UQAR
Université du Québec
à Rimouski

ANALYSES SPATIALES DE LA BIODIVERSITÉ BENTHIQUE DU GOLFE SAN JORGE, ARGENTINE

SPATIAL ANALYSES OF BENTHIC BIODIVERSITY IN SAN JORGE GULF, ARGENTINA

Mémoire présentée

dans le cadre du programme de maîtrise en océanographie

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

PAR

© JULIETA KAMINSKY

Septembre 2017

Composition du jury :

Gesche Winkler, Présidente du jury, ISMER Université du Québec à Rimouski

Philippe Archambault, Directeur de recherche, Université Laval

Martín Varisco, Codirecteur de recherche, CIT Golfo San Jorge CONICET UNPSJB

Ricardo Sahade, Codirecteur de recherche, IDEA CONICET UNC

Julio Vinuesa, Examinateur externe, CIT Golfo San Jorge CONICET UNPSJB

Dépôt initial le 28 avril 2017 Dépôt final le 13 septembre 2017

In the end we will conserve only what we love, we will love only what we understand, and we will understand only what we are taught

Baba Dioum

La meilleure façon de réaliser ses rêves, c'est de se réveiller! Autrement dit, pour faire partie de la solution, il faut passer à l'action

Phil Jackson

Ella, la mar, estaba más allá de los altos médanos, esperando. Cuando el niño y su padre alcanzaron por fin aquellas cumbres de arena, después de mucho caminar, la mar estalló ante sus ojos. Y fue tanta la inmensidad de la mar, y tanto su fulgor, que el niño quedó mudo de hermosura. Y cuando por fin consiguió hablar, temblando, tartamudeando, pidió a su padre: —¡Ayúdame a mirar!

Eduardo Galeano

REMERCIEMENTS

Ici à Rimouski, j'ai connu l'hiver. J'ai connu une latitude où en été le Soleil ne veut pas partir, mais pendant l'hiver il se cache la plupart de la journée. J'ai vu un fleuve devenir gèle et des arbres se peinturer avec deux mil couleurs. J'ai commencé une maîtrise en Océanographie, dans un autre pays, dans une autre langue, dans une autre culture. J'ai tombé en amoureuse dans la forêt. J'ai appris à continuer apprendre, mais cette fois dans une autre matrix socio-culturelle. Surtout, j'ai rencontré des expériences académiques et scientifiques différentes, enrichissantes, pour toute ma vie. Je garde avec moi une panoplie des réflexions, des amis et des paysages, inoubliables. Merci pour ce voyage.

Tout d'abord, j'aimerais remercier le Programme BEC.AR (Argentina) pour m'avoir offert la bourse de maîtrise qui m'a permis de poursuivre cette merveilleuse expérience au Québec.

Je voudrais remercier l'ISMER-UQAR de m'avoir accepté pour poursuivre mes études de maîtrise en océanographie.

Merci beaucoup à Philippe Archambault de m'avoir accepté comme étudiante dans le Laboratoire benthique. Également, je voudrais remercier Martín Varisco et Ricardo Sahade d'avoir accepté la codirection de mon projet de maîtrise.

Merci beaucoup au Comité du jury pour vos commentaires et modifications suggérées qui ont enrichies mon mémoire.

Je voudrais remercier mes professeurs d'Océanographie générale et d'Océanographie expérimentale de m'avoir fourni un ensemble de concepts et d'outils pour aborder ma maîtrise.

Je voudrais remercier l'INIDEP, et particulièrement Mónica Fernández, de m'avoir offert un ensemble de données qui a permis de développer le présent projet. Également, je voudrais remercier Agustina Ferrando pour les données de polychètes, Marta Commendatore pour les données de sédiments et Gabriela Williams pour les données de bathymétrie.

Merci infiniment à Alain Caron pour m'avoir aidé à réfléchir dans les différentes étapes des analyses et de me donner une boîte d'outils statistiques. Merci de votre patience dans chaque rencontre où je suis arrivée avec ma feuille des questions.

J'aimerais remercier énormément Nathalie Landreville du CAR-UQAR pour son aide extraordinaire dans l'édition de mes présentations en français.

J'aimerais remercier Gustavo Ferreyra et Irene Schloss pour m'avoir accompagné dans chaque étape de la maîtrise, pour m'avoir orienté et m'avoir encouragé avec esprit et cœur.

Merci beaucoup au Laboratoire benthique pour l'aide dans différents moments de ma maîtrise. Je voudrais remercier spécialement Jésica Goldsmith, Cindy Grant, Gonzalo Bravo, Heike Link, Charlotte Moritz, Blandine Gaillard et Mylène Dufour de vos apports.

Merci beaucoup Pierre-Arnaud Desiage et Noela Sánchez-Carnero pour votre aide dans différents moments de mes analyses.

Je voudrais remercier Martine Belzile, Nancy Lavergne et Brigitte Dubé pour leur collaboration dans chaque étape. Merci à Marcel David pour m'avoir aidé dans mes voyages à la bibliothèque de l'UQAR.

