
0.4
Turbidity (NTU)
2.0
1.5
1.0
0.5
Small Zooplankton
mg AFDM/m3
12.0
8.0
4.0
0.0
Wind speed (m/s)
12.0
8.0
4.0
0.0
Large Zooplankton
mg AFDM/m3
8.0
6.0
4.0
2.0
0.0
0
1
2
3
4
5
6
7
8
Distance from the coast (km)
Distance from the coast (km)

Figure 5

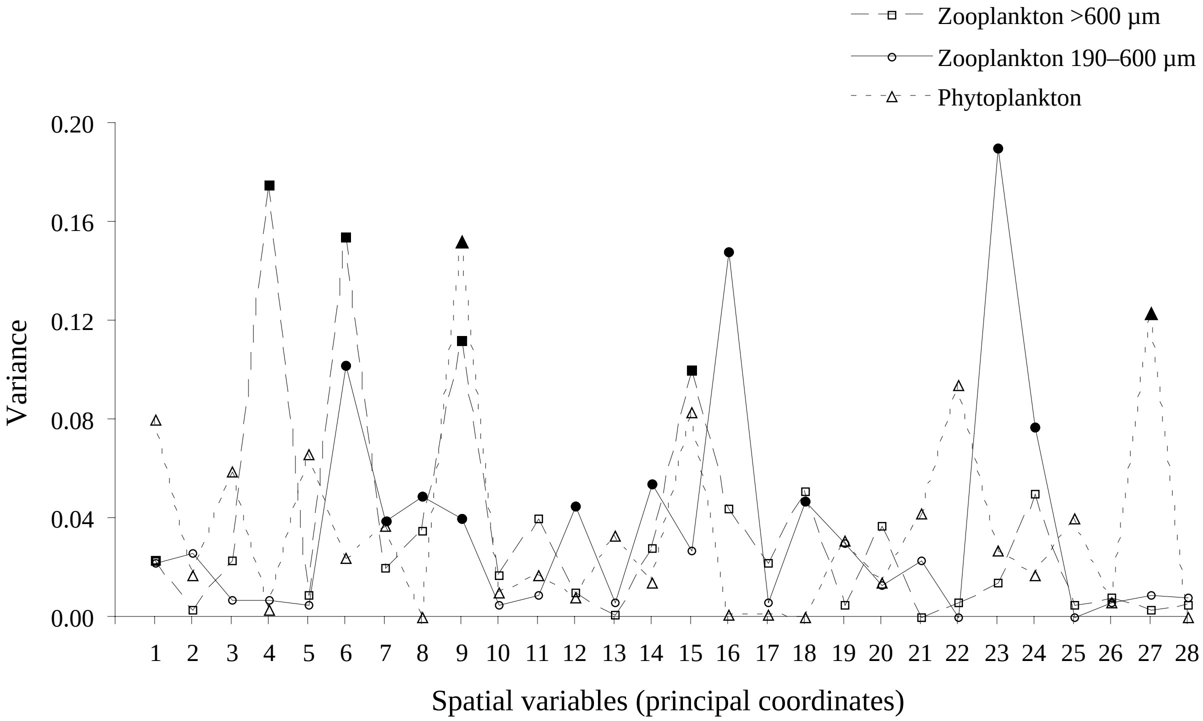

Zooplankton >600 µm
Zooplankton 190–600 µm
Phytoplankton
Variance
0.20
0.16
0.12
0.08
0.04
0.00
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28
Spatial variables (principal coordinates)

Figure 6

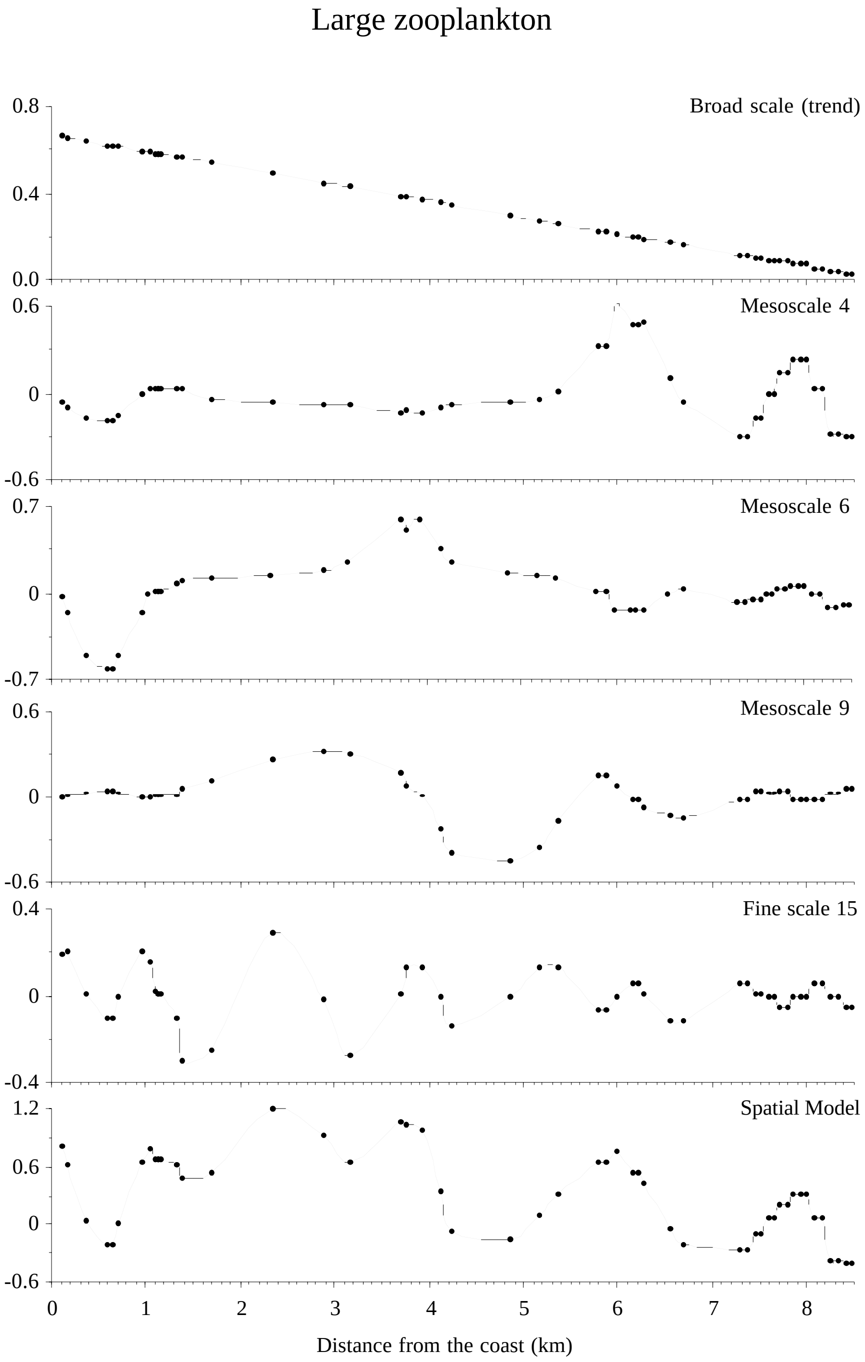

Large zooplankton
Broad scale (trend)
0.8
0.4
0.0
Mesoscale 4
0.6
0
-0.6
Mesoscale 6
0.7
0
-0.7
Mesoscale 9
0.6
0
-0.6
Fine scale 15
0.4
0
-0.4
Spatial Model
1.2
0.6
0
-0.6
0
1
2
3
4
5
6
7
8
Distance from the coast (km)

Figure 7

Small zooplankton

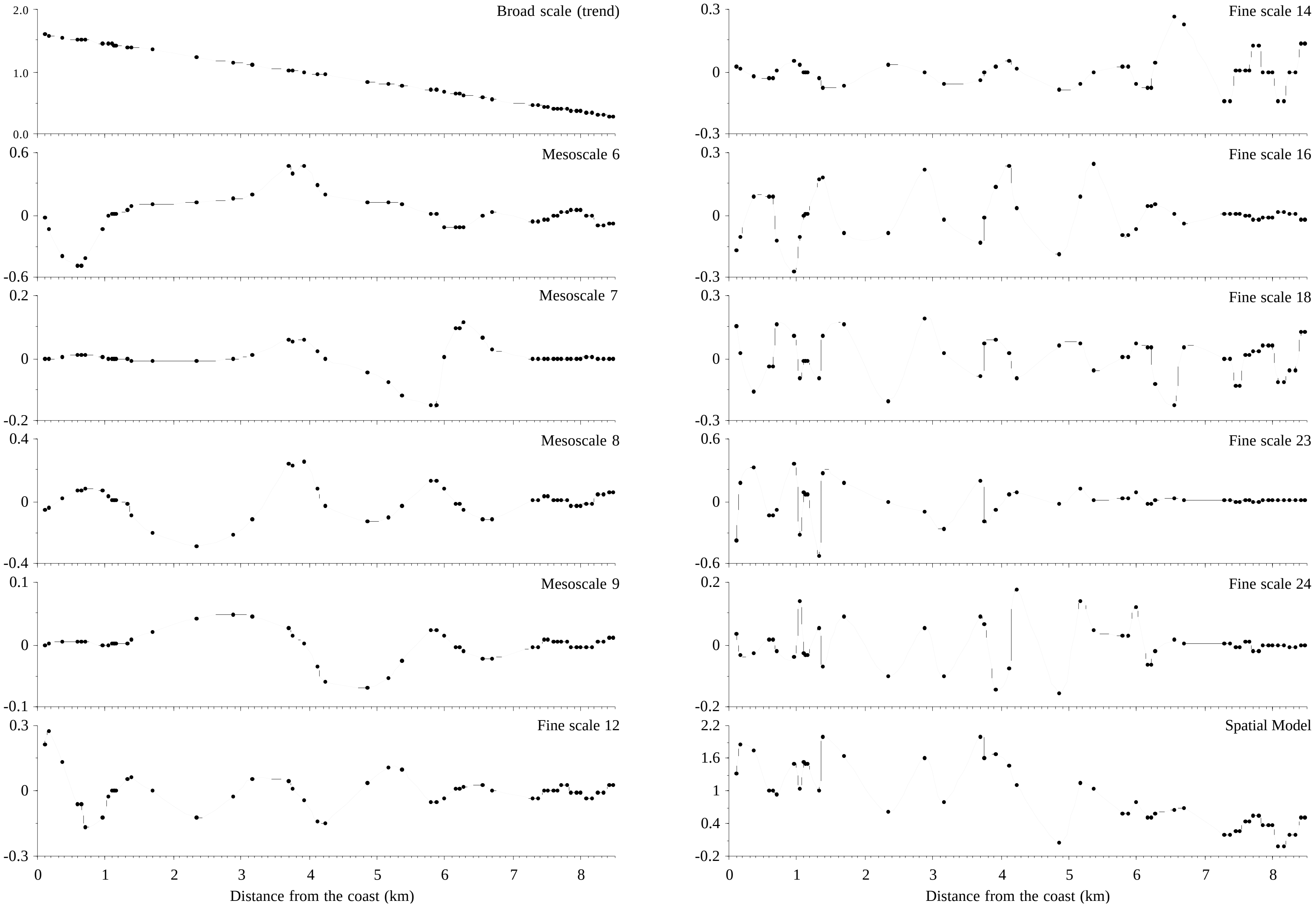


Figure 8

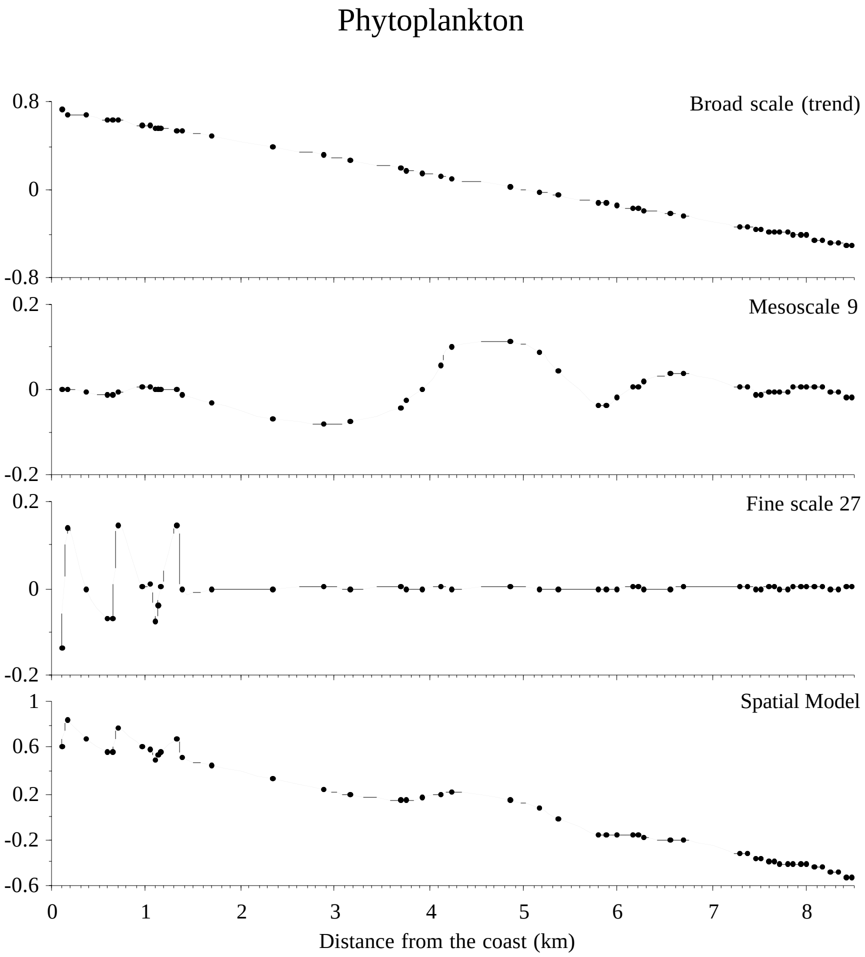
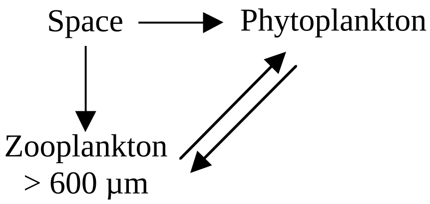

Phytoplankton
Broad scale (trend)
0.8
0
-0.8
Mesoscale 9
0.2
0
-0.2
Fine scale 27
0.2
0
-0.2
Spatial Model
1
0.6
0.2
-0.2
-0.6
0
1
2
3
4
5
6
7
8
Distance from the coast (km)

Figure 9

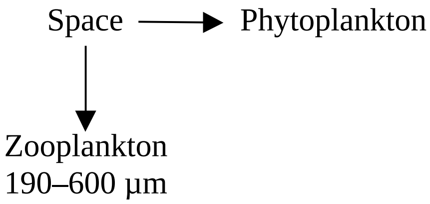
(a) Zooplankton > 600 µm-Phytoplankton-Space relationships

	> 600 µm	Phyto	Space
> 600 µm	–	-0.062 ns	0.023 ns
Phyto	-0.143 **	–	0.823 ***
Space	0.131 *	0.827 ***	–



(b) Zooplankton 190–600 µm-Phytoplankton-Space relationships

	190–600 µm	Phyto	Space
190–600 µm	–	0.393 ***	0.423 ***
Phyto	0.087 ns	–	0.823 ***
Space	0.191 **	0.789 ***	–



CHAPITRE 6

PATRONS SPATIAUX DE L'ABONDANCE ET DE LA BIOMASSE DU ZOOPLANCTON TROPICAL : ROLE DE L'ÉCHELLE ET DES FACTEURS ENVIRONNEMENTAUX

6.1 Résumé de l'Article en Français

Une étude a été réalisée pour estimer les processus physiques et biologiques qui influencent les patrons spatiaux du mésozooplancton tropical dans un lagon récifal côtier en Guadeloupe (Antilles Françaises, Mer des Caraïbes), en considérant deux classes de taille (190–600 µm et > 600 µm). La variabilité spatiale de la biomasse et de l'abondance du mésozooplancton a été examinée le long d'un transect et mise en relation avec l'hétérogénéité environnementale. En utilisant une pompe à plancton, l'échantillonnage a été réalisé pendant la saison sèche (Mars 1999) à 51 stations disposées le long d'un transect allant de la côte vers le large. La méthode des coordonnées principales des matrices de voisin, une nouvelle forme d'analyse multiéchelle, a été utilisée pour déterminer les patrons spatiaux du zooplancton de petite à grande échelles. Les patrons spatiaux pour les deux fractions de mésozooplancton changent le long du continuum d'échelles. (1) Bien que les échelles de dépendance spatiale du petit et du gros zooplancton sont différentes, les deux fractions montrent les mêmes patrons à certaines échelles spatiales. (2) Le petit zooplancton (190–600 µm) a une variabilité multiéchelle de la biomasse et de l'abondance plus élevée que celle du gros zooplancton (> 600 µm). (3) Les échelles spatiales de la biomasse et de l'abondance du petit zooplancton sont identiques, alors que (4) le gros zooplancton présente différents patrons multiéchelles pour la biomasse et l'abondance. Nos résultats suggèrent que l'hydrodynamique locale, les influences océaniques et côtières, la structure spatiale du phytoplancton, le comportement du zooplancton et l’hétérogénéité de l’habitat génèrent les patrons spatiaux observés. Les types et les effets de ces processus dépendent de l’échelle spatiale.

6.2 Article 4 : Spatial Patterns in Abundance and Biomass of Tropical Zooplankton: The Role of Scale and Environmental Factors (soumis à *Marine Ecology Progress Series*)

Abstract – A study was conducted to assess the leading physical and biological processes influencing the spatial patterns of tropical mesozooplankton in a coral reef lagoon in Guadeloupe (French West Indies, Caribbean Sea), considering two size classes (190–600 µm and > 600 µm). The spatial variability of mesozooplankton biomass and abundance was examined along a transect, and related to environmental heterogeneity. Using a high capacity pump, sampling was carried out during the dry season (March 1999) at 51 stations arranged along a cross-shelf transect from the coast to the open sea. The method of principal coordinates of neighbour matrices—a new form of multiscale analysis—was used to determine the spatial patterns of zooplankton from fine to broad scales. Spatial patterns for mesozooplankton fractions changed along the continuum of scales. (1) Although the small and large zooplankton displayed different scales of spatial dependency, they showed common patterns at some scales. (2) The small zooplankton (190–600 µm) exhibited more multiscale variability in biomass and abundance than large zooplankton (> 600 µm). (3) The spatial scales of variability in biomass and abundance of the small zooplankton were similar, whereas (4) large zooplankton presented different multiscale patterns for biomass and abundance. Our results suggest that local hydrodynamics, coastal and oceanic influences, phytoplankton patchiness, zooplankton behaviour, and habitat patterning generated the observed spatial patterns. The types and effects of these processes depended upon spatial scale.

Introduction

All ecological systems exhibit spatial patterns–the non-random spatial variability of populations, communities or ecosystems–over a broad range of scale. This variability is fundamental to population dynamics, community organization, and element cycling. Such variability is encountered in zooplankton communities in which the overwhelming majority of species show over-dispersed (aggregated) dispersal patterns along the horizontal and vertical axes (Haury & Wiebe 1982). In marine environments, zooplankton patchiness has been observed at different scales (e.g. Haury et al. 1978, Legendre et al. 1986); the size patch varying from a few centimetres (micro-scale: 1 cm–1 m) to thousands of kilometres (mega-scale: 10^3–10^4 km). The implications of zooplankton spatial heterogeneity for the structure and functioning of marine ecosystems (Pinel-Alloul 1995) have been highlighted with respect to various processes: species reproduction (Hamner & Carleton 1979, Haury & Wiebe 1982, Folt & Burns 1999), population dynamics (Noda et al. 1998, Froneman et al. 2000), and prey-predator interactions (Tiselius 1992, Ribes et al. 1996, Folt & Burns 1999). They are also important to determine sampling strategies at the population and community levels (Omori & Hamner 1982, Avois et al. 2000). Most investigations have focused on zooplankton spatial variability in temperate and tropical oceanic areas (e.g. Piontkovski & Williams 1995, Marguerit et al. 1998, Seuront & Lagadeuc 2001), but little attention has been paid to the spatial structure of coastal tropical zooplankton. There is a pressing need to monitor coastal reef ecosystems (Hughes 1994) in order to assess the spatial and temporal scales of the damages that may be occurring through natural disturbances (Hughes 1994) and impacts of human activities (Sale 1999). The study of the structure and dynamics of coastal tropical zooplankton is also of fundamental importance to understand the mechanisms involved in the functioning of these systems.