De plus, j'aimerais remercier toutes les personnes avec qui j'ai partagé des expériences au Québec. Merci avec tout mon cœur aux filles argentines Maité, Xime, Elo et Ari pour partager ce voyage extraordinaire ensemble. Je vous admire énormément. Merci à toute la communauté argentine de Rimouski. Vous êtes merveilleux. Merci à Jesi, Nacho et Licho pour chaque mate et sourire partagés. Merci à María et Santiago pour votre belle amitié épicée. Merci à l'équipe de volley *les étrangers* pour jouer ensemble.

Merci à mes oncles Arlène et James pour m'avoir ouvert les portes à votre monde génial, pour m'avoir accompagné et nourri l'âme et l'esprit. Vous êtes inoubliables.

Merci à mon ami Marwen pour les réflexions collectives sur nos cultures, nos familles et nos vies. Je t'admire beaucoup. Merci à mes colocs pour la construction d'un *Bercail* à Rimouski. Merci aux Bombones, et spécialement à Louis Poulain, à Sara Dignard et à Tom Jacques, pour m'avoir fait rire, lire, écouter vraiment beaucoup. Merci Geneviève pour ton amitié, toujours pleine de réflexions et de mots tellement enrichissants.

Merci beaucoup à mes parents Mirta et Goyo, à mon frère Javier, à ma grand-mère Olga et aux amis en Argentine pour m'envoyer les plus belles énergies.

Merci à David, à ta magique famille, à notre petit Paprika et aux plantes pour l'amour.

AVANT-PROPOS

Le présent projet de recherche fait partie du programme PROMESse-MARES, développé par des institutions de l'Argentine et du Québec. Ce programme vise à décrire l'état présent de l'écosystème du golfe San Jorge (Argentine). Dans ce cadre, j'ai obtenu une bourse du programme BEC.AR (Argentine) pour poursuivre des études de maîtrise en océanographie à l'ISMER-UQAR. Pour la présentation écrite de mon devis de recherche, le Comité d'évaluation de l'ISMER m'a donnée une mention d'excellence. Je voudrais également souligner l'aide financière que j'ai reçu du Service aux Étudiantes de l'UQAR pour participer dans la mission océanographique du programme Pampa Azul au golfe San Jorge. Cette mission a été menée à bord du navire de recherche *Puerto Deseado* pendant le mois de novembre 2016. Cette expérience m'a permis de connaître mon site d'étude, faire des échanges avec des scientifiques qui travaille dans le même environnement et améliorer l'interprétation de mes résultats de maîtrise.

Durant la période de 2 ans, ce projet a été présenté dans les événements scientifiques suivants :

- ✓ Kaminsky J, Varisco M, Sahade R, Archambault P. *Spatial analyses of benthic biodiversity in the San Jorge Gulf*. Présentation des résultats de maîtrise. Mars 2017, Workshop PROMESse, Rimouski, Québec

- ✓ Kaminsky J, Varisco M, Sahade R, Archambault P. *Functional benthic ecology in an Argentinean Patagonian gulf: what is where?* Affiche. Novembre 2016, Assemblée Générale Annuelle Québec Océan, Rimouski, Québec

- ✓ Bravo G, Flores Melo X, Giménez E, Kaminsky J, Klotz P, Nocera A, Latorre M. *Naviguons dans le Golfe San Jorge, Patagonie Argentine*. Stand avec de l'information audiovisuel. Mars 2016, La nature dans tous ses états, UQAR, Rimouski, Québec

- ✓ Kaminsky J, Archambault P, Varisco M, Sahade R. *Analyse spatiale de la biodiversité benthique dans le golfe San Jorge, Argentine*. Affiche. Novembre 2015, Assemblée Générale Annuelle Québec Océan, Québec, Québec

Les principaux résultats de recherche seront publiés à partir d'un thème spécial dans le journal scientifique *Oceanography* avec l'ensemble des résultats du PROMESse.

RÉSUMÉ

La distribution de la biodiversité benthique est liée à la complexité des habitats. Dans un contexte d'augmentation des pressions anthropiques, il est nécessaire de développer des modèles de biodiversité selon la distribution des habitats afin d'améliorer la gestion et la conservation des écosystèmes marins et côtiers. Le golfe San Jorge (45° - 47° S, Argentine) fait partie du *Patagonian Shelf Large Marine Ecosystem*, l'un des écosystèmes les plus productifs de l'hémisphère sud. L'objectif de cette étude était de caractériser la distribution spatiale de la biodiversité benthique du golfe de San Jorge (SJG). Nous avons décrit les caractéristiques de l'environnement benthique. Ensuite, nous avons exploré la présence des assemblages taxonomiques et fonctionnels pour l'épifaune et l'endofaune. Ensuite, nous avons évalué la relation entre l'environnement benthique et la distribution des assemblages pour estimer la probabilité de présence des assemblages. Nos hypothèses étaient que la distribution des assemblages est associée à la profondeur, à la granulométrie et à la matière organique, et que les assemblages les plus divers sont dans les zones à forte matière organique. Les données des missions R/V Oca Balda (2000) et R/V Coriolis (2014) ont été utilisées. Nos résultats montrent la présence des assemblages d'épifaune taxonomique et fonctionnels. La région centrale avec concentrations de matière organique plus élevées était caractérisée par d'opportunistes rampant et déposivores de subsurface creuseur. Dans le nord, près de l'embouchure et dans les côtes l'assemblage d'épifaune est composé par déposivores de subsurface, suspensivores sessile ou creuseur. Cet assemblage a été corrélé avec basses concentrations d'oxygène et de matière organique. Au contraire, l'épifaune est composée par prédateurs nageur, prédateurs rampant, opportunistes rampant et suspensivores sessile près de Cape Tres Puntas. Dans le cas de l'endofaune, aucun modèle spatial n'a été identifié, probablement en raison de l'effort d'échantillonnage. Les cartes avec les habitats préférentiels permettent de prédire la distribution de la biodiversité benthique dans le SJG, en particulier selon la disponibilité d'oxygène dans l'eau de fond et les concentrations de la matière organique de sédiments.