Spatial patterns of zooplankton are linked to physical processes: climatic and hydrodynamic regimes such as currents, eddies, turbulent mixing, internal waves, and tidal and regional wind forcing (Mackas et al. 1985, Pinel-Alloul 1995, Petersen et al. 1998, Incze et al. 2001).

Biological processes have recently been shown to contribute to zooplankton spatial patterns (reviewed by Folt & Burns 1999), whereas physical mechanisms alone proved insufficient to explain many spatial patterns found in plankton (e.g., Wiafe and Frid 1996). New studies about fine-scale biological processes (Tiselius 1998) have altered our perception of the behavioural capacity and flexibility of zooplankton. They also grappled with the quantitative assessments of the relative contributions of biology and physics to spatial structures (Pinel-Alloul 1995, Alvarez-Cadena et al. 1998), and the extent to which biological processes counteract physical driving forces (Folt & Burns 1999). Four biological mechanisms associated with the underlying individual behaviour of zooplankton (Folt & Burns 1999) are often cited for their potential responsibility in creating zooplankton spatial patterns: 'diel vertical migrations', 'locating food patches', 'predator avoidance', and 'mating behavior' (Bollens & Frost 1991, Tiselius 1992, Yen et al. 1998). The physical and biological mechanisms responsible for structuring zooplankton in space refer to the 'multiple driving forces hypothesis' (Pinel-Alloul 1995). The relative importance of these processes corresponds to a gradation in effects over scales, the physical effects predominating at broad spatial scales while biological effects predominate at finer scales.

Because the environment is a spatially structured and dynamic system, the ecological patterns and the generating processes are dependent on space and time. All physical and biological processes operate at specific spatial and temporal scales (Legendre et al. 1986), generating scale-dependent patterns (Haury et al. 1978, Mackas et al. 1985). Scales and patterns are intertwined. The idea of considering the spatial variability of planktonic communities as a 'multiscale process' was introduced into marine biology nearly 30 years ago by Platt & Denman (1975). It was developed and elaborated further (Haury et al. 1978) to the level of a paradigm called the 'multiscale spatial and temporal variability of marine ecosystems'. Recent studies have described the multiscale spatial patterns of zooplankton in marine environments (e.g. Pascual et al. 1995, Ribes et al. 1996, Marguerit et al. 1998, Avois-Jacquet et al. *submitted*). The intensity and spatial scales of zooplankton spatial structures differ with respect to size and swimming capacity or motility (Haury & Wiebe 1982, Mackas et al. 1985). Indeed, the swarms formed by macrozooplankton typically show more intense and finer spatial aggregates than do the smaller and less mobile micro- and mesozooplankton (Piontkovski & Williams 1995). This trend is also observed from phytoplankton to macrozooplankton (Mackas et al. 1985, Piontkovski et al. 1995). Larger freshwater zooplankton seems, however, to be less patchy than small zooplankton (Pinel-Alloul et al. 1988). These authors suggested that greater aggregation might allow small zooplankters to avoid predators and locate mates, while reduced patchiness in large species may decrease competition. On the other hand, if environmental forcing tends to disperse aggregates (e.g. turbulent mixing, random resource distributions), then larger, more mobile organisms might be able to maintain themselves in large social aggregates (Haury et al. 1990, Ribes et al. 1996). When physical processes overwhelm zooplankton locomotion, physical mechanisms may aggregate zooplankton with algae passively, particularly if the organisms are similar in shape, buoyancy or motility (Yen et al. 1998). These authors recognize that turbulence, which is a key factor regulating zooplankton dynamics at the population and community levels (Davis et al. 1991), affects a range of biological processes related to the size and the taxa of organisms (Petersen et al. 1998).

The spatial scales of variability also differ between zooplankton community composition and zooplankton biomass (Mackas 1984). Indeed, a large fraction of biomass variability occurs within the confines of fairly uniform community patches. This implies that the dominant generating processes differ across spatial scales for community composition versus biomass variability (Mackas et al. 1985). Salas-de-Leon et al. (1998) showed that zooplankton biomass was affected by river inputs through nutrient run-off and upwelling, whereas the spatial variability of community composition was controlled by the general hydrodynamics of the bay, which occurred at larger spatial scale. In contrast, the multiscale spatial patterns of zooplankton biomass and abundance seem to be similar, which suggests that they are generated by the same processes. In coastal tropical areas, several studies have evidenced a decreasing gradient in zooplankton biomass and abundance as well as an increasing gradient in species number from the coast to the open sea (e.g. Moore & Sander 1979, Alvarez-Cadena et al. 1998, Hassett & Boehlert 1999). Phytoplankton distribution (Webber et al. 1992, Rios-Jara 1998, Hassett and Boehlert 1999), predation (Moore & Sander 1979, Noda et al. 1998), wind-driven currents (Alvarez-Cadena et al. 1998, Hassett & Boehlert 1999) and tidal-induced mixing, as well as internal waves (Leichter et al. 1998), have been suggested to explain the biomass-abundance gradient, but the scales of spatial dependency of zooplankton biomass and abundance, and of their generating processes, have not been studied.

In the present study, we examined the spatial variability of mesozooplankton abundance and biomass with respect to scales and environmental heterogeneity. Tropical zooplankton samples were collected in the Grand Cul-de-Sac Marin lagoon (GCSM) in Guadeloupe (French West Indies). We considered two size classes of zooplankton (190–600 µm and > 600µm). The aims of our study were to i) describe the multiscale spatial patterns of mesozooplankton biomass and abundance, ii) assess the leading physical and biological processes hypothesized to be responsible for the mesozooplankton spatial patterns, and iii) test the hypothesis that the biomass and abundance variabilities of zooplankton display the same scales of spatial dependency; an alternative hypothesis was that the largest zooplankters show more intense and finer-scale variability than the smaller organisms.

Materials and Methods

Study site

The GCSM lagoon is a shallow coastal reef lagoon (mean depth = 5 m, maximum depth = 30 m) on the northern coast of Guadeloupe in the eastern Caribbean Sea (61°34’W, 16°18’N). The lagoon is characterized by a barrier coral reef with several passes allowing connections between the lagoon and the Caribbean Sea; an extensive shallow area with cays; and a deeper channel system in the middle of the lagoon (Fig. 1). The dominant winds are easterlies (i.e. trade wind direction) and generate north-easterly surface currents which push water outside the lagoon through the Grande Coulée pass (Fig. 1). The tide has a mixed character (i.e. diurnal or semi-diurnal) ranging from 50 to 60 cm. The hydrodynamics of the GCSM lagoon generates a complex circulation forming two distinct dynamic areas: a northern area (from the barrier reef to site 17) where the anticyclonic gyre action allows renewal of the water with the support of waves and surface wind-driven currents, and a southern area (from the coast to site 17) which is semi-sheltered and where water renewal is limited (Assor & Julius 1987). The physics and chemistry of the GCSM lagoon confirm the existence of low-energy dynamics in the southern and eastern portions of the lagoon (Assor & Julius 1987). This coastal reef lagoon shelters various habitats, including the barrier coral reef, the cays (i.e. shallows located inside the lagoon, inhabited by sea grasses and/or coral), the seagrass meadows dominated by *Thalassia testudinum*, and the mangroves located on the intertidal mud flats. All these features are found along the transect ranging from the island coast to the open sea (Fig. 1). The GCSM lagoon forms a transition zone between the marine and insular systems. It is highly vulnerable to natural disturbances like hurricanes (Bouchon et al. 1991) and impacts of human activities (Bernard 1995).

Sampling and processing

Mesozooplankton and phytoplankton were sampled using a high capacity pump (Monarch BSGF-8 self-priming centrifugal pump). Sampling was diurnal (from 8:00 to 16:00); it was carried out during the dry season (March 1999) at 51 sites arranged along a cross-shelf transect, 8.4 km in length, from the coast to the Caribbean Sea (Fig. 1). This transect followed a gradient of temperature, salinity and sedimentology (Assor & Julius 1987) crossing the different habitats of the GCSM lagoon. Samples were collected in all habitats crossed by the transect; two or three sites were selected in each type of habitat (Table 1). Sites not exceeding 5 m in depth were sampled one metre from the bottom, while the others sites whose depth exceeded 5 m were sampled one metre below the sea surface. Due to the irregular distribution of the types of habitat, the distance between neighbouring sampling sites was not regular; the sampling interval varied from 100 to 500 m. The width of the lagoon imposed the extent of the observations (8.4 km in length), while the volume of pumped seawater defined the size of the sampling units (grain size: 2.5 m^3 for zooplankton and $2 \cdot 10^{-3}$ m^3 for phytoplankton).

Eleven environmental variables were measured at each site: temperature, dissolved oxygen, turbidity, salinity, maximum depth, transparency, wind direction and speed, swell height, cloud coverage, and concentration of total chlorophyll *a* (i.e. chlorophyll *a* + phaeopigment). Each site was also described in terms of habitat features (Table 1). Each zooplankton sample was divided in two parts using a Folsom splitter. One of the sub-samples was used for measuring zooplankton biomass, the other for abundance. Zooplankton biomass was estimated by ash-free dry mass (AFDM), considering the two fractions of zooplankton (190–600 µm and > 600µm) separately. The sampling design as well as the field and laboratory methods (except for zooplankton abundance) are described in Avois-Jacquet et al. (*submitted*).

An optical plankton counter (*OPC–1L Lab. Unit*, Focal Technologies Inc. 1992a) was used to quantify zooplankton abundance, by measuring the optical surface area of the organisms. Particles passed into a flow-through tunnel where they crossed a thin rectangular light beam, which measured the profile area of each individual target. The electronic size of each particle was converted into an equivalent spherical diameter (ESD). The OPC provided measurements of targets, ranging in size from 100 µm to 3 mm in ESD, at a rate up to 200 counts per second. The OPC assemblage measuring the abundance and size spectrum of zooplankton organisms included the following elements: an aquarium (14 L) put down on magnetic agitators, a peristaltic pump owning a linear flow upper to 0.5 $m \cdot s^{-1}$ (Watson-Marlow 603 S/R), intake and discharge hoses (∅ ≈ 2 m), a collector with a sifter of 53 µm mesh size, an OPC detector (*OPC–1L Lab. Unit*, Focal Technologies Inc. 1992a), a data converter (*OPC–2D Deck Unit*, Focal Technologies Inc. 1992a) and a computer equipped with a data acquisition software (*OPC*

Lab Windows® Data Acquisition Software, Focal Technologies Inc. 1992b). Mesozooplankton abundance was expressed in ind·m^{-3} for both size classes.

Statistical analyses

The method of Principal Coordinates of Neighbour Matrices (PCNM, Borcard & Legendre 2002) was used to identify the multiscale spatial variability in zooplankton abundance and biomass. This new method of multiscale analysis, which is based on the neighbourhood relationships among sampling sites, permits to detect and quantify spatial patterns over a wide range of scales. The spatial analysis was carried out separately for the zooplankton biomass and abundance data (considering the two size classes of zooplankton separately), as well as for phytoplankton biomass. The first step of PCNM was to remove the spatial trend from the data in order to achieve stationarity. Trend extraction, by linear regression (Legendre & Legendre 1998) on the latitudinal geographic coordinate of the sites, was carried out for each zooplankton and environmental variable. Determining the trend of the zooplankton variables was equivalent to modelling the spatial pattern of zooplankton at the broadest scale, which is that of the lagoon. After modelling and extracting the trend, the residuals (i.e. the detrended data) of the zooplankton variables were used in the PCNM analyses. PCNM analysis was carried out from the latitude coordinate of the sampling sites. The longitude coordinate was not used because our hypothesis concerned a latitudinal gradient; in any case, the differences in longitude were small. The four response variables were regressed against the PCNM spatial variables. The regression coefficients were tested using permutations of the residuals of the full regression model (ter Braak 1990).

The environmental data were used to explain the spatial patterns i.e., corresponding to the trends, while the residuals of the environmental variables (i.e. after detrending) were used to explain the zooplankton spatial patterns provided by the PCNM analysis. Redundancy analysis (RDA) with a forward-selection procedure, which is available in the program CANOCO™

version 3.10 (ter Braak 1990), was used to select the environmental variables that significantly explained each spatial pattern of zooplankton biomass and abundance for each size class (i.e. 190–600 µm and > 600 µm). The results were also tested by permutations of the residuals of the full regression model (ter Braak 1990). The steps of the statistical analyses are fully described in Avois-Jacquet et al. (*submitted*).

Results

Spatial patterns across scales

Table 2 reports the spatial variance of the abundance and biomass of mesozooplankton, as well as that of phytoplankton biomass, detected at various scales. The total variance in biomass of small zooplankton was higher than that of the large zooplankton and phytoplankton, while large zooplankton exhibited higher total variance in abundance than small zooplankton. Although mesozooplankton and phytoplankton exhibited multiscale spatial patterns, their variance spectrum differed strongly. For large zooplankton, the spatial variability in abundance and biomass represented about 23-26% of the total variance. Small zooplankton showed a higher amount of spatial variability: 62-69% of the total variance in biomass and abundance was spatial. The two size classes of mesozooplankton showed markedly different scales of spatial dependency; two spatial patterns of abundance were common to both fractions, however: scales 8 and 12. The biomass and abundance variability of small zooplankton displayed the same scales of spatial dependency from broad to fine scales, except for fine scales 16 and 17, whereas variability in abundance of large zooplankton was detected at spatial scales that differed from the scales of biomass variability. Spatial patterns of abundance of large zooplankton were detected at meso- and fine scales, while biomass presented its strongest spatial variability at broad scale (i.e., the scale of the lagoon). Phytoplankton biomass showed great spatial variability across scales accounting together for 92% of the total variance.

The spatial patterns of mesozooplankton and phytoplankton varied a lot across scales. Trend extraction found the same spatial linear model for the two zooplankton fractions and phytoplankton. The model described a decreasing gradient of biomass from the coast to the barrier reef at the broadest scale (i.e., the scale of the GCSM lagoon, 8.4 km) (Figs. 2, 3, 4). The variability of small zooplankton abundance over broad scale (trend) also described the decreasing gradient from the coast to the barrier reef (Table 2), but no pattern was found for large zooplankton abundance at that scale. Large zooplankton showed spatial structure across the whole transect for abundance at meso- (i.e., 1–5 km) and fine (i.e., 400-1000 m) scales, but only at mesoscale for biomass.

Spatial variability in abundance and biomass of small zooplankton was found in limited areas at mesoscales 2 and 3, while patchiness was detected across the transect at other scales (Fig. 3). At mesoscale 2, two distinct depressions shape the spatial pattern of abundance and biomass; a depression on the seagrass beds near the coast (i.e., from 0.7 to 1.7 km off the coast, sampling sites 6 to 15) and another located in the northern part of the lagoon from 6.7 to 8.1 km off the coast (sampling sites 34 to 46). At mesoscale 3, however, a patch was only found near the barrier reef; the pattern was characterized by lower biomass and abundance on the seagrass meadows than on the barrier reef. At finer mesoscales, small zooplankton also presented spatial variability in abundance and biomass in the north of the lagoon (5.8 km from the coast) at scale 10, and from the coast to 5.8 km at mesoscale 11. The spatial structuring in abundance and biomass was also concentrated in the first 5.8 km of the transect (sampling sites 1 to 28) at fine scale 12, but only for biomass at fine scales 16 and 17 (Fig. 3). Small zooplankton presented inverse patterns at scales 16 and 17 in the southern part of the lagoon (from the coast to 3.8 km, sampling sites 1 to 20), but the same spatial pattern from the centre of the lagoon to the barrier reef where spatial variability was low in the northern region, further than 5.8 km from the coast.

Phytoplankton and the two size classes of mesozooplankton showed some common scales of spatial dependency (Table 2). Like zooplankton, phytoplankton biomass formed a decreasing gradient from the coast to the barrier reef at broad scale (Fig. 4); the highest amount of spatial variability of phytoplankton biomass was found at that scale (Table 2). At mesoscale 6, however, the spatial pattern of phytoplankton biomass was opposed to that of the biomass of large zooplankton (Figs. 2 and 4). Fine-scale spatial patterns of phytoplankton was detected along the cross-shelf transect with decreasing variability towards the northern part of the lagoon (scales 12 and 13). Phytoplankton biomass also exhibited smaller fine-scale variability (i.e., 100–400 m) in the southern part of the lagoon, from the coast to 3.8 km (sampling sites 1 to 20).

Physical and biological factors

Tables 3, 4 and 5 report the environmental variables that were found, by multiple regression, to significantly explain the spatial patterns identified in Table 2 to be of interest for zooplankton biomass and abundance and for phytoplankton biomass. Partial standard regression coefficients are reported in these tables because they indicate the partial contributions of the environmental variables after controlling for the effect of the other variables in the spatial model. The biomass spatial structure of the two size classes of mesozooplankton was linked to the variables describing the types of habitats (Bms to Reef in Table 3) across meso- and fine scales, while the chemical, hydrodynamic and biological factors (Depth to Phyto in Table 3) were mostly implicated in the broad- and mesoscale patterns of zooplankton variability. Since small zooplankton showed the same spatial patterns in abundance and biomass (except for scales 16 and 17), the environmental factors implicated in the abundance patterns were the same as those explaining the biomass patterns.

The broad-scale pattern of biomass of the two mesozooplankton fractions, describing a decreasing gradient from the coast to the barrier reef, was mostly explained by phytoplankton biomass ($b = 0.548$) and wind direction ($b = 0.348$, Table 3). While biomass variability was positively linked to these variables, the relationship was negative with swell height and salinity. The broad-scale pattern of phytoplankton biomass was also explained by wind direction and swell height (Table 4) with great influence of the northerly winds ($b = 0.760$) on phytoplankton spatial structure. At mesoscales, climatic (i.e., wind direction and cloud coverage) and hydrodynamic variables (i.e., swell height) associated with the variables describing the types of habitat explained a large amount of variability of the small zooplankton and phytoplankton (Tables 3 and 4). At mesoscale 2, small zooplankton responded negatively to the seagrass beds located near the coast ($b = –0.125$) and near the barrier reef ($b = –0.606$) and to the bare sand ($b = –0.601$), and on the inner reef flat ($b = –0.525$). These habitats were shallow ($b = 0.244$ for depth) and dissolved oxygen ($b = 0.479$) was lower near the coast (DO = 4 $\text{mg}\cdot\text{L}^{-1}$) than near the barrier reef (DO ≥ 8 $\text{mg}\cdot\text{L}^{-1}$). While swell height was negatively linked to the biomass and abundance of small zooplankton ($b = –0.265$) at mesoscale 2, the relationship was positive ($b = 0.286$) at mesoscale 3. At that scale, variability in abundance and biomass of small zooplankton was only detected in the northern part of the lagoon. The organisms were less abundant on seagrass beds ($b = –0.461$), on cays covered solely with seagrass ($b = –0.234$), and on bare sand ($b = –0.388$) than on the barrier reef where biomass was high. During the sampling campaign, winds were easterlies in this area ($b = 0.189$) and cloud coverage ($b = –0.322$) was more important on the seagrass meadows that on the barrier reef. Phytoplankton spatial structure at mesoscales 2 and 3 was explained by the same factors as in the case of the small zooplankton, except for wind factor (Table 4). The northerly winds, which had a positive effect on the spatial variability of phytoplankton biomass at broad scale, had a negative, but small ($b = –0.298$), influence at mesoscale 2. Northerly winds were only observed in the southern part of the lagoon (i.e., from the coast to 4.3 km).

At mesoscale 8, the spatial patterns of small zooplankton and phytoplankton were linked to the type of substrate and the coverage by seagrass and/or coral (Tables 3 and 4). High biomass was found on bottoms with high seagrass coverage, for example on seagrass beds with 76–100%

coverage (*b* = 0.224), while muddy bottoms (*b* = –0.340) were characterized by low biomass of small zooplankton and phytoplankton. Although the variability in abundance and biomass of the small zooplankton detected in the northern part of the lagoon was negatively linked to cloud coverage at mesoscale 3, this relationship was positive at mesoscale 10. At this scale, variability of the small zooplankton was negatively linked to dissolved oxygen (*b* = –0.295) which was low on cays (DO ≤ 6 $\text{mg}\cdot\text{L}^{-1}$) and high on seagrass beds (DO ≥ 10 $\text{mg}\cdot\text{L}^{-1}$). At mesoscale 11 and fine scales, the spatial pattern of small zooplankton from the coast to the middle of the lagoon was mainly explained by the types of habitat. At these scales, seagrass beds always harboured high biomasses of small zooplankton except at fine scale 12 where biomass was negatively linked to seagrass on muddy bottoms (*b* = –0.302), but positively linked to seagrass on sandy bottoms (*b* = 0.264). At fine scale 12, the spatial patterns of small zooplankton and phytoplankton were also explained by turbidity (*b* = 0.254), which was high on muddy bottoms (*b* = 0.577) and low on seagrass beds. At fine scale 17, the same relationship was observed between biomass of small zooplankton, habitat and turbidity: high biomass on seagrass beds (*b* = 0.299) was associated with low turbidity (*b* = –0.346).

Despite the positive relationship between large zooplankton and phytoplankton biomass (*b* = 0.548) at broad scale, the biomass of large zooplankton was negatively linked to phytoplankton biomass (*b* = –0.266) at mesoscale 6 (Table 3). At this scale, only the large zooplankton and phytoplankton exhibited a spatial pattern mostly explained by habitat variables. No hydrodynamic or climatic factors were implicated in these patterns. The spatial pattern of phytoplankton that was the opposite of that of the large zooplankton (Figs. 2B and 4): seagrass beds were characterized by high phytoplankton biomass (*b* = 0.447) whereas cays (*b* = –0.578) had low phytoplankton biomass (Table 4). At mesoscale 5, the inner reef flat (*b* = 0.383) and the seagrass beds near the coast (*b* = 0.214), which were characterized by low turbidity (*b* = –0.323), presented high abundance of large zooplankton. Large zooplankton showed the same spatial pattern of abundance as the small zooplankton at scales 8 and 12 (Figs 2 and 3). At fine scale 12, however, the abundance variability of large zooplankton was also explained by phytoplankton, as it was the case at mesoscale 5 (Table 5). Although the relationship between phytoplankton and zooplankton biomass was negative at mesoscle 6, the abundance of large zooplankton was positively linked to phytoplankton biomass across scales. Phytoplankton exhibited the same spatial pattern as large zooplankton at fine scale 12 (Fig. 4), but no phytoplankton pattern was detected at mesoscale 5 (Table 2). Like the abundance of large zooplankton, the variability of phytoplankton biomass was positively linked to the presence of shallow muddy bottoms ($b = 0.577$) which were characterized by high turbidity ($b = 0.254$), but negatively linked to the seagrass beds near the coast ($b = –0.302$) characterized by low turbidity (Table 4).

Discussion

In the present study, mesozooplankton and phytoplankton communities exhibited multiscale spatial variability from broad to fine scales, but they differed strongly in the spectral composition of their spatial structure, displaying different scales of spatial dependency. These results are in agreement with previous findings obtained by Pascual et al. (1995), Marguerit et al. (1998), Seuront & Lagadeuc (2001). Piontkovski et al. (1995) reported that the heterogeneity of spatial distributions increased with the size of the organisms, from phytoplankton (chl *a*) through mesozooplankton to macrozooplankton. Contrary to these findings, the 190–600 µm zooplankton in the GCSM lagoon showed more intense and finer-scale variability in biomass and abundance than zooplankton > 600 µm. This tendency has also been observed for larger freshwater zooplankton which seems to be less patchy than small zooplankton (Pinel-Alloul et al. 1988). These authors suggested that greater spatial aggregation might allow small zooplankters to avoid predators and locate mates, while reduced patchiness in the large species may decrease competition. The known types of aggregation of planktonic copepods, which represent up to 75% of the total zooplankton abundance in tropical waters (e.g., Moore & Sander 1979), are swarms (dense, discrete patches, 5 to 10^3 times denser than normal patches, often composed of a single species, where movement and orientation, but not necessarily spacing, are random) and schools (monospecific, with individuals oriented parallel to one another) (Haury & Yamazaki 1995, Leising & Yen 1997). Swarming, which is widespread among tropical copepods in reef lagoons (Emery 1968, McKinnon 1991), is one example of the complex behavioural adaptations that have evolved in resident plankton species to survive within reef ecosystems (Hamner & Carleton 1979). Swarms form and are maintained in response to individual behaviour such as predator avoidance, which is the most common adaptive explanation for the swarming of copepods, food exploitation, as well as social interactions including mating encounters. Indeed, swarming enhances copepod mating encounters and success, bringing together adult males and females in high concentrations (Buskey 1998). For example, *Dioithona oculata* is a cyclopoid copepod which commonly forms swarms in mangrove and coral reef environments. This species exhibits a diel behavioural pattern that allows the individuals to synchronize their mating and reproductive behaviour to the daily pattern of swarm formation and dispersal (Ambler et al. 1991). Subdividing the population into swarms is also an evolutionary response by demersal organisms with highly patchy distributions to ensure preferential protection from predation (Hamner & Carleton 1979). Indeed, swarms, which are always located slightly above the bottom, are not available to benthic filtering feeders; the protection against predators is reinforced by water coloration that decreases visibility. Moreover, swarming behaviour may reduce predation rate on egg-bearing females which form large, high-contrast targets for planktivorous fish (Buskey 1998). These behaviours are usually accompanied by a tendency to aggregate in more compact swarms during daytime (at dawn) and disperse at dusk, which is also a predation-avoidance strategy (Hamner & Carleton 1979, Omori & Hamner 1982, Ribes et al. 1996).

In the GCSM lagoon, swarms may represent the main form of spatial pattern for the mesozoooplankton detected at meso- to fine scales (Figs. 2 and 3). These scales were linked to the presence of various types of habitat (Tables 3 and 5). Swarm size, structure, and distribution are adapted to habitat topography (Hamner & Carleton 1979, Ribes et al. 1996). Substratum heterogeneity enhances densities of organisms on and near the bottom (Rios-Jara & Gonzalez 2000). However, the nature of the substratum and the type of habitat may alter zooplankton swarming. For example, copepods may be found individually or in small swarms near patch reefs (Emery 1968). Zooplankton in these areas, which are often characterized by shallow depth, is strongly affected by wind and/or tidal effects that are not favourable to the maintenance of aggregates. This corroborates the low abundance and biomass of small zooplankton observed on cays, at mesoscales, where swell height and easterly winds were favourable to the dispersion of small organisms such as the 190–600 µm zooplankton (Table 3) and phytoplankton (Table 4). The dispersal effect of swell height and wind observed on small zooplankton inhabiting cays also seems to influence the organisms living in seagrass beds (Table 3). Although the abundance and biomass of zooplankton are generally high in seagrass beds (Connolly 1997 and references therein), this also depends on turbulent mixing in these habitats. Waves, which increase the exchange between the water column and the water mass within the meadows (Koch & Gust 1999), may affect mesozooplankton pattern in seagrass beds by horizontal (Haury et al. 1990) and/or vertical dispersal (Incze et al. 2001) of organisms. Turbulence is a ubiquitous feature of the marine environment and has a substantial effect on the structure and dynamics of planktonic organisms across spatial scales. The distribution of copepods and fish larvae may be modified by variations in turbulence intensity (Haury et al. 1990), and turbulent mixing may affect zooplankton behaviour (Saiz 1994). Experimental studies have clearly shown that small-scale turbulence can influence the large components of plankton, such as copepods (Kiørboe & Saiz 1995), through changes in shear velocity and modifications of the searching and feeding behaviour (Saiz 1994). Different species respond to turbulence differently (Mackas et al. 1993), however. Assuming that the species associations near the barrier reef differ from those found in seagrass beds (Alvarez-Cadena et al. 1998, Suàrez-Morales & Gasca 2000), this may explain the high abundance and biomass of small zooplankton on the barrier reef where swell height was strongest, whereas the presence of small organisms in seagrass beds increased with decreasing swell height.

At broad scale, mesozooplankton and phytoplankton formed a decreasing gradient of biomass and/or abundance from the coast to the barrier reef (Figs. 2 and 3); this is consistent with the findings of previous studies in tropical environments (e.g., Moore & Sander 1979, Rios-Jara 1998, Alvarez-Cadena et al. 1998). Several investigators found a positive correlation between phytoplankton and zooplankton (e.g. Moore & Sander 1979, Webber et al. 1992, Rios-Jara 1998), which we also found in our results at broad scale (Table 3). In general, zooplankton variability in coastal tropical waters is associated with changes in phytoplankton standing stocks (Rios-Jara 1998) and with the combined effects of regional climatology (Yoshioka et al. 1985, Rios-Jara 1998) and local patterns of water movements (Webber et al. 1996). Fluctuations of zooplankton abundance and biomass are closely related to the rainfall pattern with associated nutrient input from land drainage and a consequent increase in phytoplankton productivity (Hopcroft & Roff 1990, Webber et al. 1992). Although nutrient input probably declines during the dry season (i.e., sampling period), the phytoplankton standing stock can remain high during that period (Rios-Jara 1998) due to autochthonous nutrient remineralization intensified by wind (Hopcroft & Roff 1990); increases in netplankton chlorophyll are more strongly related to wind than in the case of nanophytoplankton. In the semi-sheltered system close to the southern coast, long water residence time (Assor & Julius 1987) combined with northerly winds (Table 3) are probably responsible for the high phytoplankton biomass observed near the coast (Fig. 5), which is available to the zooplankton communities. An additional source of nutrients in tropical lagoons is obtained by coupling with adjacent communities. Coastal tropical lagoons are frequently associated with fringing mangroves at the land-sea interface, or with mangrove islands; both are found in the GCSM lagoon (Fig. 1). Mangroves can provide an important source of nutrients to adjacent areas (Rivera-Monroy et al. 1998), either directly through detritus mineralization, or indirectly through excretion by the associated fauna, which may be important contributors to lagoon primary production (Koch & Madden 2001). A plausible mechanism is that shifts in wind direction and reduction of the overall mean wind velocity near the southern coast of the GCSM lagoon may simply increase the residence time of water. The residence time of cells in this system may be long enough for the biomass to increase, if several generations of larger cells are produced in the enriched nutrient climate of this region, as suggested by Hopcroft & Roff (1990).

Ours estimates of total chlorophyll a concentration from the coast to the open sea are comparable to the data observed in neritic and oceanic waters of Jamaica (Roff et al. 1995). The decreasing gradient of phytoplankton biomass from the coast to the open sea corresponds to a trophic gradient from eutrophic to oligotrophic status. The tropical oceanic environment is characterized by oligotrophic water where pico- (< 2 µm) and nano- (2 to 20 µm) phytoplankton organisms dominate. In contrast, the coastal tropical environment tends to be dominated by netplankton (> 20 µm), especially when the overall phytoplankton biomass is high (Hopcroft & Roff 1990). However, major differences in total phytoplankton biomass may be largely attributable to variations in the net- and nanoplankton biomass, rather than picoplankton, because of the relative constancy of the picoplankton size fraction of the phytoplankton (Hopcroft & Roff 1990 and references therein). The positive relationship between phytoplankton and mesozooplankton biomass detected at broad scale (Table 3) thus suggests that zooplankton does benefit from the high phytoplankton production. The mesozooplankton community along the cross-shelf transect was dominated by small zooplankton species (i.e. 190–600 µm) in terms of biomass and abundance (Fig. 5a, b), particularly in regions with high values of phytoplankton biomass (i.e., near the coast). Although both size classes of mesozooplankton showed a decreasing gradient of biomass from the coast to the open sea, no broad-scale pattern was detected for large zooplankton abundance. Piontkovski et al. (1995) suggest that, in regions where the phytoplankton turnover rate is high, zooplankton is mainly represented by smaller organisms; their contribution to total abundance of individuals considerably exceeds that of larger organisms. In regions with low phytoplankton turnover rate, the contribution of the large zooplankton organisms becomes more significant. This corroborates the fact that in eutrophic environments (i.e. near the coast), the community is numerically dominated by small species (Hopcroft et al. 1998b) in comparison to oligotrophic waters (i.e. oceanic waters) where the community is numerically dominated by larger species (Webber & Roff 1995a, b, Hopcroft et al. 1998b). However, we did not observe an increase of the relative contribution of large zooplankton from the coast to the open sea; on the contrary, small zooplankters also dominated strongly near the barrier reef (Fig. 5). The fact that the size-spectrum of the copepod community shifts towards smaller species and earlier developmental stages, with nauplii becoming relatively more abundant because reproduction is continuous in tropical waters (Webber & Roff 1995a, b, Hopcroft et al. 1998a, b), may explain our results. Another suggestion is the size-spectrum of resources utilized by copepods, which increases with body size (Berggreen et al. 1988). Smaller species and development stages are able to exploit the smaller, more abundant food particles (Webber & Roff 1995b), whereas large species and stages appear to become increasingly food-limited (Hopcroft et al. 1998a), presumably as they exploit progressively larger, but more sparse, food particles (Roff et al. 1995), especially in oceanic waters (Webber & Roff 1995b). The high availability of food may explain the high copepod abundance (Calbet et al. 2000), with dominance of copepodites (CI-V stages) and nauplii (Gotsis-Skretas et al. 2000), compared to adjacent oceanic waters. Rollwagen-Bollens & Landry (2000) also showed that while mesozooplankton abundance and biomass increased inside patches, relative to the outside levels, in response to the phytoplankton standing stock, the small animals (202–500 µm) accounted for most of the mesozooplankton increase, most of it being attributable to small calanoid copepods, copepod nauplii, and larvaceans. Thus, the broad-scale variability in abundance of small organisms, compared to the absence of spatial structure of large zooplankters, would be partly the result of an enhancement in nauplii, copepodites, and small species in response to the phytoplankton standing stock. However, the size distribution and abundance of the mesozooplankton community in the GCSM lagoon may also be controlled by factors such as predation. Moore & Sander (1979) noted that carnivorous zooplankters (e.g. siphonophors, chaetognaths, and euphausids) are more abundant in offshore than inshore waters. Predation on larger mesozooplankton in combination with dominance of the small-size fractions in the food resource may explain the relative scarcity of larger zooplankters, as suggested by Calbet et al. (2000) in their work in Kaneohe Bay (Hawaii).

In previous work, although the increase in zooplankton appeared to be due to a proliferation in response to phytoplankton biomass (Webber et al. 1992, Rios-Jara 1998), zooplankton biomass showed less fluctuation than zooplankton abundance, because the community was dominated by smaller juveniles stages and copepodites, which contributed little biomass (Webber et al. 1992). In the GCSM lagoon, the small and large mesozooplankton showed higher total variability and higher spatial structuring in abundance than in biomass at mesoscales, but the small zooplankton exhibited higher spatial variability in biomass than in abundance at broad scale (Table 2). High spatial structuring in abundance and biomass was probably the result of several factors. The positive relationship between phytoplankton and mesozooplankton detected at broad scale (Table 3) may be the result of the food searching behaviour. Locating food patches is one of the mechanisms explaining zooplankton spatial patterns; aggregation in regions of high food concentration may be a strong driver of zooplankton patchiness (Folt & Burns 1999). The mesozooplankton and phytoplankton patterns, however, may also be the result of the spatial redistribution of existing variability, as highlighted by Avois-Jacquet et al. (submitted). These authors showed that the relationship between phytoplankton and small zooplankton (190–600 µm) biomass was generated by their common spatial structure, whereas the relationship between phytoplankton and large zooplankton (> 600µm) was negative and significant after controlling for the effect of spatial distance. They suggested that, in the GCSM lagoon, the broad-scale pattern of small zooplankton, which is less mobile than large zooplankton, is generated by wind-induced currents, like the phytoplankton pattern, while the broad-scale pattern of large zooplankton results from an active response of large zooplankton to phytoplankton caused by their food searching and grazing behaviour. The broad-scale patterns of temperature, salinity, and phytoplankton support this hypothesis (Table 3), given that these variables are passive tracers of hydrodynamic features (Geyer 1997). Zooplankters are either passive (Castel & Viega 1990) or active (Davis et al. 1992) drifters; that depends on their swimming capacity and on the hydrodynamic conditions. Our results support the hypothesis that large zooplankton (> 600 µm) are more mobile than the 190–600 µm organisms; they are active drifters. Except for the broadest scale, hydrodynamic processes did not influence large zooplankton, while these processes had some effect on the spatial structures of the small zooplankton and phytoplankton (Tables 3–5). It is known that hydrodynamic processes affect a range of biological processes, mostly related to the taxa and the size of the organisms (Petersen et al. 1998). Patches may be formed by accumulation, i.e., passive aggregation (Noda et al. 1998), particularly if the zooplankton organisms are similar in shape, buoyancy, or motility, and when turbulence overwhelms zooplankton motility (Yen et al. 1998). At broad scale, the abundance and biomass of mesozooplankton as well as the phytoplankton biomass were positively correlated with the northerly winds, i.e., found from the barrier reef to the coastline, while the relationship was negative with swell height (Table 3) which particularly high around the barrier reef. Thus, in the GCSM lagoon, wind-induced currents may produce an accumulation of zooplankton near the coast and a transport of oceanic fauna towards the lagoon; this has already been observed (Alvarez-Cadena et al. 1998). On the other hand, the broad-scale pattern of large zooplankton may result from the combination of active behavioural swimming by the organisms during food searching and grazing, combined with passive hydrodynamic accumulation.

The discrepancy between the two size classes of mesozooplankton may be explained by a difference in grazing impact relative to the organism's size, by the effect of turbulence on feeding and/or by an underestimation of the small organisms. Phytoplankton and small zooplankton showed the same meso- and fine scales of spatial dependency (Table 2), but there was no significant relationship between theirs patterns. Instead, the meso- and fine scale patterns of large zooplankton were linked to phytoplankton (Tables 3 and 5). Rollwagen-Bollens & Landry (2000) found that small mesozooplankton (202–500 µm) in the eastern equatorial Pacific consistently accounted for a lower portion of the total grazing rate than the 500–2000 µm fraction. In general, grazing impact on daily primary production by mesozooplankton (e.g., copepods) is low in marine ecosystems (reviewed by Sutton et al. 2001). These authors suggested that the grazing impact may be locally intense at smaller spatial scales than suggested by the negative correlation between large zooplankton and phytoplankton biomass found in our results (Table 3). They also emphasized the importance of carrying out concomitant high-resolution sampling of zooplankton and their food supply, which is heterogeneously distributed at fine scales. This corroborates the high spatial structuring of the biomass of small zooplankton and phytoplankton observed at meso- and fine scales (Table 2, Figs 3 and 4). At mesoscales, turbulence generated by swell, which has a negative effect on the abundance and biomass of small zooplankters (Table 3), may have a negative influence on the feeding behaviour of these organisms. Specifically, beyond a certain level, turbulence may impair the copepod’s rate of ingesting food by eroding the feeding current, interfering with the remote detection of prey, or increasing the pursuit time (Kiørboe & Saiz 1995). The effect of turbulence on prey encounter rates in planktivorous predators depends strongly on the feeding behaviour of the predator (i.e., swimming predator, ambush predator, suspension feeder), on the motility of the predator and prey, and on the scales at which the predator operates (Kiørboe & Saiz 1995). Underestimation of most of the copepodite stages due to inadequate mesh size of the nets may also explain the reported low grazing impact (Sutton et al. 2001). The 190 µm mesh size used during our study undersampled or ignored nauplii, copepodites, and small copepod species (Chisholm & Roff 1990, Hopcroft et al. 1998a,b), all of which are important in terms of abundance and production (Hopcroft et al. 1998a,b) and as trophic intermediaries between the classical and microbial food webs (Roff et al. 1995). This role may be especially significant in oligotrophic ecosytems, where pico-sized (0.2–2 µm), auto- and heterotrophic phytoplanktonic organisms comprise much of the system biomass (Hopcroft & Roff 1990), while we used a 0.7 µm pore size filter to estimate the phytoplankton biomass. Gotsis-Shretas et al. (2000) reported that the total mesozooplankton abundance was positively correlated with total chlorophyll *a* biomass, as shown in our results (Tables 3 and 5). However, negative relationships were found between abundances of copepodites and nauplii and the relative proportion of picoplankton. Adult copepod abundance was negatively associated with microplankton and positively correlated with picoplankton. This may be due to the fact that herbivorous adult copepods graze on phytoplankton cells larger than 7 µm with higher efficiency, whereas cells of 5 to 7 µm in size approach the lower limit of their prey size spectrum (Berggreen et al .1988) and are thus grazed with lower efficiency. On average, copepods feed on prey that are about 18 times smaller than their linear body size (e.g. large copepods generally graze netplankton, which is > 20 µm; Berggreen et al. 1988), whereas small copepods tend to feed on prey that are much closer to their own body size (Hansen et al. 1994). Although neither the adult calanoids nor the cyclopoids seem to efficiently feed on particles smaller than 5 µm (Hansen et al. 1994), Calbet et al. (2000) reported that some small calanoids and cyclopoids (i.e. *Parvocalanus crassirostris*, *Oithona nana* and *O. simplex*) do feed at high rates on particles smaller than 5 µm (or even smaller than 3 µm).