Mots clés : environnement benthique, assemblages, diversité fonctionnelle, modèle de distribution de la biodiversité, habitats préférentiels

ABSTRACT

Benthic biodiversity distribution is closely related to habitat complexity. In the context of increasing anthropogenic pressures, it is necessary to develop biodiversity models considering habitat distribution to improve management and conservation of marine and coastal ecosystems. San Jorge Gulf (45° - 47° S, Argentina) is part of the *Patagonian Shelf* Large Marine Ecosystem, one of the most productive ecosystems of the Southern Hemisphere. The general objective of this study was to characterize the spatial distribution of benthic biodiversity of the San Jorge Gulf (SJG). First, we described the physic-chemical characteristics of the benthic environment. Then, we explored taxonomic and functional assemblages for epifauna and infauna organisms. Afterwards, we evaluated the relationship between benthic environment and assemblages' distribution to estimate habitat suitability for assemblages. We hypothesized that the distribution of benthic assemblages is associated with depth, sediment size and concentration of sediment organic matter as environmental factors, and that the most diverse assemblages are present in areas with higher concentrations of organic matter. Data from R/V Oca Balda (2000) and R/V Coriolis (2014) oceanographic missions in SJG were used. Our results show the presence of epifauna taxonomic and functional assemblages. The central area of SJG with high organic matter is characterised by opportunist crawlers and deposit subsurface burrowers. In the north, close to the mouth and along the southern coastal area (Mazarredo), the epifauna assemblage was mainly composed by deposit subsurface feeders, filter burrowers and sessile feeders. This assemblage was correlated with low oxygen availability and low organic matter concentrations. On the contrary, assemblages close to Cape Tres Puntas were characterised by predator swimmers, predator crawlers, opportunist crawlers and filter sessile feeders. In the case of infauna, no spatial patterns were identified, probably related with the sampling effort. Habitat suitability maps might enable to predict benthic biodiversity distribution in the SJG, particularly considering oxygen availability in bottom water and organic matter in sediments.

Keywords: benthic environment, assemblages, functional diversity, biodiversity distribution model, habitat suitability

TABLE DES MATIÈRES

LISTE DES TABLEAUX

LISTE DES FIGURES

LISTE DES ABRÉVIATIONS, DES SIGLES ET DES ACRONYMES

PROMESse	Programa Multidisciplinario para el Estudio del ecosistema y la geología marina del golfo San Jorge y las costas de las provincias de Chubut y Santa Cruz.
MARES	Marine ecosystem health of the San Jorge Gulf: Present status and Resilience capacity.
INIDEP	Instituto Nacional de Investigación y Desarrollo Pesquero (Argentina).
SJG	San Jorge Gulf.
TOM	Total organic matter.
TOC	Total organic carbon.
TN	Total nitrogen.

INTRODUCTION GÉNÉRALE

PRÉDIRE LA DISTRIBUTION DE LA BIODIVERSITÉ BENTHIQUE

La distribution de la biodiversité benthique est fortement liée à la complexité des habitats des écosystèmes côtiers et marins (Brown et al. 2011, Kovalenko et al. 2012, Moritz et al. 2013, Carvalho et al. 2017). Les habitats benthiques peuvent être décrits comme des régions de fonds marins qui sont géo-statistiquement différentes de leur environnement en termes de caractéristiques physiques, chimiques et biologiques, en considérant des échelles d'observations spatiales et temporelles précises (Lecours et al. 2015). Une panoplie de facteurs environnementaux qui varient sur les plans spatiaux et temporels déterminent la présence d'une grande hétérogénéité d'habitats dans les environnements benthiques. Parmi ces facteurs, ont été principalement décrites des variations dans la topographie (Archambault et Bourget 1996, Archambault et al. 1999), la présence des structures physiques (Carvalho et al. 2017) et la taille de sédiments (Gray et Elliot 2009). La circulation des masses d'eau détermine fortement les caractéristiques physico-chimiques, comme la température, la salinité et la présence de nutriments. La dynamique dans la colonne d'eau peut conditionner le couplage pélagique-benthique et la disponibilité et la qualité des apports de matière organique qui arrivent au fond (Wassmann 1997). De plus, la topographie, les structures physiques et les courants peuvent déterminer la connectivité entre les habitats. La biodiversité benthique est plus diversifiée dans un environnement benthique marqué par une grande complexité d'habitats (Tokeshi et Arakaki 2012).

Les activités humaines représentent des facteurs de stress multiples qui ont des impacts sur la biodiversité et sur la complexité des écosystèmes benthiques (Breitburg et al. 1998, Crain et al. 2008). Les principales pressions anthropiques sur ces écosystèmes sont la pêche au chalut, l'extraction de pétrole et de gaz, le développement des villes côtières, le tourisme et l'exploitation minière (Williams et al. 2010, Harris 2012, Cook et al. 2013). Ces activités peuvent entre autres modifier et fragmenter les habitats benthiques, favoriser l'établissement d'espèces envahissantes, entraîner des extinctions locales d'espèces et la diminution de la diversité génétique (Solan et al. 2004, Stachowicz et al. 2007, Hooper et al. 2012, Grabowski et al. 2014). Fait à noter, les écosystèmes côtiers présentent les impacts cumulés les plus importants (Halpern et al. 2008, 2015). Dans un contexte d'augmentation des pressions anthropogéniques sur les écosystèmes côtiers et marins, il devient nécessaire de développer des modèles temporels et spatialement explicites qui permettent de comprendre les rapports entre la distribution de la biodiversité et les habitats benthiques (Lecours et al. 2015, Mokany et al. 2016).

Les modèles de distribution spatiale de la biodiversité explorent les relations entre la distribution de la diversité et des variables environnementales (Field et al. 1982, Robinson et al. 2011). La distribution spatiale de la diversité peut être décrite à partir de l'identification d'assemblages, définis selon la composition et l'abondance des espèces (Moritz et al. 2013). Ensuite, les modèles de distribution spatiale de la biodiversité traitent de l'information sur l'environnement benthique pour identifier quelles variables environnementales déterminent la distribution spatiale des assemblages. Les modèles permettent d'élaborer de cartes d'habitats représentant la distribution actuelle des communautés et leur possible distribution, définie selon la probabilité de présence des assemblages (Moritz et al. 2013, Brown et al. 2012). De plus, ils rendent possible l'identification des *hotspots* et des *coldspots*, définis respectivement comme des habitats riches ou pauvres en biodiversité (Link et al. 2013, Marchese 2015). La présence d'espèces emblématiques chez les assemblages permet de suivre l'état des habitats (Torn et al. 2017).

Dans l’ensemble, ces modèles fournissent de l'information pour comprendre l'hétérogénéité spatiale de la biodiversité observée et les impacts possibles des activités humaines. En contrepartie, cette information offre la possibilité d'améliorer les stratégies de gestion et de conservation tout en répondant aux besoins anthropogéniques et en conservant le fonctionnement écosystémique à long terme (Lévesque et al. 2012, Copeland et al. 2011, Vierod et al. 2014).

LA DIVERSITÉ FONCTIONNELLE DANS LES ASSEMBLAGES BENTHIQUES

Les études développées pendant les dernières années dans les écosystèmes marines et côtiers ont cherché à comprendre comment des modifications dans la biodiversité déterminent des changements dans le fonctionnement écosystémique (Loreau et al. 2001, Worm et al. 2006, Stachowicz et al. 2007, Duffy et al. 2009, Gamfeldt et al. 2015). Les principaux résultats ont identifié que la biodiversité affect multiples fonctions de l’écosystème et que les assemblages avec une grand richesse sont généralement plus productives et efficients dans l’utilisation de ressources par rapport aux assemblages moins riches. Cependant, les impacts cumulés de pressions anthropiques, comme la surexploitation, la pollution, l’introduction des espèces envahissantes et les modifications des habitats (Cardinale et al. 2012**)**, peuvent réduire la richesse et modifier la composition et l’abondance des espèces dans différents niveaux trophiques (Cardinale et al. 2006, Worm et al. 2006, Duffy et al. 2007). Cette diminution de la biodiversité peut affecter négativement les processus écosystémiques liés avec la productivité, les interactions trophiques et les cycles biogéochimiques (Loreau et al. 2001, Solan et al. 2004, Balvanera et al. 2006, Cardinale et al. 2012, Gamfeldt et al. 2015), ainsi qu’affecter la stabilité et la capacité de résilience des écosystèmes (Hooper et al. 2005, Worm et al. 2006). Les impacts seront différents selon l’identité des espèces disparues (Cardinale et al. 2006, Harvey et al.

2013), et ils seront plus fortes quand multiples fonctions écosystémiques sont considérées (Hector and Bagchi 2007, Byrnes et al. 2014, Lefcheck et al. 2015).

Parmi les approches proposées pour explorer le fonctionnement écosystémique, la diversité fonctionnelle décrit la variété de fonctions réalisées par les organismes (Díaz et Cabido 2001). La diversité fonctionnelle considère les caractéristiques morphologiques, physiologiques et comportementales des espèces liées à l'acquisition et à l'utilisation des ressources, à la modification des réseaux trophiques et aux impacts sur l'occurrence et la magnitude des perturbations (Chapin et al. 1997, Tilman 2001). Au-delà des approches utilisées pour décrire la diversité fonctionnelle, les traits fonctionnels classifient les espèces en relation avec le cycle des matières et le flux d'énergie, les préférences pour l'habitat, les modes de vie des espèces, les caractéristiques morphologies comme la taille, entre autres (Roth et Wilson 1998, Pearson 2001, Rosenberg 2001, Gray et Elliot 2009).