While the biomass of large zooplankton was negatively linked to phytoplankton biomass at scale 6 (Table 3), the relationship between the abundance of large zooplankton and phytoplankton biomass was positive (Table 5). These patterns are best ascribed by a combination of correlations with phytoplankton biomass, local turbidity, and habitat heterogeneity. In estuaries, Roman et al. (2001) noted the high turbidity values are the frequent areas of enhanced zooplankton concentration. The abundance of food in the form of detritus, protozoa, and phytoplankton, in addition to the convergence associated with estuarine circulation, may result in high zooplankton concentrations (Roman et al. 2001). Our findings suggest that the relationship between turbidity and the zooplankton and phytoplankton standing stocks depends on the type of habitat. Indeed, shallow muddy bottoms characterized by high turbidity sheltered high abundances of large zooplankton and high phytoplankton biomass, while these relationships were negative in seagrass beds and on the barrier reef (Table 5). Seagrass meadows are known to alter both the physical and biological characteristics of their surrounding environment (e.g., flow, turbulent mixing, turbidity) by their ability to attenuate waves and decrease current velocity, and by increasing light availability due to sediment accretion (Koch & Gust 1999). Seagrass meadows in lagoons are also recognized as supporting high primary production (Koch & Madden 2001). Moreover, the presence of large plants of *Thalassia testudinum* can offer a refuge from predation for zooplankton organisms (Edgar 1999) and thus contribute to increase zooplankton abundance (Alvarez-Cadena et al. 1996, Connolly 1997).

Over meso- and fine scales, the influence of habitat patterning (i.e., the heterogeneity and division of habitats; Addicott et al. 1987) on mesozooplankton abundance and biomass increases while the effects of hydrodynamic processes decrease (Table 3 and 5). Habitat patterning is known to influence community structure by modifying the biomass (Rios-Jara 1998), diversity (Eggleston et al. 1999), and the distribution and abundance of the dominant organisms (Eggleston et al. 1998). Habitat patterning is also known to affect many ecological processes, including larval dispersal and recruitment (Eggleston et al. 1998), predation intensity (Gonzàlez & Tessier 1997), and predation avoidance (Alvarez-Cadena et al. 1998). Predation may explain the spatial variability in abundance and biomass of mesozooplankton among the types of habitat at mesoscales and within the same type of habitat at fine scales (Figs 2 and 3). Planktivory by fish may be intense. It can affect zooplankton and larval abundance as water masses pass over reefs or through seagrass beds (Bullard & Hay 2002). Numerous reef and seagrass zooplankters possess traits such as demersalism (Emery 1968, Walters & Bell 1994), schooling behaviour (Hamner & Carleton 1979), chemical defenses (Poulet & Ouellet 1982), and rheotactic abilities (hydromechanical signals; Visser 2001) that reduce their susceptibility to planktivorous fishes. The widespread incidence of defences and escape behaviour among resident reef and seagrass zooplankton suggests that planktivory may act as a significant selective force in these habitats (Bullard & Hay 2002). It may explain the variability in biomass and abundance between the barrier reef and the seagrass beds at mesoscales (Table 3). In the GCSM lagoon, Baelde (1990) reported that primarily coral-reef fish species (e.g., Apogonidae, Pomacentridae, Scorpaenidae) were apparently restricted to seagrass beds near the coral barrier reef. It is also in seagrass beds that many juvenile coral-reef fish (e.g., Lutjanidae, Scaridae), big enough to have taken up residence on the coral reefs, were present (Baelde 1990). They used the coral reefs as shelter and the nearby seagrass beds as foraging ground. The threat of predation can also vary dramatically over small spatial scales in the same habitat, as shown in our results. Indeed, fish densities and predation risk, in the seagrass beds, were highest along the edge of the seagrass beds and were lower inside the bed and on the sand plain (Bullard & Hay 2002). So, certain habitats could serve as spatial refuges for resident zooplankton, while nearby locations would present significant dangers. For transient zooplankters, including marine larvae, they should avoid certain areas or move through these areas quickly (selective transport) or during times of lower predation risk by visually foraging fishes (Bullard & Hay 2002).

Conclusion

Our results support the hypothesis that spatial structuring of mesozooplankton biomass and abundance depends on the spatial scales (Haury et al. 1978, Mackas et al. 1985, Legendre et al. 1986). Mesozooplankton spatial variability in the GCSM lagoon seems to exist at three spatial scales: broad- (> 5 km), meso- (1–5 km), and fine (400–1000 m) scales. Our findings also support the hypothesis that zooplankton spatial structuring is size-specific (Haury & Wiebe 1982, Mackas et al. 1985, Piontkovski & William 1995); the intensity and spatial scales of the mesozooplankton spatial patterns differ with respect to their size and their swimming capacity or motility. Small zooplankters (190–600 µm), however, show more intense and finer-scale variability than do zooplankton > 600 µm. The spatial structures of abundance and biomass of large zooplankton displayed different scales of spatial dependency. These organisms seem to be more influenced by the spatial patterns of phytoplankton than by local hydrodynamics across scales. Behavioural processes such as food searching and grazing constitute important mechanisms for the creation of spatial structures in large zooplankton. On the contrary, hydrodynamic processes such as wind-induced currents generate the spatial patterns of small zooplankton and phytoplankton from broad- to meso-scales.

At mesoscales, mesozooplankton spatial structuring and generating processes differed from communities in areas influenced by fresh water inputs and areas influenced by the open ocean. Different areas in the same region may offer zooplankton widely different environmental conditions (Webber et al. 1996, Alvarez-Cadena et al. 1998, Gotsis-Skretas 2000). Along the cross-shelf transect, three areas, corresponding to different mesozooplankton abundance and biomass values, divide the GCSM lagoon into regions, which are influenced by waters of different origins. The coastal sites (1 to 15; from the coast to 1.7 km) form an area of consistently high zooplankton abundances and biomass, which is influenced by the coastal water masse; the spatial structure of the zooplankton is influenced by the spatial patterns of the phytoplankton. The sites in the middle of the lagoon (16 to 26; 2.3–5.4 km from the coast) are found in an area representing intermediate condition. The gradient observed in zooplankton abundance and biomass may result from the mixture of oceanic and coastal waters. The sites in the northern part of the lagoon (27 to 51; 5.8 km from the coast) are found in an area which is only influenced by oceanic water. The spatial structures of mesozooplankton in this area were mostly influenced by local hydrodynamics and turbidity.

Over meso- and fine scales, both size classes of mesozooplankton respond to habitat patterning which influences the community structure by modifying the biomass, abundance, and distribution of organisms. Predation intensity and predator avoidance may also explain the fine-scale spatial patterns. Others processes, however, must be invoked to explain the fine-scale variability of mesozooplankton. Biological processes including feeding (Tiselius 1992, Yen et al. 1998) and reproduction (Folt & Burns 1999) have been evidenced to affect fine-scale spatial structures of zooplankton. Fine-scale spatial structuring is regulated not only by biological, but also by physical processes (Haury et al. 1990). Further studies conducted at fine scales; in which hydrodynamic (i.e. turbulence) and biological (i.e. swimming, feeding, predation, reproduction) processes will be considered, are needed to establish the relationship between fine-scale spatial structuring of mesozooplankton and environmental heterogeneity. These mechanisms, which affect spatial patterns of zoooplankton, are likely to be species-specific (Bollens & Frost 1991, Rios-Jara & Gonzalez 2000). Thus, the identification of species associations, which differ according to water masses (Webber et al. 1996, Alvarez-Cadena et al. 1998) and habitat characteristics (Alvarez-Cadena et al. 1998, Rios-Jara 1998, Suàrez-Morales & Gasca 2000), may help establish the physical and biological processes responsible not only for the fine-scale patterns of zooplankton, but also for the multiscale spatial spatial structuring of these organisms.

Acknowledgements – This study is part of a research programme on the multiscale spatial variability of zooplankton in the GCSM lagoon, which was submitted as part of the requirements for a Ph.D. degree at Université de Montréal (Canada) and Université Paris 6 (France). This work was supported by a doctoral fellowship from the Ministère de la Recherche et de l’Enseignement Supérieur and the Ministère des Affaires Étrangères of France granted to C.A.-J. Field work was financed by Ministère de la Recherche (France), Parc National de la Guadeloupe, and NSERC (Canada) grant number OGP7738 to P. Legendre.

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Table 1 Habitat features at the various sampling sites along the transect. d: distance from the coast (km); depth (m); (% coverage).

Site	d	Depth	Habitat	Site	d	Depth	Habitat
1	0.10	2.1	Bare mud (shallow bottom)	27	5.79	0.4	Cay — Corals
2	0.24	4.8	Bare mud (shallow bottom)	28	5.79	1.5	Cay — Sea-grasses
3	0.36	7.3	Bare mud (deep bottom)	29	5.98	1.4	Cay — Sea-grasses
4	0.61	1.3	Sea-grass beds on mud (76-100%)	30	6.16	0.8	Cay — Corals
5	0.61	1.4	Sea-grass beds on mud (76-100%)	31	6.16	2.0	Cay — Sea-grasses
6	0.70	1.2	Sea-grass beds on mud (76-100%)	32	6.28	1.0	Cay — Corals
7	0.97	1.9	Sea-grass beds on mud (76-100%)	33	6.55	3.1	Sea-grass beds on sand (51-75%)
8	1.03	1.5	Sea-grass beds on mud (76-100%)	34	6.70	1.7	Sea-grass beds on sand (51-75%)
9	1.09	3.3	Sea-grass beds on muddy sand (76-100%)	35	7.28	1.9	Bare sand
10	1.12	0.6	Cay — Corals	36	7.28	2.1	Bare sand
11	1.12	0.8	Cay — Corals	37	7.46	2.0	Sea-grass beds on sand (51-75%)
12	1.15	1.7	Sea-grass beds on muddy sand (76-100%)	38	7.46	2.1	Sea-grass beds on sand (51-75%)
13	1.33	0.9	Cay — Corals	39	7.58	1.7	Sea-grass beds on sand (51-75%)
14	1.40	1.8	Sea-grass beds on muddy sand (76-100%)	40	7.58	1.9	Sea-grass beds on sand (51-75%)
15	1.70	10.8	Bare mud (deep bottom)	41	7.70	2.0	Bare sand
16	2.34	15.5	Bare mud (deep bottom)	42	7.70	1.8	Bare sand
17	2.88	3.8	Sea-grass beds on muddy sand (0-25%)	43	7.86	1.1	Inner reef flat
18	3.15	19.5	Bare mud (deep bottom)	44	7.86	1.4	Inner reef flat
19	3.70	1.7	Cay — Mixed sea-grasses and corals	45	7.86	1.4	Inner reef flat
20	3.76	0.9	Cay — Mixed sea-grasses and corals	46	8.07	2.6	Reef front
21	3.91	1.0	Cay — Mixed sea-grasses and corals	47	8.07	2.6	Reef front
22	4.13	1.7	Cay — Mixed sea-grasses and corals	48	8.25	9.8	Outer slope of barrier reef
23	4.25	10.3	Bare mud (deep bottom)	49	8.25	9.5	Outer slope of barrier reef
24	4.85	16.4	Bare mud (deep bottom)	50	8.40	21.8	Outer slope of barrier reef
25	5.16	6.2	Sea-grass beds on sand (26-50%)	51	8.40	16.3	Outer slope of barrier reef
26	5.37	3.0	Sea-grass beds on sand (26-50%)				

Table 2 Spatial variance of zooplankton (> 600 µm and 190–600 µm) and phytoplankton (Phyto) biomass, and of zooplankton abundance, detected at different scales. The percentage of the total variance explained either by the all-scale model or by each significant explanatory variable is shown in parentheses. *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$.

	Biomass			Abundance	
	> 600 µm	190–600 µm	Phyto	> 600 µm	190–600 µm
Total	0.3790	0.4976	0.1746	0.9618	0.6369
Model	0.0870 (23.0***)	0.3439 (69.1***)	0.1607 (92.1***)	0.2467 (25.8**)	0.3964 (62.2***)
Trend	0.0629 (16.6***)	0.1357 (27.3***)	0.1322 (75.7***)		0.1170 (18.4***)
Scale 2		0.0267 (5.4**)	0.0040 (2.3**)		0.0388 (6.1*)
Scale 3		0.0519 (10.4***)	0.0017 (1.0*)		0.0508 (8.0***)
Scale 5				0.0889 (9.3*)	
Scale 6	0.0241 (6.4*)		0.0014 (0.8*)		
Scale 8		0.0113 (2.3**)	0.0009 (0.5*)	0.1237 (12.9**)	0.0929 (14.6***)
Scale 10		0.0299 (6.0**)			0.0354 (5.5**)
Scale 11		0.0389 (7.8***)			0.0350 (5.5**)
Scale 12		0.0150 (3.0**)	0.0122 (7.0***)	0.0341 (3.6*)	0.0260 (4.0**)
Scale 13			0.0022 (1.3**)		
Scale 15			0.0038 (2.2**)		
Scale 16		0.0195 (3.9**)			
Scale 17		0.0150 (3.0*)			
Scale 23			0.0023 (1.3**)		
Residuals	0.2920	0.1537	0.0139	0.7151	0.2405

Table 3 Partial standard regression coefficients of environmental variables, which significantly explained the spatial patterns of biomass of large and small zooplankton and the abundance of small zooplankton at different scales.

	Trend	Scale 2	Scale 3	Scale 6	Scale 8	Scale 10	Scale 11	Scale 12	Scale 16	Scale 17
Depth		0.244								
T°	0.181		–0.295							
Salinity	–0.260									
DO		0.479				–0.295				
NTU								0.254		–0.346
Cloud			–0.322			0.265				
Swell	–0.091	–0.265	0.286							
North	0.348									
East			0.189							
Phyto	0.548			–0.266						
Bms								0.577		
Bmd					–0.340					
Sm				–0.466	0.224		0.334	–0.302		
Sms0					–0.279		0.440		0.281	
Sms76		–0.125								
Ss26				0.189				0.264	0.362	0.299
Ss51		–0.606	–0.461							
Cs			–0.234							
Cm				0.575	0.566					
Bs		–0.601	–0.388							
Reef		–0.525								
Total	0.93^{***}	0.69^{***}	0.73^{***}	0.69^{***}	0.63^{***}	0.18^{**}	0.28^{***}	0.65^{***}	0.32^{***}	0.20^{**}

T°: temperature, DO: dissolved oxygen, NTU: turbidity, Cloud: cloud coverage, Swell: swell height, Speed: wind speed, North or East: Northerly or easterly wind, Phyto: phytoplankton biomass, Bms: shallow bare muddy bottom, Bmd: deep bare muddy bottom, Sm: sea-grass beds on mud (76–100% coverage), Sm0 and 76: sea-grass beds on mud-sand (0–25% and 76–100% coverage), Ss26 and 51: sea-grass beds on sand (26–50% and 51-75% coverage), Cs: cay—sea-grass beds, Cm: cay—mixed sea-grass beds and coral species, Bs: bare sand, Reef: inner reef flat, Total: fraction of the total variance explained by all selected environmental variables in the model. $^{***}p \leq 0.001$, $^{**}p \leq 0.01$, $^{*}p \leq 0.05$.

Table 4 Partial standard regression coefficients of environmental variables which significantly explained the spatial patterns of phytoplankton biomass at different scales. Variable codes: see Table 3.

	Trend	Scale 2	Scale 3	Scale 6	Scale 8	Scale 12	Scale 13	Scale 15
Depth		0.331						
T°			–0.295					
Salinity							0.224	
DO		0.451						
NTU						0.254		
Cloud			–0.322					
Swell	–0.255		0.286					
North	0.760	–0.298						
East			0.189					
Bms						0.577	0.427	0.353
Bmd					–0.340			
Sm				0.447	0.224	–0.302		
Sms0					–0.279			
Sms76		–0.149						
Ss26						0.264	–0.533	
Ss51		–0.507	–0.461					
Cs			–0.234					
Cm		0.251		–0.578	0.566			
Bs		–0.495	–0.388					
Reef		–0.356						
Total	0.79 ***	0.71 ***	0.73 ***	0.61 ***	0.63 ***	0.65 ***	0.49 ***	0.12 **

Table 5 Partial standard regression coefficients of environmental variables which significantly explained the spatial patterns of abundance of large zooplankton at different scales. Variable codes: see Table 3.

	Scale 5	Scale 8	Scale 12
NTU	–0.323		0.272
Phyto	0.401		0.284
Bms			0.524
Bmd		–0.383	
Sm	0.214	0.200	–0.349
Sms0		–0.293	
Ss26			0.223
Cm		0.551	
Reef	0.383		
Total	0.56 ***	0.63 ***	0.67 ***

Figure Legends

Figure 1 Distribution of the habitats in the Grand Cul-de-Sac Marin (GCSM) lagoon. Location of the sampling sites along the South-North transect from the coast to the Caribbean Sea. Mangroves cover most of the shorelines, seagrass beds are found at 0-10 m depth, and muddy bottoms at depths greater than 10 m.

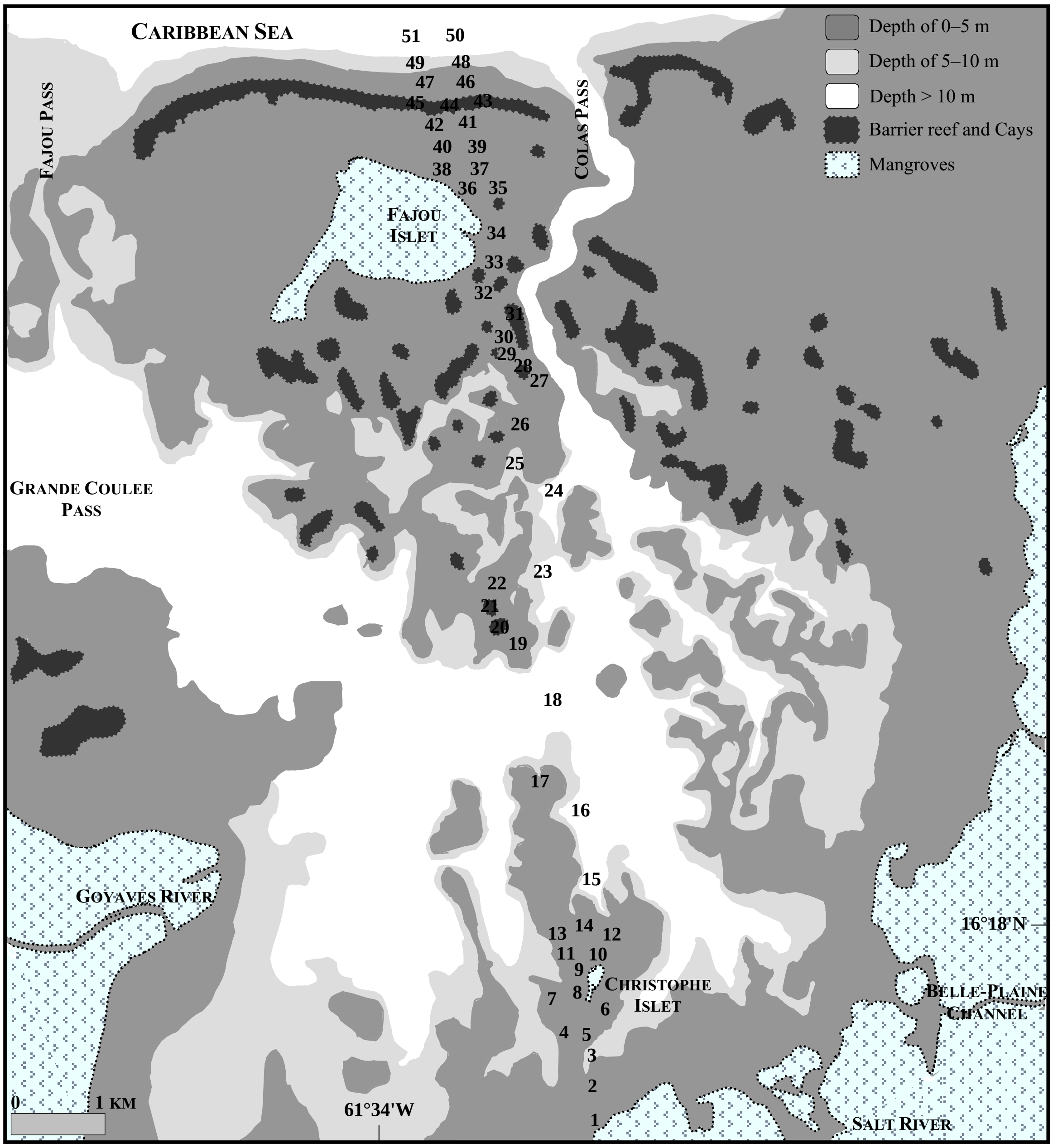
Figure 2 Significant spatial patterns of abundance (a) and biomass (b) of large zooplankton (> 600 µm) detected at the various scales. Abscissa: distance from the coast (km). Ordinate: fitted values to the spatial variable.

Figure 3 Significant spatial patterns of biomass and abundance of small zooplankton (190–600 µm) detected at the various scales. The spatial patterns at fine scales 16 and 17 are only detected in zooplankton biomass. Abscissa: distance from the coast (km). Ordinate: fitted values to the spatial variable.

Figure 4 Significant spatial patterns of phytoplankton biomass detected at the various scales. Abscissa: distance from the coast (km). Ordinate: fitted values to the spatial variable.

Figure 5 Large and small zooplankton: (a) Biomass in mg ash-free dry mass (AFDM) per m^3 of water and (b) abundance observed along the cross-shelf transect. (c) Phytoplankton biomass estimated by total chlorophyll *a* (µg/L) along the cross-shelf transect.

Figure 1


CARIBBEAN SEA
Depth of 0–5 m
Depth of 5–10 m
Depth > 10 m
Barrier reef and Cays
Mangroves
FAJOU PASS
COLAS PASS
FAJOU ISLET
GRANDE COULEE PASS
GOYAVES RIVER
CHRISTOPHE ISLET
BELLE-PLAINE CHANNEL
SALT RIVER
16°18'N
61°34'W
0
1 KM
51 50
49 48
47 46
45 44 43
42 41
40 39
38 37
36 35
34
33
32
31
30
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13 12
11 10
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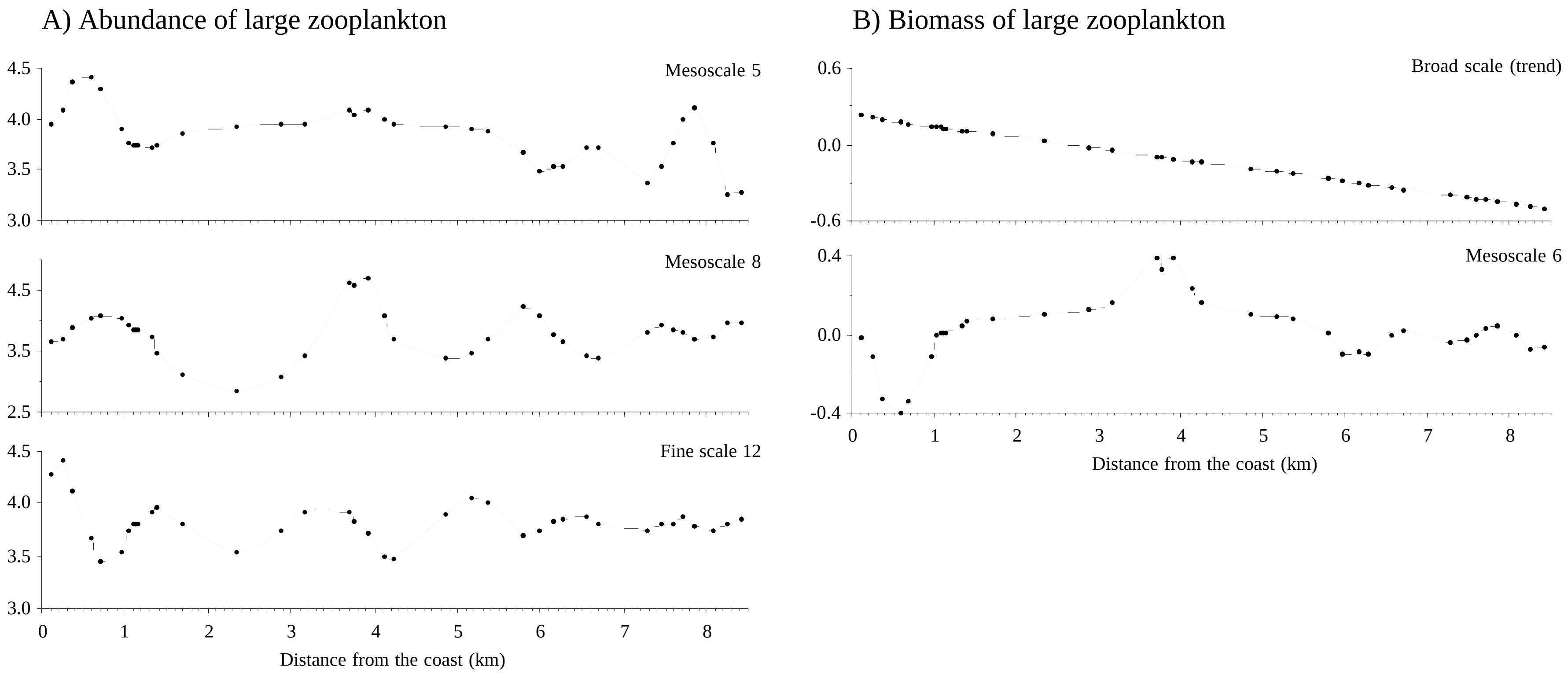
3
2
1

Figure 2



A) Abundance of large zooplankton

B) Biomass of large zooplankton

Figure 3

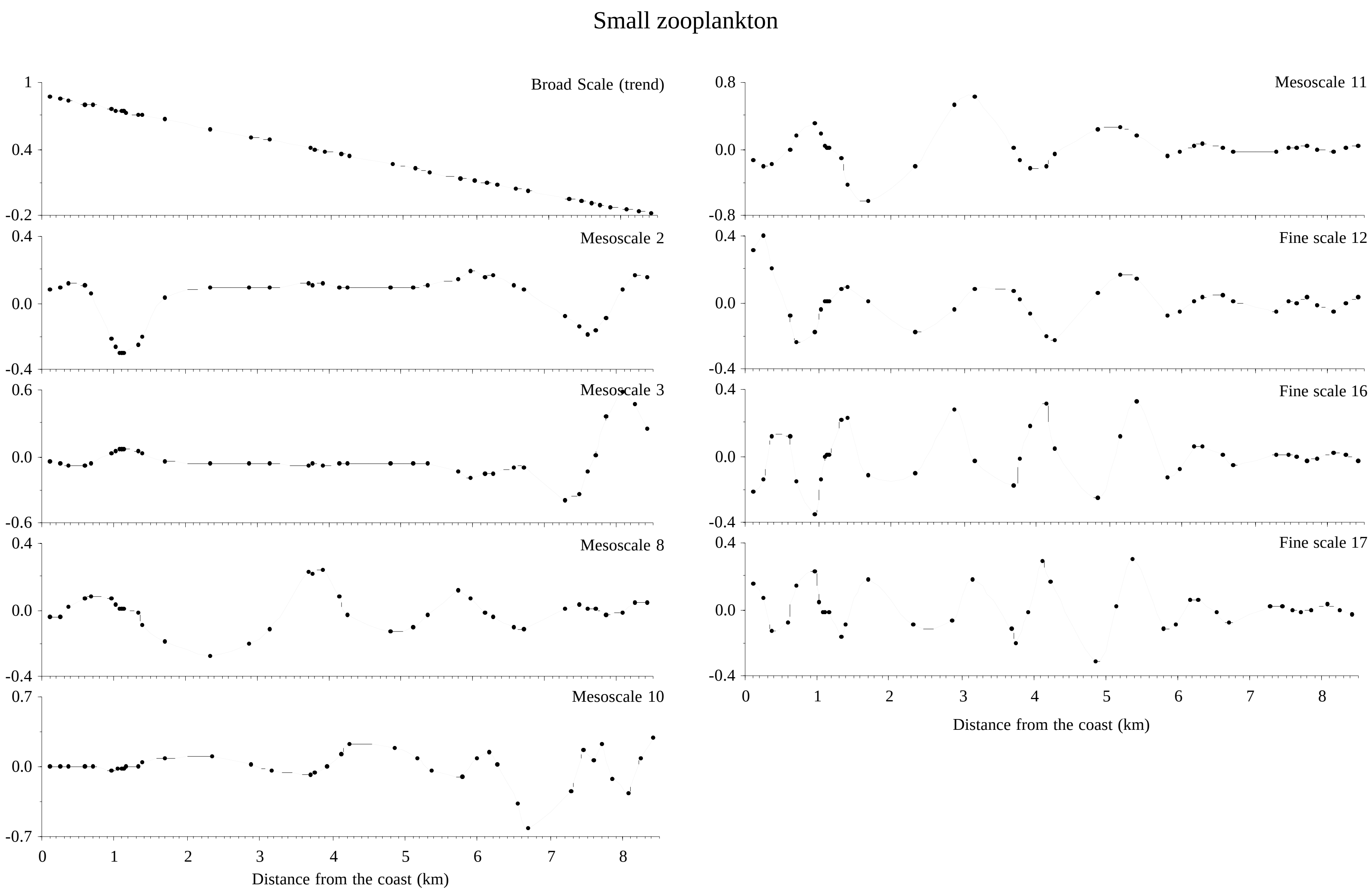

Small zooplankton
Broad Scale (trend)
1
0.4
-0.2
Mesoscale 2
0.4
0.0
-0.4
Mesoscale 3
0.6
0.0
-0.6
Mesoscale 8
0.4
0.0
-0.4
Mesoscale 10
0.7
0.0
-0.7
0
1
2
3
4
5
6
7
8
Distance from the coast (km)
Mesoscale 11
0.8
0.0
-0.8
Fine scale 12
0.4
0.0
-0.4
Fine scale 16
0.4
0.0
-0.4
Fine scale 17
0.4
0.0
-0.4
0
1
2
3
4
5
6
7
8
Distance from the coast (km)

Figure 4

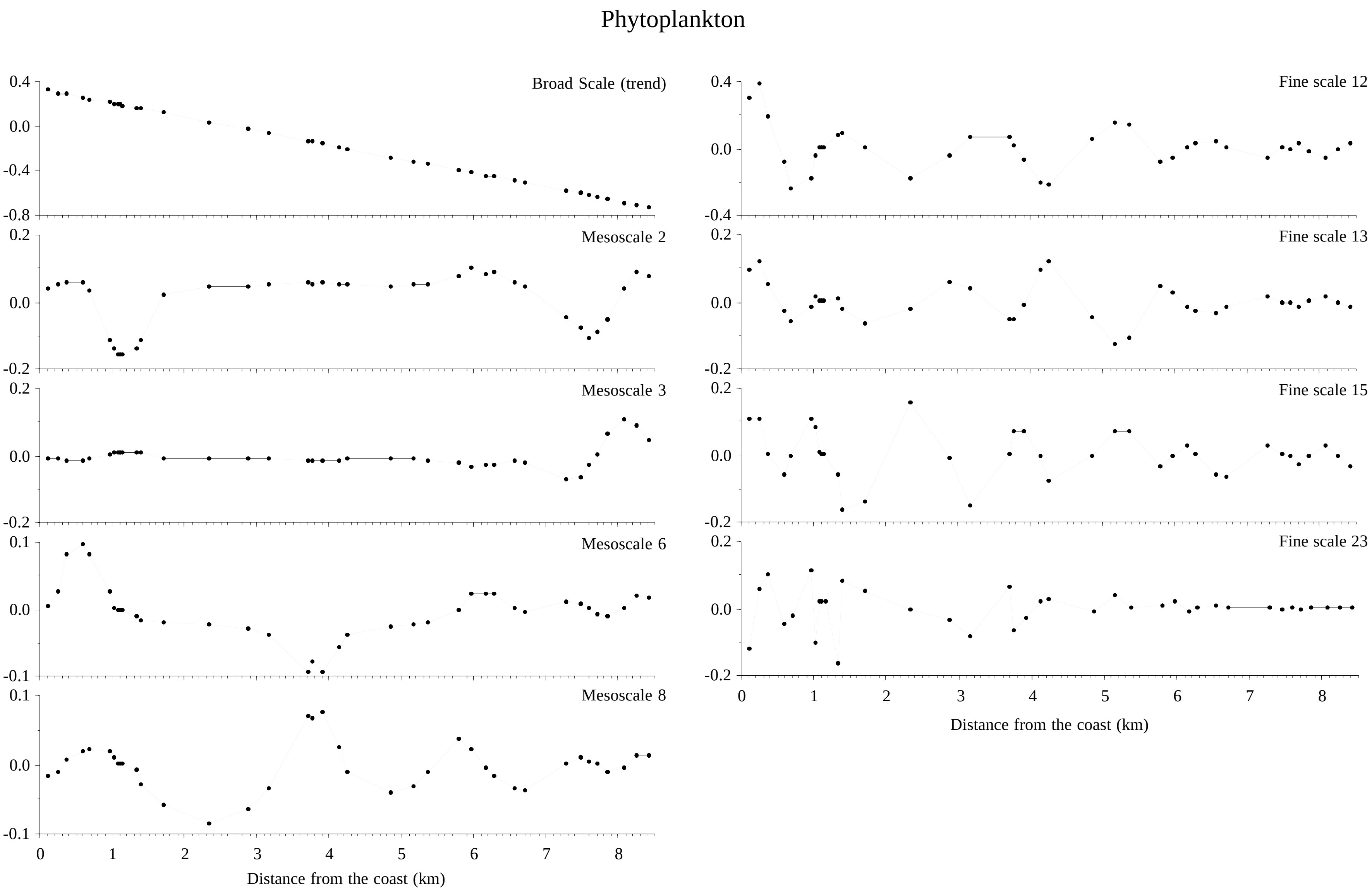
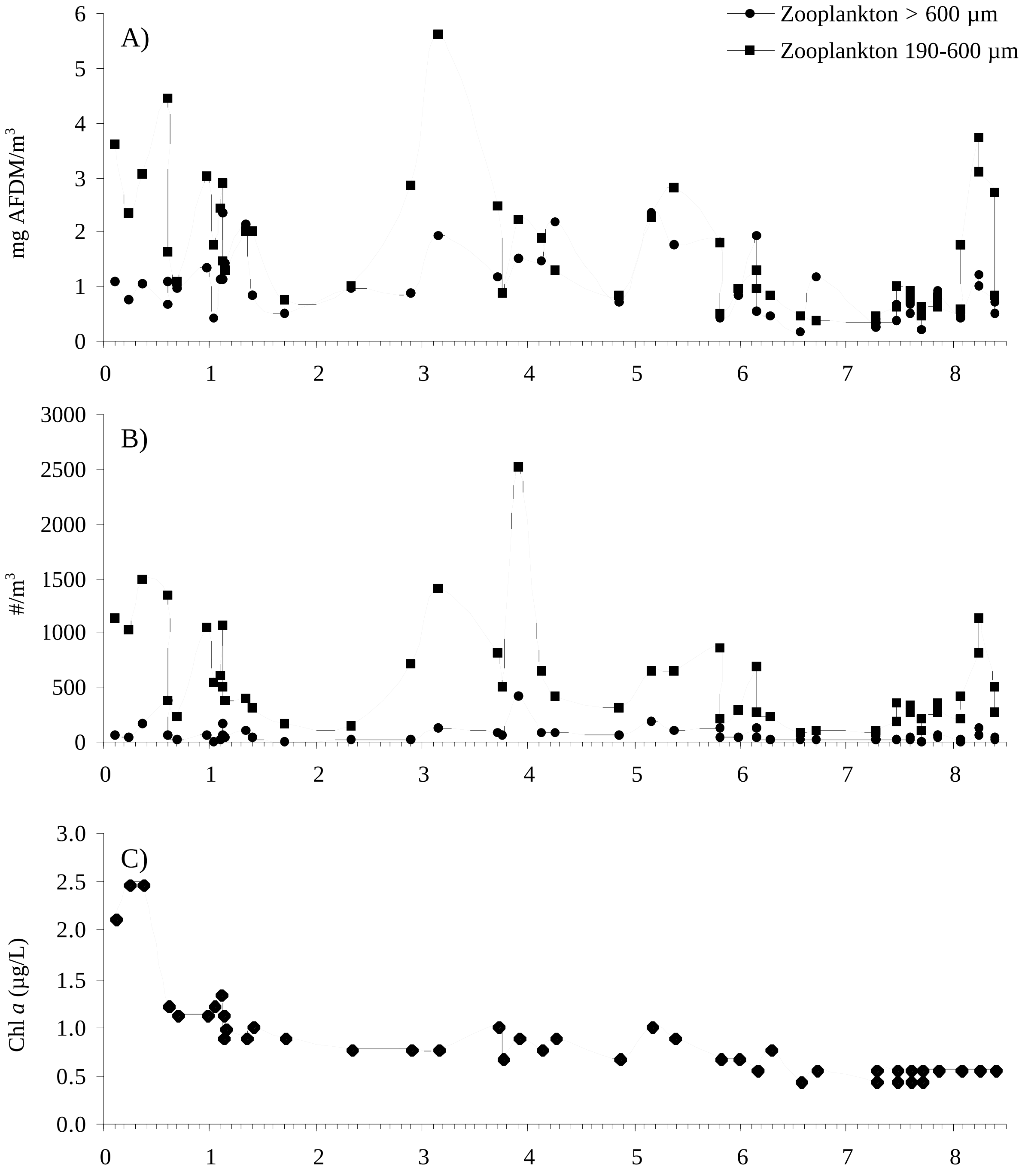

Phytoplankton
Broad Scale (trend)
0.4
0.0
-0.4
-0.8
Mesoscale 2
0.2
0.0
-0.2
Mesoscale 3
0.2
0.0
-0.2
Mesoscale 6
0.1
0.0
-0.1
Mesoscale 8
0.1
0.0
-0.1
0
1
2
3
4
5
6
7
8
Distance from the coast (km)
Fine scale 12
0.4
0.0
-0.4
Fine scale 13
0.2
0.0
-0.2
Fine scale 15
0.2
0.0
-0.2
Fine scale 23
0.2
0.0
-0.2
0
1
2
3
4
5
6
7
8
Distance from the coast (km)

Figure 5


A)
mg AFDM/m3
6
5
4
3
2
1
0
Zooplankton > 600 µm
Zooplankton 190-600 µm
0
1
2
3
4
5
6
7
8
B)
#/m3
3000
2500
2000
1500
1000
500
0
0
1
2
3
4
5
6
7
8
C)
Chl a (µg/L)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
1
2
3
4
5
6
7
8

CHAPITRE

7

CONCLUSIONS ET PERSPECTIVES

7.1 Conclusions Générales

Deux thèmes fondamentaux et interconnectés en écologie sont le développement et le maintien des patrons spatiaux et temporels et les conséquences de ces patrons dans la dynamique des populations et des écosystèmes. Ces deux thèmes ne peuvent être abordés sans considérer les échelles spatiales des patrons et des processus écologiques puisque, d'une part, les processus physiques et biologiques varient avec l'échelle spatiale et, d'autre part, chaque individu et chaque espèce expérimentent l'environnement à des échelles spatiales et temporelles différentes et de ce fait répondent individuellement à l'hétérogénéité environnementale. **Dans ce contexte, le travail de recherche présenté dans ce manuscrit a montré comment le changement d'échelle spatiale, dans le cadre de l'analyse multiéchelle, a permis de mettre en évidence différents niveaux d'organisation de la communauté zooplanctonique associée au lagon du GCSM et d'identifier les échelles de dépendance spatiale des patrons du zooplancton et des processus physiques et biologiques responsables de la variabilité spatiale multiéchelle du zooplancton.**