Dans les écosystèmes benthiques, la diversité fonctionnelle a été traditionnellement associée avec la variété de stratégies d'alimentation des organismes et la bioturbation, considérées comme des facteurs qui déterminent plus fortement la structure d'écosystèmes (Pearson et Rosenberg 1978, Norling et al. 2007, Kristensen et al. 2012, Mermillod-Blondin et al. 2005). Même si dans la plupart de communautés benthiques il manque encore de l'information sur des espèces, particulièrement sur la variabilité phénotypique et les effets des interactions positifs comme la facilitation (Rosenberg 2001), une panoplie de différentes catégories écologiques de traits fonctionnels est disponible pour explorer la diversité fonctionnelle (Pearson 2001, Bremner et al. 2003, Petchey et Gaston 2006, Link et al. 2013). Dans la présente étude, la diversité fonctionnelle a été explorée à partir de la combinaison de traits fonctionnels pour essayer de considérer la multifonctionnalité des organismes.

À partir de la classification des espèces selon les traits fonctionnels, il est possible de décrire la composition et d'estimer la richesse fonctionnelle définie comme le nombre de groupes fonctionnels (Link et al. 2013). Cette richesse locale de groupes fonctionnels est aussi définie comme l'indice de diversité alpha (α). La diversité de groupes fonctionnels peut également être décrite à l'aide d'autres indices de diversité. La diversité gamma (γ) indique la richesse régionale et la diversité bêta (β) décrit l'hétérogénéité de l'habitat (Gray 2001, Cusson et al. 2007). De plus, les modèles de distribution de la biodiversité peuvent être développés avec des assemblages identifiés en considérant des groupes fonctionnels. Ces modèles permettent d'explorer la distribution de la diversité fonctionnelle et les relations avec l'environnement benthique (D'Amen et al. 2015).

LE GOLFE SAN JORGE

Le golfe San Jorge (45° - 47° S, SJG) se trouve dans le plateau continental d'Argentine, considéré comme un des écosystèmes les plus productifs de l'hémisphère Sud (Longhurst 2007, Miloslavich et al. 2011, Fig. 1). Le SJG est caractérisé par la présence de variations spatiales et saisonnières des facteurs environnementaux qui favorisent une variété d'habitats marins et côtiers (Roux et al. 1995, Fernández et al. 2003, 2005, Zaixso et al. 2015). Ces habitats soutiennent une diversité des stratégies de vie comme des oiseaux migratoires, des mammifères marins, des crustacés, des poissons et d'autres organismes qui trouvent nourriture, refuge et une place pour la reproduction dans le golfe (Yorio 2009).

Les pressions anthropogéniques dans le SJG viennent de la pêche avec principalement des chaluts, de la présence de villes côtières, du tourisme et des activités liées au transport des hydrocarbures (Commendatore et Estevez 2007, Góngora et al. 2012, Bovcon et al. 2013, Marinho et al. 2013). Les espèces d'intérêt pour la pêche sont la crevette *Pleoticus muelleri* (Fernández et al. 2007), le merlu *Merluccius hubbsi* (Louge et al. 2009) et le crabe royal *Lithodes santolla* (Vinuesa et al. 2013). Différentes stratégies de gestion ont été implantées comme l'interdiction de la pêche dans des régions sélectionnées (aire Mazzaredo), quotas de captures maximal, et l'établissement d'un parc marin côtier dans le nord en 2006 (Yorio 2009, Góngora et al. 2012). Récemment, l'initiative PAMPA AZUL créée en 2014 et la promulgation de la loi PROMAR (loi 27.167/2015) en Argentine ont établi la région du golfe San Jorge entre les zones prioritaires dans l'intention de promouvoir la recherche, de développer des stratégies d'utilisation durable des ressources et de protéger la biodiversité.

Pendant les dernières décades, la plupart des études benthiques développées dans le golfe San Jorge ont été liées à la surveillance de la pêche (Roux et al. 1995, Bovcon et al. 2013). La plupart de ces efforts d'échantillonnage ont été faits avec des méthodes pour étudier l'épifaune, mais l'endofaune était moins représentée. De plus, les approches fonctionnelles pour décrire la biodiversité benthique sont encore à développer. Finalement, la relation entre la distribution des assemblages et des facteurs environnementaux n'a pas encore été explorée à l'échelle du golfe. Dans ce contexte, le présent projet a cherché à apporter de l'information sur la biodiversité benthique, en considérant des traits taxonomiques et fonctionnels dans l'intention de promouvoir des modèles intégratifs de biodiversité (Mokany et al. 2016) qui permettent d'améliorer la compréhension des dynamiques dans les écosystèmes benthiques du SJG.