Les résultats de notre étude suggèrent que la variabilité du zooplancton dans le lagon du GCSM est observable à trois échelles spatiales différentes, grande (5–10 km), moyenne (1–5 km) et petite (400–1000 m) échelles. Deux types de patrons caractérisent la structure spatiale des deux classes de taille du zooplancton. Le premier, à l'échelle du lagon (8 km), représente un gradient de la biomasse et de l'abondance (du petit zooplancton seulement) décroissant de la côte vers le large et le deuxième, à moyennes et à petites échelles, caractérise des agrégats de zooplancton. Ces patrons spatiaux, caractéristiques des communautés zooplanctoniques dans les écosystèmes tropicaux côtiers (Emery 1968, Hamner & Carleton 1979, Moore & Sander 1979, Youngbluth 1980, Le Borgne et al. 1989, Ambler et al. 1991, McKinnon 1991, Alvarez-Cadena et al. 1998, Hassett & Boehlert 1999) varient, non seulement, avec l'échelle spatiale ce qui caractérise des phénomènes échelle-dépendants, mais également avec la taille des organismes et la variable-réponse considérée (biomasse ou abondance, Avois-Jacquet et al. Article 4). Bien que les deux classes de taille du zooplancton montrent une variabilité spatiale multiéchelle, l'amplitude et l'échelle spatiale de leur variabilité diffèrent fortement, particulièrement à moyennes et à petites échelles. Le petit zooplancton (190–600 µm) montre une forte variabilité spatiale de grande à petite échelles alors que les patrons spatiaux du gros zooplancton (> 600 µm) sont observables seulement à l'échelle du lagon et à moyennes échelles ; cette fraction montre une forte variabilité non structurée dans l'espace. Concomitants avec ces résultats sont les processus physiques et biologiques impliqués dans les patrons spatiaux du zooplancton dont la nature, l'amplitude et les effets varient également avec l'échelle spatiale, la taille des organismes et la variable-réponse considérée (Avois-Jacquet et al. Articles 3 et 4). Ces résultats corroborent les faits que l'hétérogénéité fonctionnelle des organismes, c'est-à-dire l'hétérogénéité environnementale qu'ils perçoivent et à laquelle ils répondent, diffèrent d'un individu à un autre (Kolasa & Rollo 1991) et que la variabilité spatiale du zooplancton est un phénomène taille-dépendant (Piontkovski et al. 1995a, Piontkovski & Williams 1995). **Les résultats de cette étude suggèrent donc que les organismes zooplanctoniques dans le lagon du GCSM perçoivent et répondent différemment à l'hétérogénéité environnementale en fonction de leur taille et, par conséquent, les échelles de dépendance spatiale de leur variabilité sont différentes.**

Bien que le petit et le gros zooplancton montrent la même structure spatiale à l'échelle du lagon (un gradient décroissant de la côte vers le large), les processus environnementaux responsables de ce patron spatial diffèrent entre les deux classes de taille. **Les résultats suggèrent que le forçage hydrodynamique induit par les vents et les courants dans le lagon du GCSM est responsable de la variabilité spatiale du petit zooplancton à grande échelle**

alors que le patron spatial du gros zooplancton à cette même échelle est le résultat d'une réponse active du zooplancton à la distribution spatiale du phytoplancton. La différence des processus impliqués dans la structure spatiale des deux fractions de zooplancton peut être attribuée à la taille des organismes (Avois-Jacquet et al. Article 3). Les petits organismes zooplanctoniques, dont la capacité natatoire est plus restreinte que celle des gros organismes (Mackas et al. 1985, Tiselius 1998), sont dispersés ou agrégés par les courants comme les cellules phytoplanctoniques alors que le gros zooplancton est capable de nager activement (Davis et al. 1992a, Wiafe & Frid 1996) pour chercher sa nourriture et maintenir une position favorable dans les agrégats de phytoplancton (Tiselius 1992, Yen et al. 1998). Si les patrons spatiaux du zooplancton à l'échelle du lagon sont maintenus par des processus hydrodynamiques agissant sur le petit zooplancton et par des processus biologiques associés aux comportements du gros zooplancton (recherche de nourriture, broutage), le gradient de biomasse et d'abondance décroissant de la côte vers le large semble être généré par la présence d'une forte biomasse de phytoplancton près de la côte qui est disponible pour le zooplancton et par l'impact de la prédation sur les organismes zooplanctoniques présents sur la barrière récifale (Avois-Jacquet et al. Article 4). Le gradient décroissant de la biomasse de phytoplancton qui représente un gradient trophique des eaux côtières eutrophiques aux eaux océaniques oligotrophiques peut expliquer pourquoi la communauté mésozooplanctonique dans le lagon du GCSM est dominée, en termes d'abondance et de biomasse, par les petits organismes (190–600 µm), particulièrement près de la côte où la biomasse de phytoplancton est la plus élevée (Avois-Jacquet et al. Article 4). Dans les eaux eutrophiques, la communauté zooplanctonique est généralement dominée par les petites espèces (Hopcroft et al. 1998b) et par les nauplii et les copépodites (Gotsis-Skretas et al. 2000) par comparaison avec les eaux oligotrophiques où la communauté est numériquement dominée par de plus grosses espèces zooplanctoniques (Webber & Roff 1995a, b, Hopcroft et al. 1998b). Les petites espèces zooplanctoniques ainsi que les nauplii et les copépodites sont capables d'exploiter de petites cellules phytoplanctoniques, comme le pico- (< 2 µm) et le nanophytoplancton (2–20 µm), très abondantes (Webber & Roff 1995b) particulièrement dans les eaux oligotrophiques (Hopcropft & Roff 1990) alors que les grosses espèces de zooplancton apparaissent limitées par la nourriture (Hopcroft et al. 1998a). Ces derniers se nourrissent de particules phytoplanctoniques plus grosses (microphytoplancton > 20 µm) mais plus diluées dans l'environnement (Roff et al. 1995), particulièrement dans les eaux océaniques (Webber & Roff 19995b). Bien que les eaux tropicales côtières tendent à être dominées par le microphytoplancton, notamment lorsque la biomasse du phytoplancton est élevée (Hopcroft & Roff 1990), la disponibilité du microphytoplancton comme source de nourriture ne semble pas affecter l'abondance du gros zooplancton (> 600 µm) dans le lagon du GCSM (Avois-Jacquet et al. Article 4). L'augmentation de la biomasse et l'abondance du mésozooplancton en fonction de la disponibilité des cellules phytoplanctoniques est souvent attribuable aux petits organismes zooplanctoniques comme les petits copépodes, les copépodites et les nauplii qui constituent la majorité du mésozooplancton (Rollwagen-Bollens & Landry 2000). **Par conséquent, la variabilité spatiale de l'abondance du petit zooplancton (190–600 µm) à l'échelle du lagon, comparée à l'absence de patron spatial du gros zooplancton à cette échelle, peut être en partie le résultat de la dominance des nauplii, des copépodites et des petites espèces zooplanctoniques en réponse à la disponibilité du phytoplancton comme source de nourriture. Une dominance de petites cellules phytoplanctoniques combinée avec la prédation sur le gros zooplancton peut expliquer sa faible abondance par rapport à celle du petit zooplancton et l'absence de patron spatial pour ce dernier à l'échelle du lagon.**

Il est clair qu'à moyennes échelles, l'hétérogénéité de l'habitat et le forçage hydrodynamique sont des facteurs importants de la variabilité spatiale des deux classes de taille de zooplancton qui se caractérise par des agrégats. Les résultats de l'étude suggèrent que les organismes zooplanctoniques vivant dans les herbiers à phanérogames marines ne sont pas adaptés à de fortes conditions hydrodynamiques alors que les organismes présents sur les cayes peuvent maintenir leur position dans un environnement turbulent (Avois-Jacquet et al. Article 3). Le comportement natatoire des organismes zooplanctoniques peut être un processus biologique important pour la formation et le maintien des agrégats en réponse à l'intensité lumineuse (Hamner & Carleton 1979, Buskey et al. 1995), à la prédation (Emery 1968, Hamner & Carleton 1979, Walters & Bell 1994, Bullard & Hay 2002), à la reproduction (Ambler et al. 1991, Buskey 1998, Folt & Burns 1999) et aux agrégats de phytoplancton (Tiselius 1992). Cependant les pics de biomasse et d'abondance de zooplancton observés dans les différents habitats ne requièrent pas nécessairement la mobilité des organismes, mais peuvent résulter d'une accumulation hydrodynamique passive des organismes à un endroit particulier (ou plus justement dans un site hydrodynamique particulier). La profondeur et la topographie du fond influencent la direction et la vitesse des courants induisant des turbulences locales (Castaing et al. 1984) qui affectent la structure spatiale du zooplancton (Avois-Jacquet et al. Article 3). L'effet de la turbulence sur les patrons spatiaux du zooplancton dépend non seulement de l'intensité de la turbulence, mais également de la taille des organismes, de leur motilité et des espèces zooplanctoniques eux-mêmes (Petersen et al. 1998). De plus, différentes associations d'espèces zooplanctoniques attribuées aux caractéristiques physiques, chimiques et biologiques des masses d'eau (Webber et al. 1996, Alvarez-Cadena et al. 1998) et aux caractéristiques de l'habitat (Alvarez-Cadena et al. 1998, Rios-Jara 1998, Suàrez-Morales & Gasca 2000) ont été observées dans les écosystèmes tropicaux côtiers le long d'un gradient côte-large. **Les caractéristiques des espèces zooplanctoniques associés aux différents habitats et la taille des organismes peuvent expliquer les différents patrons spatiaux du zooplancton observés dans le lagon du GCSM à moyennes échelles et qui résulteraient de processus d'agrégation active des organismes zooplanctoniques et/ou d'accumulation hydrodynamique passive.**

Les résultats de l'étude (Avois-Jacquet et al. Article 4) ont permis de mettre en évidence trois régions géographiques dans le lagon du GCSM qui se distinguent à moyennes échelles par les patrons spatiaux de zooplancton et les processus physiques et biologiques sous-jacents. La région près de la côte est caractérisée par une biomasse et une abondance très élevées de zooplancton qui est influencé par les mêmes masses d'eau côtière et par la présence de phytoplancton. La partie centrale du lagon représente une zone intermédiaire de mélange des eaux océaniques et côtières où la structure spatiale du zooplancton est influencée par la topographie des fonds et l'hydrodynamique local. La troisième région localisée dans le nord du lagon, près du récif-barrière, est sous l'influence des masses d'eau océanique où les organismes zooplanctoniques répondent fortement à l'hydrodynamique locale, à la turbidité et à la prédation.

À petites échelles (400–1000 m), comme à moyennes échelles (1–5 km), l'hétérogénéité de l'habitat influence la structure de la communauté zooplanctonique du lagon du GCSM en modifiant leur abondance, leur biomasse et leur distribution spatiale (Avois-Jacquet et al. Articles 3 et 4). Il est reconnu que la taille, la structure et la distribution des agrégats sont adaptées à la topographie de l'habitat (Hamner & Carleton 1979, Omori & Hamner 1982, Ribes et al. 1996) et que la nature du substrat affecte les densités d'organismes sur le fond (Emery 1968, Villiers & Bodiou 1996, Rios-Jara & Gonzalez 2000). Bien que le petit zooplancton montre une forte variabilité spatiale et des patrons spatiaux différents tandis que le gros zooplancton ne montre aucune structure spatiale à ces échelles, les données de l'étude ne permettent pas de déterminer d'autres processus physiques et biologiques responsables de ces patrons spatiaux. Dans les eaux côtières, il semble que les processus hydrodynamiques comme la turbulence (Haury et al. 1990) et le comportement individuel du zooplancton incluant le broutage (Tiselius 1992, Yen et al. 1998), la prédation (Ribes et al. 1996, González & Tessier 1997, Alvarez-Cadena et al. 1998, Bullard & Hay 2002) et la reproduction (Haury & Wiebe 1982, Ambler et al. 1991, Buskey 1998, Folt & Burns 1999) sont des sources de variabilité dans les communautés zooplanctoniques à petites échelles spatiales. Ces mécanismes qui affectent la structure spatiale du zooplancton sont espèce-dépendants et taille–dépendants (Ohlhorst 1982, Bollens & Frost 1991, Folt et al. 1993, Petersen et al. 1998, Rios-Jara & Gonzalez 2000). **Pour établir les relations spatiales à petite échelle entre la variabilité du zooplancton et l'hétérogénéité environnementale, il serait nécessaire de réaliser de nouvelles études en**

considérant la turbulence, les processus biologiques associés aux comportements individuels des organismes zooplanctoniques ainsi que les assemblages d'espèces associés aux différents habitats des écosystèmes tropicaux côtiers et les caractéristiques des espèces zooplanctoniques (taille, motilité, mode d'alimentation), ce qui peut constituer de nombreuses perspectives de recherche.

7.2 Perspectives de Recherche

7.2.1 – Échantillonnage du Zooplancton

La pompe à plancton a permis d'échantillonner le zooplancton avec la même technique dans les différents habitats du lagon du GCSM (récif-barrière, cayes, herbiers à *T. thalassia*, fonds vaseux) ce qui était préférable pour l'analyse et l'interprétation des données (Avois-Jacquet et al. Article 3). Bien qu'elle possède certains avantages comme l'échantillonnage à des échelles spatiales et temporelles biologiquement pertinentes et l'échantillonnage simultané de toutes les classes de taille dans le même espace-temps (Miller & Judkins 1981, Taggart & Leggett 1984, Rahkola et al. 1994), cette technique génère certains problèmes avec la collecte des organismes zooplanctoniques incluant l'endommagement et la destruction de certains organismes et l'évitement du tuyau d'aspiration par d'autres (Taggart & Leggett 1984). Cette technique d'échantillonnage permet de collecter des échantillons à des endroits spécifiques et de couvrir une aire d'étude plus rapidement et plus précisément que le filet à plancton, mais elle ne permet pas un échantillonnage en continu. De plus, elle requière un certain temps passé à chaque station ce qui limite le nombre d'échantillons qui peuvent être collectés par jour (Avois-Jacquet et al. Articles 3). Cette technique ne permet donc pas un échantillonnage en continu à haute-fréquence ce qui limite la puissance des analyses multiéchelles (voir § 7.2.2) et, par conséquent, l'interprétation des patrons spatiaux du zooplancton.

Au cours de ces vingt dernières années, trois techniques d'échantillonnage ont été développées. Elles permettent de résoudre certains problèmes liés à l'échelle spatiale d’observation (limitation de la taille du grain d’échantillonnage et/ou de l’étendue de l’échantillonnage) qui influence les analyses spatiales et, par conséquent, l’identification des patrons et des processus écologiques (Avois-Jacquet et al. Article 1). Il s’agit : i) des **compteurs à particules** comme le compteur optique à plancton (Optical Plankton Counter, OPC ; Herman 1992) et le détecteur lumineux (Dual Light Sheet sensor, DLS ; Sutton et al. 2001), ii) des **détecteurs optiques** comme l’enregistreur vidéo à plancton (Video Plankton Recorder, VPR ; Davis et al. 1992b), la caméra vidéo *in situ* (in situ video camera, Tiselius 1998) et l’enregistreur de l’évaluation du profil imagé des particules (Shadow Image Particle Profile Evaluation Recorder, SIPPER ; Sutton et al. 2001) et iii) des **détecteurs acoustiques multi-fréquences** (Sameoto et al. 1993, Greene et al. 1998, Swartzman et al. 1999, Coyle 2000). Bien que chacune de ces techniques soit limitée techniquement (se référer à Williamson et al. 1992, Pinel-Alloul 1995, Folt & Burns 1999, Sutton et al. 2001 pour une revue exhaustive), ces nouvelles méthodes d’échantillonnage permettent d’acquérir des données *in situ* et en continu et/ou de couvrir une grande aire d’étude sans compromettre la résolution haute-fréquence des données aux petites échelles spatiales. Il est possible d’acquérir des données *in situ* et en continu en utilisant des détecteurs optiques qui comptent, mesurent et donnent même une image des particules. De telles informations permettent de visualiser des patrons quasi-synoptiques de la distribution des organismes. L’OPC est un exemple d’appareil comptant et mesurant les particules et qui peut collecter des données biologiques sur une grande échelle spatiale sans compromettre la résolution des données à petite échelle. Bien qu’elle ne permette pas l’identification des espèces, cette technique d’échantillonnage permet de déterminer les distributions spatiales du zooplancton du kilomètre au millimètre (e.g. Currie et al. 1998). Les détecteurs optiques qui sont capables d’imager les particules donnent des informations intéressantes sur les patrons spatiaux verticaux et horizontaux des organismes à petites échelles (Sutton et al. 2001, Avois-Jacquet non publié). Ces techniques optiques peuvent être augmentées avec des détecteurs acoustiques multi-fréquences qui fournissent également des informations sur la distribution spatiale du zooplancton et des poissons par classe de taille (Sameoto et al. 1993, Greene et al. 1998, Swartzman et al. 1999, Coyle 2000). Cependant ces nouvelles techniques d’échantillonnage sont difficilement applicables, voir inapplicable, pour le moment dans les environnements tropicaux côtiers à cause de la faible profondeur et de la topographie du milieu (Avois-Jacquet et al. Article 2).

Un autre problème dans l’acquisition des données biologiques dans les systèmes aquatiques est que les procédures diffèrent pour les différents groupes d’organismes pélagiques (phytoplancton, microzooplancton, mésozooplancton, poissons qui possèdent des échelles de dépendance spatiale différentes). Chaque groupe requiert des méthodes spécifiques d’échantillonnage. Les données physiques et biologiques sont souvent obtenues à des échelles spatiales et temporelles différentes. L’acquisition des données physiques est généralement rapide avec un enregistrement *in situ* en continu alors que les données biologiques sont souvent acquises après des procédures laborieuses qui prennent du temps, particulièrement en planctonologie. L’utilisation d’un échantillonneur haute-fréquence multi-détecteur (Sutton et al. 2001) incluant un compteur à particules, un détecteur optique, un fluorimètre ou un cytomètre en flux, une sonde température-conductivité-profondeur, des filets à plancton et des bouteilles d’échantillonnage permettrait des analyses à haute-résolution des variables de l’écosystème pour l’étude des patrons spatiaux des organismes de grande à petite échelle ainsi que des facteurs qui influencent ces patrons. Cependant ces techniques demandent un soutien logistique et financier qui n’est pas toujours disponible. De nouvelles techniques d’échantillonnages adaptées aux eaux tropicales côtières (Avois-Jacquet et al. Article 2) restent encore à être développées ce qui aiderait à identifier les échelles de dépendance spatiale des patrons du zooplancton, mais également des autres groupes pélagiques, dans les différents habitats et à comprendre les processus physiques et biologiques sous-jacents.

7.2.2 – Analyse Multiéchelle

La méthode des coordonnées principales des matrices de voisin (Principal Coordinates of

Neighbour Matrices, PCNM ; Borcard & Legendre 2002) a permis de détecter et de quantifier les patrons spatiaux du zooplancton qui ont été corrélés aux facteurs environnementaux mesurés dans le lagon du GCSM. L'approche multiéchelle a donc permis d'apprécier la nature et l'importance des sources de variabilité et d'identifier les échelles de dépendance spatiale des patrons du zooplancton et des processus physiques et biologiques sous-jacents (Avois-Jacquet et al. Articles 3 et 4). Bien qu'elle ait montré son efficacité avec des données discrètes mesurées à intervalle irrégulier, le degré avec lequel la PCNM détecte les patrons spatiaux est sensible à l'échelle d'observation. Dans l'étude, la puissance de la PCNM a été limitée par la 'fenêtre d'observation' imposée par l'intervalle d'échantillonnage.

La description de tous systèmes dépend de l'échelle spatiale, temporelle et organisationnelle choisie par l'observateur. Il est donc essentiel de comprendre non seulement comment les patrons et les processus écologiques varient avec l'échelle, mais également comment les patrons détectés à une échelle sont les manifestations des processus opérant à une autre échelle (Avois-Jacquet et al. Article 1). Par exemple, les courants induits par le vent à grande échelle peuvent générer une diminution de la variabilité spatiale du zooplancton à moyennes échelles qui se caractérise par une faible agrégation des organismes zooplanctoniques (Piontkovski & Williams 1995). De même, on peut se demander comment le comportement du zooplancton à petites échelles affecte sa variabilité et ces patrons spatiaux à moyennes échelles. Dans ce contexte, la PCNM n'a pas pu quantifier ces relations interéchelles puisque, par définition, les variables spatiales (i.e. les coordonnées principales) sont indépendantes les unes des autres (i.e. orthogonales). Il serait pertinent, dans cette perspective, de développer une méthode d'analyse multiéchelle qui permettrait d'identifier et de quantifier les relations interéchelles entre les patrons et les processus écologiques.

7.2.3 – Variabilité Spatiale du Zooplancton à Petite Échelle

Les variables physiques et biologiques considérées dans l'étude (Avois-Jacquet et al. Articles 3 et 4) ont expliqué une fraction importante de la variabilité spatiale de la biomasse et de l'abondance du zooplancton à grande et à moyenne échelles (entre 42 et 93 % de la variabilité spatiale). Par contre, seule une petite fraction de la variabilité spatiale du zooplancton a été expliquée à petites échelles (> à 30 % de la variabilité spatiale). Les seules variables environnementales retenues dans les modèles spatiaux à petites échelles ont été celles qui caractérisaient l'habitat. Il est reconnu que le type et la structure de l'habitat influencent la structure des communautés zooplanctoniques en modifiant la biomasse (Rios-Jara 1998, Avois-Jacquet et al. Article 3), la diversité (Porter et al. 1978, Alvarez-Cadena et al. 1996, Conolly 1997, Eggleston et al. 1999), la distribution et l'abondance des organismes (Emery 1968, Villiers & Bodiou 1996, Eggelston et al. 1998, García-Charton & Pérez-Ruzafa 1999, Rios-Jara & Gonzalez 2000, Avois-Jacquet et al. Article 4). L'habitat peut affecter la variabilité spatiale du zooplancton à petite échelle en modifiant l'intensité de la prédation (González & Tessier 1997, Bullard & Hay 2002), l'évitement des prédateurs (Alvarez-Cadena et al. 1998, Edgar 1999, Bullard & Hay 2002), la dispersion et le recrutement larvaire (Porter et al .1978, Eggleston et al. 1998, Jenkins et al. 1998), la disponibilité de la nourriture (Koch & Madden 2001) et les caractéristiques physiques de l'environnement (e.g. courants, turbulence, turbidité ; Koch & Gust 1999). La turbulence (Haury et al. 1990) et le comportement du zooplancton concernant le broutage (Tiselius 1992, Yen et al. 1998), la prédation (Ribes et al. 1996, González & Tessier 1997, Alvarez-Cadena et al. 1998, Bullard & Hay 2002) et la reproduction (Haury & Wiebe 1982, Ambler et al. 1991, Buskey 1998, Folt & Burns 1999) sont également des sources de variabilité du zooplancton à petites échelles spatiales. Comme ces processus sont espèce-dependants et taille-dépendants (Ohlhorst 1982, Bollens & Frost 1991, Folt et al. 1993, Petersen et al. 1998, Rios-Jara & Gonzalez 2000), il serait pertinent de considérer les espèces zooplanctoniques et les assemblages qu'elles forment dans les différents habitats afin de déterminer les processus physiques et biologiques qui génèrent leurs patrons spatiaux à petite échelle.

L’identification des assemblages d’espèces zooplanctoniques associés aux différents habitats est une étape majeure pour établir les processus biologiques impliqués dans la variabilité du zooplancton à petite échelle, mais elle doit prendre en considération l’effet de la turbulence sur les organismes (Avois-Jacquet et al. Article 2). La turbulence, généralement plus importante dans les eaux côtières que dans les eaux océaniques (Petersen et al. 1998), affecte certains processus biologiques. La turbulence peut générer et disperser les agrégats de phytoplancton ce qui affecte la disponibilité de la nourriture pour les prédateurs planctivores (Kiørboe 1997) et peut induire la dérive du plancton en dehors de leur lieu de croissance ou de production (Peters & Marassé 2000). La turbulence à petite échelle augmente le taux de rencontre entre les prédateurs planctoniques et leur proie (Rothschild & Olson 1988), affecte les taux d’alimentation des prédateurs planctoniques incluant les copépodes (Saiz et al. 1992, Saiz & Kiørboe 1995, Visser et al. 2001), modifie le comportement alimentaire des organismes (Saiz & Kiørboe 1995), affecte la production du plancton (Saiz et al. 1992) et altère les taux métaboliques des organismes (Alcaraz et al. 1994). Ces effets dépendent d’un certain nombre de facteurs incluant l’intensité de la turbulence, l’espèce, la taille des organismes, leur motilité et leur mode d’alimentation (Petersen et al. 1998). L’effet de la turbulence à petite échelle sur les taux de rencontre des proies diffèrent entre les prédateurs et dépend fortement du comportement et du mode d’alimentation du prédateur (Kiørboe & Saiz 1995), de la différence de vélocité entre la proie et le prédateur induite par leur motilité et de l’échelle spatiale d’interaction entre le prédateur et sa proie (Kiørboe 1997). Dans ce contexte, une perspective de recherche serait de déterminer les échelles de dépendance spatiale des espèces zooplanctoniques en considérant leur taille, leur motilité, leur mode d’alimentation, les caractéristiques hydrodynamiques du comportement des organismes et la turbulence. Ces études devront être menées à l’échelle de l’individu puisque le broutage et la prédation ne sont pas accomplis par une population, mais par un individu et que les interactions entre le prédateur et sa proie sont des évènements discrets se produisant sur des petites échelles spatiales et temporelles. Ce type de recherche demanderait de réaliser des études en milieu naturel qui peuvent être réalisées grâce aux détecteurs optiques (caméra vidéo *in situ*, § 7.2.1), mais également des études expérimentales qui permettraient de contrôler certaines variables comme la turbulence ou la concentration en nourriture. Pour comparer ces résultats, il serait nécessaire d'incorporer l'échelle spatiale comme une variable dans les plans d'échantillonnage et expérimentaux (§ 7.2.4).

7.2.4 – L' Échelle Spatiale : Une Composante Intrinsèque des Systèmes Écologiques

L'approche multi-échelle permet d'établir d'une part le comportement des systèmes écologiques aux différentes échelles spatiales et d'autre part, l'influence de l'échelle sur la perception de ces systèmes (Avois-Jacquet et al. Article 1). Si l'échelle n'est pas un élément intégré dans les études des systèmes écologiques, il devient difficile de comparer les résultats, par exemple, sur des mêmes espèces dans des environnements différents, sur des espèces différentes dans le même environnement ou entre les études en milieu ouvert et les études expérimentales. Les études expérimentales en laboratoire et en mésocosme sont très importantes en écologie (puisqu'elles permettent de tester des hypothèses dans un environnement contrôlé), mais la possibilité d'extrapoler les résultats obtenus à partir de ces études à des systèmes naturels est problématique. Des biais évidents sont liés aux échelles spatiales et temporelles sous lesquelles les expériences sont conduites puisque les expériences à petite échelle entraînent souvent des conclusions erronées sur les patrons et les processus à grande échelle. Une solution est d'incorporer de manière explicite l'échelle spatiale dans les stratégies d'échantillonnage et dans les études expérimentales. Une perspective d'étude est de comprendre les effets des échelles spatiales et de leur changement afin de pouvoir comparer les résultats entre les différents systèmes, d'une part, et d'autre part, d'extrapoler les informations à partir des systèmes expérimentaux aux systèmes naturels.

GLOSSAIRE

Abiotique (abiotic) — Adjectif qualifiant tous les éléments inorganiques* (minéraux, eau, soleil) et les facteurs physiques incluant les facteurs climatiques (pluie, température, vent), édaphiques (humidité, composition chimique et structure du sol) et hydrodynamiques* (courant, upwelling*). Antonyme : biotique*.

Abondance (abundance) – Correspond au nombre d'individus par unité de surface ou de volume.

Agrégat (patch) – Réfère à un assemblage d'organismes dans l'espace qui forme une structure spatiale (essaim*, banc*). La densité des organismes (abondance et espace entre les individus), la composition, la dimension et la persistance sont utilisées pour caractériser un agrégat. Synonyme : tache

Alizé (trade wind) – Vent régulier soufflant toute l'année dans la zone intertropicale (du nord-est au sud-ouest dans l'hémisphère nord et du sud-est au nord-ouest dans l'hémisphère sud), dû à la quasi-permanence des anticyclones sur les régions subtropicales et de basses pressions sur les régions équatoriales.

Anthropique (anthropic) – Relatif à l'Homme.

Atoll (atoll) — Île basse formée d'un récif corallien* de forme annulaire et de dimension au moins kilométrique, entourant un lagon* et communiquant avec l'océan par des passes.

Banc (school) — Agrégat* dense dans lequel les individus, alignés parallèlement les uns aux autres, nagent dans la même direction. Ex. : Banc de poissons (Leising & Yen 1997).

Benthos (benthos) — Ensemble des espèces* aquatiques qui vivent dans ou sur le fond (i.e. sédiment ou substrat rocheux) et qui en dépend pour leur nourriture. Ces organismes, variés et abondants, peuvent être fixes (sessiles) ou mobiles (nageants, rampants, fouisseurs) comme les ascidies, les crustacés (incluant les amphipodes, les isopodes et les copépodes*), les échinodermes, les polychètes, les éponges.

Biomasse (biomass) – Masse de matière organique* produite par unité de surface ou de volume, par un organisme, une population*, une communauté* ou un écosystème*.

Biotique (biotic) — Adjectif qualifiant tous les êtres vivants incluant les virus, les bactéries, les protistes, les champignons, les végétaux, les animaux et les êtres humains. Qui a son origine dans la matière vivante. Qualifie, en écologie, les facteurs qui permettent la vie. Antonyme : abiotique*.

Caye (cay or key) — Îlot de sable situé sur de petites formations coralliennes à l'intérieur du lagon* dans des eaux peu profondes (Sorokin 1993).

Circulation de Langmuir (Langmuir circulation) — Les cellules de Langmuir disposées perpendiculairement à la direction du vent peuvent être de plusieurs kilomètres de long, mais seulement de quelques mètres de large et de profondeur. Elles sont générées par les interactions entre le vent et la dérive de surface associée aux vagues (Figure 1).

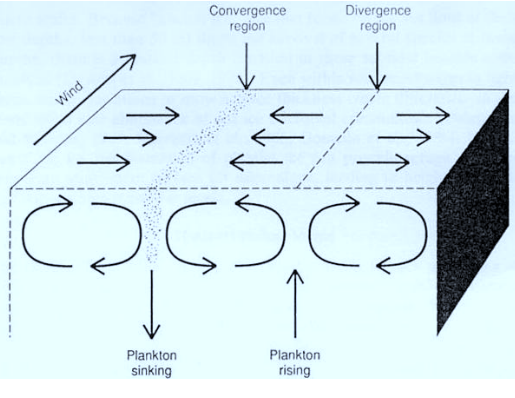


Figure 1 Dessin conceptuel de la circulation de Langmuir montrant la concentration du plancton en surface au niveau de la zone de convergence. La région de convergence correspond à un front (Barry & Dayton 1991).

Communauté (community) — Groupement d'êtres vivants appartenant à certaines espèces* bien déterminées, indépendantes les unes des autres, qui vivent dans les mêmes conditions et dans le même espace.

Continuum (continuum) — Série finement graduée dont chaque degré se fond imperceptiblement avec le suivant, l'ensemble formant une ligne droite représentant le changement dans une seule direction (gradient continu).

Copépode (copepod) — Crustacés entomostracés pourvus d'appendices natatoires développés qui ont une grande importance écologique dans les eaux marines et les eaux douces. Les copépodes (Photo 1) peuvent être libre, symbiotique ou parasite (voir http://www.nmnh.si.edu/iz/copepod/ pour plus d'informations incluant une liste taxonomique).

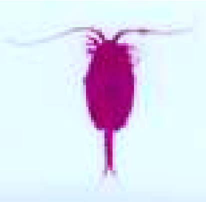


Photo 1 *Calanopia americana* (Copépode, Calanoide)

Démersal (demersal) — Se rapporte aux organismes aquatiques épibenthiques (épibenthos*) qui accomplissent des migrations verticales* dans la colonne d'eau.

Dynamique des populations (population dynamics) – Ensemble de modifications continues affectant la population, qui proviennent d'événements (reproduction, survie, mortalité) survenus pendant une période donnée.

Échelle (scale) – En écologie, les phénomènes à grande échelle implique des domaines d'espace et de temps grands (échelle d'un océan ou de l'année) ; les phénomènes à petite échelle, des domaines d'espace et de temps petits (échelle d'un lagon* ou de la journée). Pour les géographes, l'échelle est le rapport entre la taille linéaire d'un objet sur une carte et sa taille dans la nature (petite échelle 1 : 100000 ; grande échelle 1 : 25000).

Écologie (ecology) – Science qui étudie les conditions d'existence des êtres vivants, leurs comportements et les interactions de toutes natures qui existent entre des êtres vivants et le milieu extérieur.

Écosystème (ecosystem) — Ensemble d'un milieu naturel et des êtres vivants qui y vivent. L'écosystème est l'unité fonctionnelle de base en écologie, puisqu'elle inclut à la fois les êtres vivants et le milieu dans lequel ils vivent, avec toutes les interactions entre le milieu et les organismes.

Effet bottom-up (bottom-up effect) — Paradigme basé sur les processus physiques et géochimiques. Le modèle du contrôle environnemental suggère un rôle dominant des facteurs physiques et chimiques le long des gradients trophiques environnementaux ou dans les écosystèmes* limités en nutriments*. Ces facteurs constituent les processus agissant du bas vers le haut (Pinel-Alloul et al. 1995). Antonyme : effet top-down*.

Effet top-down (top-down effect) — Paradigme basé sur les cascades trophiques. Le modèle du contrôle biologique considère les interactions trophiques entre les organismes telles que la prédation, la compétition comme étant les facteurs responsables de la structure et de la dynamique des communautés*. Ces facteurs constituent les processus agissant du haut vers le bas (Pinel-Alloul et al. 1995).

Endémique (endémique) – Se dit d’un organisme, végétal ou animal, naturellement confiné dans une région particulière de dimensions limitées.

Environnement (environment) — Ensemble des facteurs physiques, chimiques et biologiques du milieu qui agissent sur un être vivant ou une communauté* écologique et qui détermine au cours du temps sa forme et sa survie.

Épibenthos (epibenthos) — Organismes aquatiques qui vivent près du fond.

Espace (space) – Étendue indéfinie contenant, englobant tous les objets, toutes les étendues finies.

Espèce (species) – Unité élémentaire de classification des être vivants, qui regroupe tous les individus de même aspect, partageant des caractères distinctifs et se reproduisant entre eux.

Essaim (swarm) — Agrégat* dense (5 à 10^3 fois plus dense qu’un agrégat normal), souvent composé d’une seule espèce*, dans lequel le mouvement et l’orientation, mais pas nécessairement l’espace entre les individus, sont aléatoires contrairement aux bancs* que peuvent former certains organismes (Leising & Yen 1997).

Eurytope (eurytopic) — Qualifie une espèce* qui supporte de fortes variations de conditions écologiques d'un milieu. Antonyme : sténotope*.

Front océanique (oceanic front) — Région de contact entre deux masses d’eau qui diffèrent dans les valeurs de certains facteurs incluant la température, la salinité et la concentration en nutriments* (Figure 1).

Habitat (habitat) – Milieu géographique qui réunit les conditions nécessaires à l'existence et à la prolifération d'une espèce animale ou végétale.

Hétérogénéité (heterogeneity) – Caractère de ce qui est formé d’éléments ou de parties de nature différentes. Antonyme : homogénéité*.

Holoplancton (holoplankton) — Ensemble des organismes aquatiques qui vivent tout leur cycle biologique en suspension dans la colonne d’eau (copépodes*, ostracodes, siphonophores, euphausiacés, salpes, chétognathes, ptéropodes, appendiculaires). Plancton* permanent. Antonyme : méroplancton*.

Homogénéité (homogeneity) – Caractère de ce qui est de la même nature, qui n’est pas formé d’éléments ou de parties différentes. Antonyme : hétérogénéité*.

Hydrodynamique (hydrodynamic) – Nom ou adjectif relatif aux mouvements de l’eau.

Inorganique (inorganic) – Dépourvu de tout caractère organique* ; sans vie.

Lagon (lagoon) — Étendue d'eau plus ou moins salée, peu profonde, séparée de la mer par un cordon littoral (lagon côtier) ou un récif-barrière* (lagon corallien ou récifal) et habituellement reliée à la mer par une ou plusieurs passes étroites.

Mangrove (mangrove) – Forêt de palétuviers (arbres halophiles) s’étendant sur les vasières de la bande littorale. Formation végétale typique des côtes marécageuses dans les pays tropicaux.

Marée (tide) – Mouvement périodique des eaux océaniques qui s’élèvent et s’abaissent chaque jour à des intervalles réguliers, provoqué par l'attraction gravitationnelle de la lune et du soleil sur l'eau des océans ainsi que par la rotation terrestre.

Marnage (tidal range) – Variation du niveau de la mer entre marée basse et marée haute.

Mer des Caraïbes (Caribbean Sea) — Autre nom de la Mer des Antilles. Basin sub-océanique de l’Atlantique Ouest situé dans l’hémisphère nord et qui borde la côte nord de l’Amérique du Sud, la côte est de l’Amérique Central et une partie du Mexique. La Mer des Caraïbes couvre une superficie d’environ 2754000 km^2.

Méroplancton (meroplankton) — Ensemble des organismes aquatiques dont une partie de leur cycle biologique est planctonique (plancton* temporaire). Ce terme est généralement utilisé pour définir tous les organismes planctoniques relevant du benthos* et du necton* (larves trocophores et véligères de vers et de mollusques, nauplii et zoés de crustacées, larves d’échinodermes, planula de cnidaires, oeufs et larves de poissons).

Migration verticale (vertical migration) — Déplacement périodique (nycthéméral* en général) du zooplancton*, vers la surface ou vers le fond. Il faut que le déplacement soit cyclique (c'est-à-dire qu'il comporte un retour) pour qu'il soit considéré comme une vraie migration.

Necton (nekton) — Ensemble des animaux marins et d’eaux douces capables de vivre en pleine eau et qui possèdent une puissance natatoire leur permettant de se déplacer activement contre les courants et d'effectuer d'importants déplacements comme les poissons, les mammifères aquatiques et certains mollusques (pieuvres, calmars).

Néritique (neritic) — S'applique à la zone marine située entre la zone littorale et le rebord du plateau continental, vers 200 m de profondeur (Figure 2).

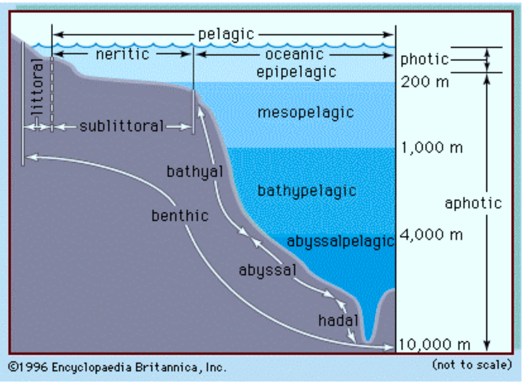


Figure 2 Diagramme schématique montrant les différentes zones de l’environnement marin qui se distinguent par leurs caractéristiques physiques, chimiques et biologiques (Britannica Encyclopedia).

Nutriment (nutrient) – Substance nutritive (organique* ou inorganique*) qui peut être directement assimilée par un organisme.

Nycthéméral (nycthemeral) – Qui se rapporte à l'alternance régulière du jour et de la nuit dont la durée relative sur 24 heures varie selon les saisons et les latitudes.

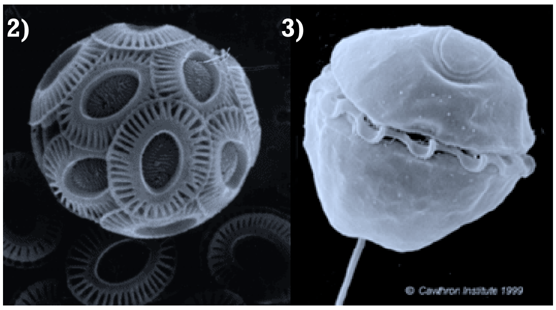
Organique (organic) – Relatif à la matière vivante. Antonyme : inorganique*.

Passe (pass) – Chenal étroit. Patrie la plus profonde d’un cours d’eau, souvent la seule navigable.

Patron (pattern) – Relatif à la forme d’un élément ou d’une structure. Les taches, les agrégats, les essaims et les bancs d’organismes sont des patrons spatiaux.