OBJECTIFS ET HYPOTHÈSES

Le présent projet fait partie du programme PROMESse-MARES (http://coriolis.uqar.ca/), qui cherche à décrire l'état présent de l'écosystème du golfe San Jorge, développé par des instituts de l'Argentine et du Québec. Dans ce cadre, l'objectif général est de caractériser la distribution spatiale de la biodiversité benthique du golfe San Jorge. Les objectifs spécifiques ont été : (1) décrire les caractéristiques physico-chimiques de l'environnement benthique du SJG, (2) identifier la présence des assemblages taxonomiques et fonctionnels avec des données pour l'épifaune et l'endofaune, et (3) évaluer les relations entre la distribution des variables environnementales et des assemblages benthiques. Les hypothèses ont été : (a) l'existence de variations spatiales dans l'environnement benthique du golfe San Jorge détermine la présence des assemblages benthiques, et particulièrement la distribution des assemblages benthiques est corrélée avec la profondeur, la taille de sédiments et la concentration de la matière organique dans les sédiments; (b) les assemblages les plus divers sont présents dans des aires avec de plus hautes concentrations de matière organique.

CHAPITRE 1

ANALYSES SPATIALES DE LA BIODIVERSITÉ BENTHIQUE DU GOLFE SAN JORGE, ARGENTINE

1.1 CONTEXTE DU PROJET

Cet article, intitulé « *Spatial analyses of benthic biodiversity in San Jorge Gulf, Argentine* », a été rédigé avec mon directeur de maîtrise Philippe Archambault et mes codirecteurs Martín Varisco et Ricardo Sahade. Mes directeurs ont proposé les objectifs du projet. Également, ils ont participé au développement de la méthodologie et à la révision de l'article. En tant que première auteur, ma contribution à ce travail fut l'essentiel de la recherche sur l'état de l'art, le développement de la méthodologie, l'exécution des analyses et la rédaction de l'article. Le manuscrit de cet article sera présenté pour publication en automne 2017 à l'éditeur de la revue scientifique *Oceanography* dans un thème spécial sur le golfe San Jorge, proposé par le programme de recherche PROMESse.

1.2 SPATIAL ANALYSES OF BENTHIC BIODIVERSITY IN SAN JORGE GULF, ARGENTINE

1.3 INTRODUCTION

Benthic biodiversity distribution is strongly related to habitat complexity of marine and coastal ecosystems (Brown et al. 2011, Zajac et al. 2013, Carvalho et al. 2017). It is widely accepted that benthic biodiversity is highly diverse in a benthic environment with higher habitat complexity (Kovalenko et al. 2012, Tokeshi and Arakaki 2012). Benthic habitats represent areas of seabed with physical, chemical and biological characteristics that are different from their surroundings (Lecours et al. 2015). Spatial and temporal variation of environmental factors determine the presence of a large habitat heterogeneity in benthic environments. Among these factors are topography (Archambault and Bourget 1996, Archambault et al. 1999), the presence of physical structures (Carvalho et al. 2017), sediment size (Gray and Elliot 2009) and water column dynamics (Wassmann 1997). Moreover, currents condition pelagic-benthic coupling which in turn modify the availability and quality of organic matter inputs arriving at the bottom.

Human activities represent multiple stressors that impact on benthic biodiversity and benthic ecosystems complexity (Breitburg et al. 1998, Crain et al. 2008). The main anthropogenic pressures on these ecosystems are bottom trawling fishing, oil and gas exploitation, coastal urban developments, tourism and mining (Williams et al. 2010, Harris 2012, Cook et al. 2013). These activities can modify and fragment benthic habitats, encourage invasive species establishment, increase local extinctions of species and decrease genetic diversity, among other impacts (Solan et al. 2004, Stachowicz et al. 2007, Hooper et al. 2012, Grabowski et al. 2014). Particularly, coastal ecosystems suffer the greatest cumulative impacts (Halpern et al. 2008, 2015). These impacts have strong consequences on richness, composition and abundances of species through different trophic levels (Cardinale et al. 2006, Worm et al. 2006, Stachowicz et al. 2007). This decrease in biodiversity can negatively affect ecosystem processes linked to productivity, trophic interactions and biogeochemical cycles (Loreau et al. 2001, Solan et al. 2004, Balvanera et al. 2006, Cardinale et al. 2012, Gamfeldt et al. 2015), as well as the stability and the resilience of ecosystems (Hooper et al. 2005, Worm et al. 2006). These impacts might variate according to the identity of lost species (Cardinale et al. 2006, Harvey et al. 2013), and they could be stronger if multiple ecosystem functions are considered (Hector and Bagchi 2007, Gamfeldt et al. 2008, Byrnes et al. 2014). In the context of increasing anthropogenic pressures on coastal and marine ecosystems, it is necessary to develop temporally and spatially explicit models that allow understanding the relationship between the distribution of biodiversity and benthic habitats, particularly considering how impacts on biodiversity distribution might affect ecosystem functioning in the long term (Lecours et al. 2015, Mokany et al. 2016).

Among approaches used to explore ecosystem functioning, functional diversity describes the variety of functions performed by organisms (Díaz and Cabido 2001, Petchey and Gaston 2006). Functional diversity considers species morphological, physiological and behavioral characteristics related to the performance in the acquisition and use of resources, modification of trophic webs, preferences for habitats and impacts in the occurrence and magnitude of disturbance (Chapin et al. 1997, Tilman 2001). In benthic ecosystems, functional diversity has been usually linked with feeding and bioturbation strategies, considered as the most important biotic factors determining ecosystem structures (Pearson et Rosenberg 1978, Norling et al. 2007, Kristensen et al. 2012, Mermillod-Blondin et al. 2005). Even though in most benthic communities, information on species is still lacking, particularly on phenotypic variability and the effects of positive interactions such as facilitation (Rosenberg 2001), a variety of different functional trait classifications are available to explore functional diversity (Pearson 2001, Bremner et al. 2003, Petchey et Gaston 2006, Link et al. 2013). In the present study, functional diversity was analysed considering the combination of functional traits to explore multifunctionality of organisms. After this classification, it is possible to analyse the functional diversity distribution considering the heterogeneity of benthic habitats (D’Amen et al. 2015).

Biodiversity spatial distribution models explore the relations between diversity and distribution of environmental variables (Field et al. 1982, Robinson et al. 2011). The spatial distribution of diversity can be described from the identification of assemblages, defined according to species or functional groups composition and abundances (Moritz et al. 2013, D'Amen et al. 2015). Then, biodiversity spatial distribution models analyse the relations between assemblages and environmental variables to identify which set of variables determines the distribution of assemblages. These models allow the development of maps representing the current and the potential distribution of assemblages considering habitat suitability, defined as the probability of presence of assemblages (Moritz et al. 2013, Brown et al. 2012). In turn, these models offer information to understand the spatial heterogeneity of observed biodiversity and could help to identify potential impacts of human activities. This information provides the opportunity to improve management and conservation strategies on ecosystem functioning by responding to anthropogenic impacts (Lévesque et al. 2012, Copeland et al. 2011, Vierod et al. 2014).

San Jorge Gulf (SJG) is part of the Patagonian Shelf Large Marine Ecosystem, in the Atlantic coast of South America (Miloslavich et al. 2011). It is located in the continental shelf of Argentina, considered one of the most productive ecosystems of the Southern Hemisphere (Longhurst 2007, Fig. 1). The SJG is characterized by spatial and seasonal variations in environmental factors that favor a variety of marine and coastal habitats (Roux et al. 1995, Fernández et al. 2003, 2005, Zaixso et al. 2015). These habitats support a high diversity of species that find food, shelter and a place for breeding in the gulf (Yorio 2009). The anthropogenic pressures in the SJG are represented by fishing, the presence of coastal cities, tourism and activities related to the transport of fossil fuel (Commendatore and Estevez 2007, Góngora et al. 2012, Bovcon et al. 2013, Marinho et al. 2013). In the SJG occur some of the main fishery resources of Argentina as the shrimp *Pleoticus muelleri* (Fernández et al. 2007), the hake *Merluccius hubbsi* (Louge et al. 2009) and the southern king crab *Lithodes santolla* (Vinuesa et al. 2013).

Different management strategies have been implemented in the SJG, as the interdiction of fishing in selected areas (Mazzaredo), maximum catch quotas, and the establishment of a coastal marine national park in 2006 (Yorio 2009, Góngora et al. 2012). Recently, the Pampa Azul initiative created in 2014 and the promulgation of PROMAR law in Argentina have established the San Jorge Gulf as a priority region for research, development of sustainable strategies of human use and biodiversity protection. During the last decades, most of the benthic studies performed in San Jorge Gulf have been linked with the fishery monitoring (Roux et al. 1995, Bovcon et al. 2013). Most of these sampling efforts were done with methods for studying the epifauna, where infauna was underrepresented. Moreover, functional approaches to describing benthic biodiversity are still to be developed, and the relationship between the distribution of assemblages and environmental factors has not been explored for the gulf scale.

In this context, the PROMESse program (http://coriolis.uqar.ca/) was executed by institutions from Argentina and Québec to describe the present state of SJG ecosystem. In this framework, the main goal of this study was to characterize the spatial distribution of benthic biodiversity of the SJG. Specific objectives were: (1) to describe the spatial distribution of physic-chemical characteristics in the benthic environment of the SJG, (2) to identify the presence of taxonomic and functional assemblages with data for epifauna and infauna, 3) to evaluate the relationship between environmental variables and assemblages, 4) to build habitat suitability maps for benthic assemblages, defined as the probability of presence of assemblages. We tested the following hypotheses: (a) benthic environment spatial variations determine the presence of benthic communities, which distribution is correlated with depth, sediment size and concentration of sediment organic matter as environmental factors, and (b) the most diverse benthic communities are present in areas with higher concentrations of organic matter.

1.4 MATERIALS AND METHODS

1.4.1 STUDY SITE

San Jorge Gulf is located in the Argentinean continental shelf, between Cape Dos Bahías and Cape Tres Puntas (Fig. 1) with an approximately surface of 39,340 km^2 (Reta 1986). The depths reach 100 m, with maximal depths close to the center and a region with shallow areas in the extreme south (Fernández et al. 2005). Grain size analyses show that the deeper area in the central region is characterised by clay and silt while close to capes region coarse granulometry dominate (Fernández et al. 2003).

Ecological dynamics in the SJG are strongly determined by circulation and by the seasonal cycle of the thermocline formatting in spring and rupturing in winter (Cucchi Colleoni and Carreto 2001, Acha et al. 2004, Rivas et al. 2006, Song et al. 2016). Circulation depends on inputs of cold and nutrient rich water from *Malvinas Current* and on a seasonal plume of low salinity current from the Magellan Strait (Acha et al. 2004, Palma and Matano 2012). Moreover, semidiurnal tides and the force of the easterlies contribute to the vertical mixing in the gulf (Palma et al. 2004, Tonini et al. 2006). In spring and autumn, tidal fronts have been identified close to northern and southern headlands (Palma et al. 2008). Recently, another seasonal thermohaline front has been described in the South of SJG, originated by a decrease in depths and the arrival of the plume from Magellan Strait (Rivas et al. 2006, Glembocki et al. 2015).