Pélagique (pelagic) — S’applique à toute la colonne d’eau dans l’environnement* aquatique (Figure 2). Les distributions horizontale et verticale des organismes pélagiques dépendent des facteurs physiques, chimiques et biologiques.

Phytoplancton (phytoplankton) — Ensemble des organismes végétaux aquatiques microscopiques (Tableau 1) qui demeurent en suspension dans l'eau, sans pouvoir opposer de résistance effective aux courants, et qui trouvent dans ce milieu leurs conditions normales d'existence (Photos 2 et 3).



Photos 2 et 3 Phytoplancton 2) Coccolithophore, *Emiliania huxleyi*, et 3) Dinoflagellé, *Gymnodinium sp.*

Plancton (plankton) — Ensemble des organismes aquatiques mono- ou pluricellulaires, pour la plupart microscopiques ou de très petite taille (Tableau 1), appartenant à des groupes très divers, vivant en suspension dans l'eau et dont les déplacements plus ou moins passifs (capacité natatoire limitée ou incapacité à nager) sont déterminés par les courants. Le plancton végétal est appelé phytoplancton* et le plancton animal est connu sous le nom de zooplancton*. Les organismes planctoniques se distinguent du necton* (animaux nageant) et du benthos* (organismes vivant sur les fonds).

Tableau 1 Classes de taille des organismes planctoniques distinguant les organismes de la boucle microbienne des organismes phytoplanctoniques et zooplanctoniques. @: classe de taille composée principalement de flagellés et de petits ciliés qui sont des membres importants de la boucle microbienne. Dans ce tableau, le femtoplancton regroupant les virus aquatiques (cellules < 200 nm) n'est pas indiqué. D'après Sieburth et al. (1978) et Catalan (1999).

Boucle microbienne		Phytoplancton		Zooplancton	
0,2–2 µm	Bactéries	0,2–2 µm	Picoplancton	2–20 µm	Nanoplancton@
2–30 µm	Flagellés	2–20 µm	Nanoplancton	20–200 µm	Microplancton
8–100 µm	Ciliés	> 20 µm	Microplancton	200–2000 µm	Mesoplancton
				> 2000 µm	Macroplancton

Pléistocène (pléistocene) – Première période (de –2 400 000 ans à 8 300 avant Jésus-Christ) du Quaternaire. Le Quaternaire est l'ère géologique la plus récente et la plus brève, marquée par l'apparition de l'homme.

Population (population) — Ensemble d'individus d'une même espèce* qui s'interfécondent librement et qui se trouvent dans une aire géographique déterminée et qui se perpétuent dans le temps.

Processus (process) – Ensemble de facteurs physiques, chimiques et biologiques qui génère une partie ou la totalité des phénomènes écologiques.

Production (production) — Quantité de matière organique* produite par unité de temps.

Productivité (productivity) — Quantité de matière organique* produite pendant un temps déterminé et sur une surface déterminée. Taux de production* ou taux de croissance relative.

Oligotrophique, Mésotrophique, Eutrophique (oligotrophic, mesotrophic, eutrophic) — Correspond respectivement à un milieu pauvre, moyennent riche et riche en nutriments* dans les environnements* aquatiques. Les critères permettant de définir l'état trophique d'une région océanique sont généralement la concentration en chlorophylle ou la concentration en nitrate (Tableau 2).

Tableau 2 Concentration en chlorophylle, surface océanique et production biologique annuelle qui caractérise chaque état trophique dans les environnements marins (d'après Antoine et al. 1996).

État Trophique	Chlorophylle	Surface	Production Biologique	
	($mg \cdot m^{-3}$)	(%)	(%)	($gC \cdot m^{-2} \cdot y^{-1}$)
Oligotrophique	[Chl] < 0,1	55,8	44,0	91,0
Mesotrophique	0,1 < [Chl] < 1	41,8	47,5	131,5
Eutrophique	[Chl] > 1	2,4	8,5	422,0

Récif-barrière (barrier reef) – Récif corallien* croissant plus ou moins parallèlement à la côte dont il est séparé par un lagon* peu profond de quelques kilomètres de large. La barrière récifale est souvent entre-coupée de passes (chenaux) permettant la communication entre le lagon et l'océan.

Récif corallien (coral reef) – Formation sous-marine de nature calcaire résultant de la production de carbonates de calcium par des espèces* coralliennes et des algues calcaires. Les récifs coralliens sont situés soit en bord de côte (récif frangeant*), soit plus au large (récif-barrière*) et peuvent encercler une île dont la lente submersion peut conduire à la formation d'un atoll*.

Récif frangeant (fringing reef) – Récif corallien* se développant sur un rivage rocheux.

Réseau trophique (food web) — En écologie, un réseau trophique (par exemple le réseau trophique microbien ou classique) est un réseau interconnecté de chaînes trophiques. Une chaîne trophique est une séquence de transferts de matière et d'énergie d'un organisme à un autre via la nourriture (Turner & Roff 1993).

Sténotope (stenotopic) — Qualifie une espèce* qui ne peut vivre que dans des conditions écologiques très étroites. Antonyme : eurytope*.

Tourbillon (eddy) — Masse d'eau tournant avec violence autour d'une dépression (Figure 3). Les tourbillons sont d'autant plus nombreux que la vitesse du courant augmente. À grande échelle* les tourbillons sont générés par la rotation de la Terre alors qu'à petite échelle ils sont le résultat de différents processus incluant le forçage par le vent sur la surface de l'eau et les upwelling* (Barry & Dayton 1991).

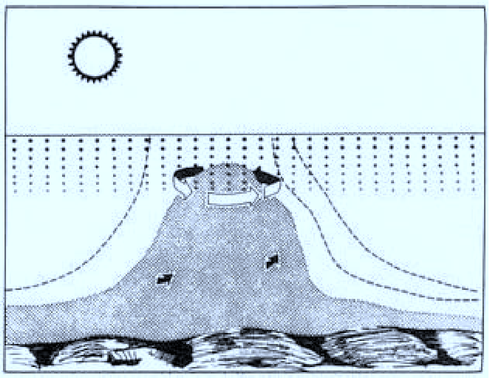
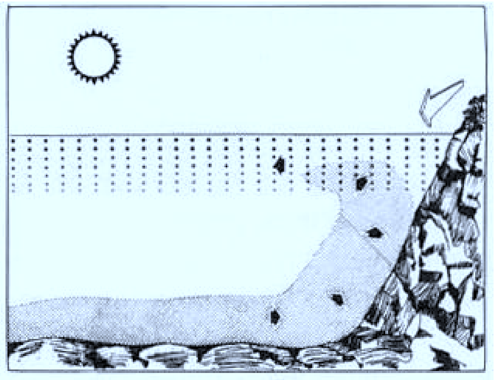


Figure 3 Diagramme schématique d'un tourbillon qui peut enrichir la zone euphotique en nutriments (Zeitzschel 1978).

Turbulence (turbulence) — Agitation irrégulière du mouvement de l'eau (Figure 3).

Turbidité (turbidity) — Réduction de la transparence d'une masse d'eau due à la présence de particules finement dispersées en suspension. La turbidité accroît la densité des eaux et peut provoquer des courants dits courants de turbidité.

Upwelling (upwelling) — Système de courant ascendant faisant remonter vers la surface des



eaux froides profondes, riches en nutriments* (Figure 4).

Figure 4 Diagramme schématique d'un upwelling rencontré le long des marges Est des bassins océaniques (d'après Zeitzschel 1978).

Vague interne (internal wave) — Formation, générée par le forçage du courant et de la marée sur les plateaux continentaux, qui se déplace entre deux masses d'eau de densités différentes. Leur période est de quelques minutes à plusieurs heures (Figure 5).

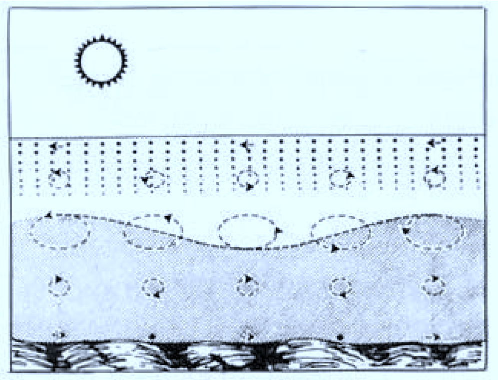


Figure 5 Diagramme schématique de vagues internes qui permettent le mélange des masses d'eau par déplacements horizontaux et verticaux (Zeitzschel 1978).

Variable (variable) – Réfère à un attribut ou à un caractère utilisé pour décrire, qualifier ou quantifier un élément ou un objet. Synonyme : descripteur. Quantité susceptible de changer de valeur.

Zooplancton (zooplankton) — Métazoaires invertébrés aquatiques dont la taille varient de quelques µm à quelques cm (Tableau 1) et qui sont dépendants du mouvement des masses d'eau, bien que certains de ces organismes possèdent des capacités natatoires. Le zooplancton est divisé en deux groupes : l'holoplancton* (zooplancton permanent comme les protozoaires et les copépodes*) et le méroplancton* (zooplancton temporaire comme les oeufs et larves de poissons, les larves de mollusques et de bivalves).

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Campagnes d'Échantillonnage

- 2001, Février 5–12 — Étude de *Periphylla periphylla* (Scyphozoaire, Coronatae) et du zooplancton dans Lurefjorden et Songefjorden, Norvège. Responsable de mission : Ulf Båmstedt, Dept Fisheries and Marine Biology, Université de Bergen, Norvège
- 1999, Mai 10–18 — ZooNyc II (Mesures Nycthémérales du Zooplancton) dans le lagon du Grand Cul-de-Sac Marin (GCSM), Guadeloupe, French West Indies
- 1999, Avril 7–10 — ZooSpace VI (Mesures de la Variation Spatiale du Zooplancton) dans le GCSM
- 1999, Mars 09–12 — ZooSpace III dans le GCSM
- 1998, Mars 21–24 — ZooSpace II dans le GCSM
- 1998, Mars 14 — Epibenthos II (Échantillonnage de l'Épibenthos) dans le GCSM
- 1998, Février 19–22 — ZooSpace I dans le GCSM
- 1998, Février 10 — Epibenthos I dans le GCSM
- 1997, Novembre 3–7 — ZooNyc I dans le GCSM
- 1995, Juillet-Août — Mesures de la Production Primaire dans le lac Croche, Canada

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- Collecte et analyse du zooplancton dans le GCSM
- Données collectées: Pompe centrifuge à zooplancton, Échantillonnage du phytoplancton et Sonde Conductivité-Température-Profondeur (CTD)
- Analyses incluent les mesures d'abondance du zooplancton, de biomasses du zooplancton et du phytoplancton, les analyses multiéchelles et multivariées
- Développement d'analyses spatiales

Recherche — Biologie du Zooplancton, Dept de Zoologie, Université de Guelph, Canada
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- Études taxonomiques et biologiques des espèces zooplanctoniques tropicales dans le laboratoire du Dr John C. Roff

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- Analyses statistiques des patrons spatiaux d'une communauté zooplanctonique lacustre pour Dr B. Pinel–Alloul
- Développement d'une méthode statistique pour déterminer les effets de la stratégie d'échantillonnage sur la variabilité des communautés zooplanctoniques avec Dr Pierre Legendre

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- 1997–2000 : Bourse d'études du Ministère des Affaires Étrangères, France
- 1997–2000 : Bourse d'études du Ministère des Relations Internationales du Québec, Canada
- Prix des Jeunes Océanographes, Mars 1999, Marseille, France
- Prix d'Excellence 2000 du Dept de Sciences Biologiques, Université de Montréal, Canada
- Prix de Voyage du GRIL (Canada) pour *ASLO Meeting 2000*, Copenhague, Danemark
- 2001 : Bourse de la Société de Secours des Amis des Sciences, Académie des Sciences, Paris

COMPETENCES

Informatique

Systèmes: Mac, DOS et Windows (5.1-2001)

Langages: Fortran, Basic

Logiciels: Progiciels Multimédias, Microsoft Office Software, FrameMarker, Progiciels Graphiques (Adobe Photoshop™, Deltagraph® Professional, Canvas™, MacGridzo) et Progiciels spécialisés en analyses (R Package, Canoco™, StatView®, SuperANOVA®, Statistica™)

Laboratoire

- Expériences avec les techniques d'incubation au ^{14}C, Compteur à scintillation, Spectrophotomètre
- Équipement limnologique/océanographique: disque de Secchi, bouteille Van Dorn, photomètre, PAR, CTD, bateaux de recherche, hors-bord
- Équipement pour collecter le plancton: filets, pompes et OPC
- Familière avec la taxonomie du zooplancton, l'appareillage standard de laboratoire, les invertébrés aquatiques et terrestres
- Équipement terrestre: compas, cartes, GPS

Formations

- Cours sur la gestion et la dynamique de groupe
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ACTIVITES

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- Secrétaire et Représentante de l'Association des Étudiants-Chercheurs en Biologie de l'Université de Montréal (AECBUM), Dept de Sciences Biologiques, Canada. Sept. 1999–Sept. 2000.
- Littérature, Arts, Gastronomie et Sport

REVISIONS D'ARTICLES

- Proceedings: Biological Sciences. The Royal Society, London, U. K. Août 2000.

CONFERENCES

- Avois C. 2001. Variabilité spatiale multiéchelle du zooplancton dans un lagon récifal côtier. INRA, Thonon-les-Bains, France.
- Avois C., Legendre, P. and D. Borcard. 2000. Role of Scales and Environmental Factors in Spatial Variability of Zooplankton Communities. NERSC (Nansen Environmental & Remote Sensing Center), Solheimsviken, Norway.
- Avois C., Legendre P. and M. Louis. 2000. Multi-scale Spatial Relationships Between Zooplankton Biomass and Environmental Heterogeneity in a Coastal Reef Lagoon. ASLO Meeting 2000, Copenhagen, Denmark.
- Avois C. and P. Legendre. 1999. Hétérogénéité Spatiale du Zooplancton Tropical Côtier. Station Biologique de Roscoff, Université Paris 6, France.
- Avois C., Legendre P. and M. Louis. 1999. Structure Spatiale du Zooplancton Tropical Laguniare – Hétérogénéité Environnementale et Échelles Spatiales. Journées du Centre des Sciences de la Mer, Observatoire Océanologique de Villefranche-sur-Mer, Université Paris 6, France.
- Avois C., Legendre P. and M. Louis. 1999. Variabilité Spatiale de la Biomasse du

Zooplancton dans un Lagon Tropical (Guadeloupe, Antilles Françaises). Forum des Jeunes Océanographes, Centre Océanographique de Marseille, France.

- Avois C. and P. Legendre. 1998. Tropical Zooplankton Heterogeneity. Dept of Biological Sciences, University of Montreal, Canada.
- Avois C., Legendre P., Masson S. and B. Pinel-Alloul. 1997. Temporal Effects in The Study of Zooplankton Spatial Variation. GRIL Symposium, University of Montreal, Canada.
- Avois C. and P. Legendre. 1996. Partitioning of Ecological Variation by Deterministic Components. Dept of Biological Sciences, University of Montreal, Canada.

PUBLICATIONS

- Avois C., Legendre P., Masson S. and B. Pinel-Alloul. 2000. Is the sampling strategy interfering with the study of spatial variability of zooplankton communities? Can. J. Fish. Aquat. Sci. 57: 1940–1956.
- Jacquet S., Prieur L., Avois-Jacquet C., Lennon J.-F. and D. Vaulot. (Accepted). Short-time-scale variability of picophytoplankton abundance and cellular parameters in surface waters of the Alboran Sea (W Mediterranean). J. Plankton Res.
- Avois-Jacquet C. and P. Legendre. (submitted to *Oikos*). Implications of Heterogeneity and Scale in Zooplankton Spatial Variability.
- Avois-Jacquet C., Legendre P. and M. Louis. (submitted to *Coral Reefs*). Coastal Tropical Zooplankton : Patterns and Processes over Spatial Scales.
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- Avois-Jacquet C., Jacquet S., Prieur L. and P. Morin. (in prep.). Relationships Between Picophytoplankton Dynamics and Environmental, Spatial and Temporal Heterogeneities in the West Mediterranean Sea.

RESUME/ABSTRACT

Variabilité spatiale multiéchelle du zooplancton dans un lagon récifal côtier

Résumé – L'identification des changements dans les patrons écologiques selon l'échelle spatiale et la compréhension des processus qui génèrent ces changements sont d'une importance considérable en océanographie. Dans ce contexte, comprendre comment une communauté biologique répond à l'hétérogénéité environnementale requiert la connaissance des processus impliqués et l'échelle spatiale à laquelle ils opèrent. Les relations spatiales entre la variabilité du zooplancton et l'hétérogénéité environnementale sont encore imprécises dans les écosystèmes tropicaux côtiers. L'objectif de ce travail de thèse a donc été de déterminer les échelles de dépendance spatiale des patrons du zooplancton associé à un lagon récifal côtier et des processus environnementaux sous-jacents. Dans ce contexte, les intérêts de cette recherche ont été de quantifier les patrons de la variabilité du zooplancton dans l'espace, de comprendre comment ces patrons changent avec l'échelle spatiale et de déterminer les processus physiques et biologiques responsables de ces patrons spatiaux. L'échantillonnage, effectué le long d'un transect de la côte vers le large dans le lagon du Grand-Cul-de-Sac Marin (Guadeloupe), a concerné deux classes de taille du zooplancton (190–600 µm et > 600 µm) pour lesquelles la biomasse et l'abondance ont été estimées. L'analyse multiéchelle a été utilisée pour caractériser les patrons du zooplancton aux différentes échelles spatiales (de l'échelle de l'habitat à celle du lagon tout entier) et pour identifier les processus responsables de ces structures spatiales. Cette étude a montré que la variabilité du zooplancton est un phénomène multiéchelle dont l'amplitude et la dépendance spatiale dépendent de la taille des organismes, de leur motilité et de la variable-réponse considérée (biomasse ou abondance). La biomasse et l'abondance du zooplancton varient en réponse à la distribution spatiale du phytoplancton, au comportement du zooplancton, à l'hétérogénéité de l'habitat, à l'hydrodynamique et aux évènements météorologiques. La nature et les effets de ces processus sont dépendants de l'échelle spatiale. Ce travail a montré comment le changement d'échelle spatiale met en évidence différents niveaux d'organisation de la communauté zooplanctonique en réponse à l'hétérogénéité environnementale.

Discipline Océanologie biologique – Environnement marin – Écologie numérique

Mots-clés Analyse multiéchelle, Échelle spatiale, Hétérogénéité environnementale, Lagon tropical, Variabilité, Zooplancton

Multiscale spatial variability of zooplankton in a coastal reef lagoon

Abstract – The identification of changes in ecological patterns with scale, and the understanding of the processes that effect these changes are of considerable importance in modern oceanographic studies. In this context, understanding how a biological community responds to the environmental heterogeneity requires the knowledge of generating processes and the spatial scale at which they operate. The spatial relationships between zooplankton variability and environmental heterogeneity are still little known in coastal tropical ecosystems. Thus the objective of the present research has been to determine the scales of spatial dependency of the patterns of zooplankton associated with a coastal reef lagoon and of the underlying environmental processes. In this way, research interests consisted in quantifying patterns of zooplankton variability in space,understanding how patterns change with scale, and determining the physical and biological processes implicated in these spatial patterns. The sampling, carried out along one transect oriented from the coast to the open sea in the Grand Cul-de-Sac Marin lagoon (Guadeloupe, French West Indies) has been focused on two zooplankton size classes

(190–600 µm and > 600 µm) for which biomass and abundance have been estimated. The multiscale analysis has been used to characterize the zooplankton patterns at different spatial scales (from the habitat scale to the lagoon scale) and to identify the processes responsible of these spatial structures. This study has shown that the zooplankton variability is a multiscale phenomenon of which the intensity and the spatial scale depend on the organism size, their motility and the response-variable considered (biomass or abundance). Biomass and abundance of the zooplankton associated with the coastal reef lagoon vary in response to the phytoplankton spatial distribution, the zooplankton behaviour, the habitat heterogeneity, the local hydrodynamics, and the meteorological events. The nature and the effects of these processes are dependent on the spatial scale. This work has also shown how the change of spatial scale underlines the different organisation levels in zooplankton community in response to the environmental heterogeneity.

Current Contents Biological Oceanography – Marine Environment – Numerical Ecology

Keywords Environmental Heterogeneity, Multiscale Analysis, Spatial Scale, Tropical Lagoon, Variability, Zooplankton