Considering the seasonal variation of the thermocline in the SJG, during winter the water column shows convective mixing that brings nutrients to the surface and the water column tends to be homogenized (Bianchi et al. 2005, Fernández et al. 2005). However, primary productivity is limited by radiation availability during this period. During spring when temperature increases, the water column starts to stratify and forms a thermocline, giving place to a phytoplankton bloom (Akselman 1996). Primary productivity is particularly high close to headlands where fronts are present (Glembocki et al. 2015).

During summer, the water column is completely stratified in the central region and primary productivity is limited by the lack of nutrients (especially nitrate). However, close to northern and southern headlands, the water column continues to be mixed by the tides. In fall, a second phytoplankton bloom has been observed, following the typical productivity pattern described for coastal temperate ecosystems (Akselman 1996, Glembocki et al. 2015).

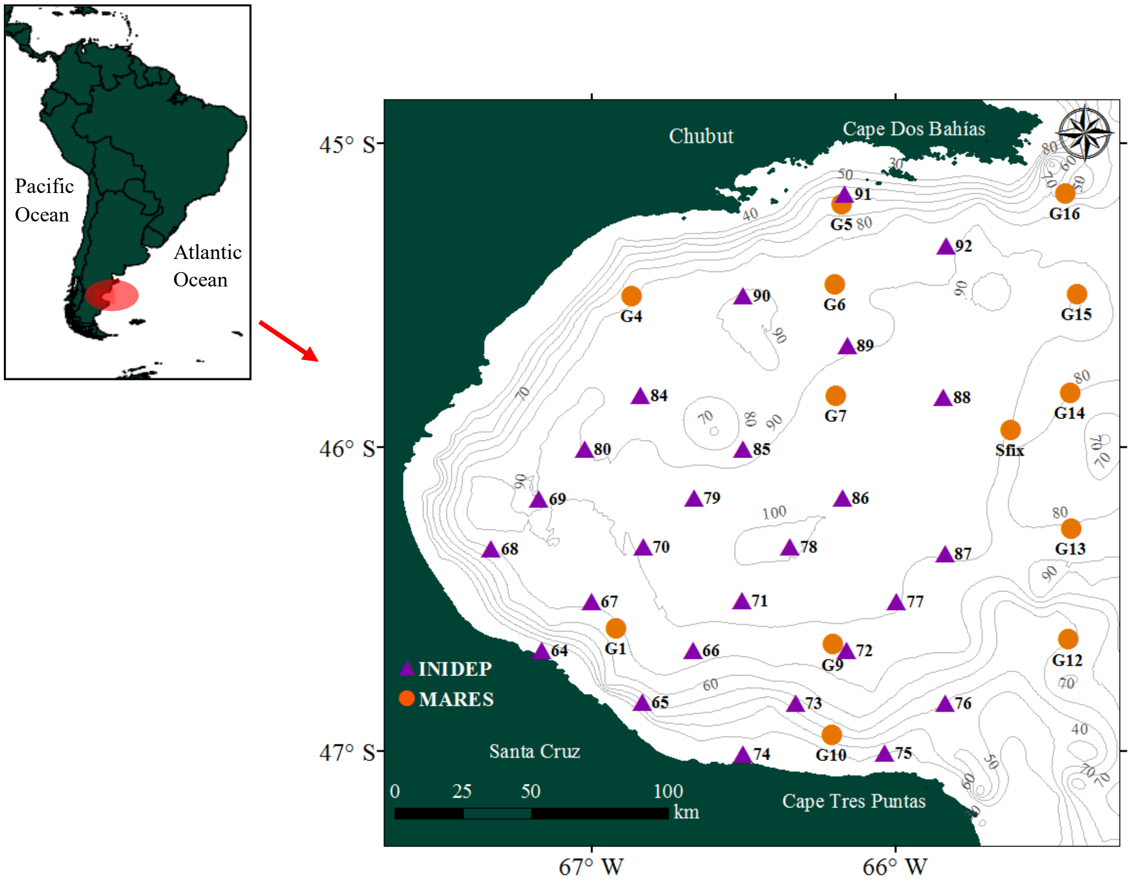

Figure 1 : Study site with sampling stations (bathymetry adapted from Carta H-365, Servicio de Hidrografía Naval, Argentina).

1.4.2 DATA ACQUISITION

In the present study, two sets of environmental and biological data were analysed. The INIDEP data was obtained from the Argentinean National Institute of Fishing while MARES data was acquired from the PROMESse Program.

INIDEP data. Sediments and bottom water characteristics in the SJG were analyzed with data from 26 stations ranging in depth from 21 m to 96 m sampled during INIDEP oceanographic missions on the R/V Oca Balda (Fig. 1 and TS1, *INIDEP* stations). Sediments samples were collected in November 1999 and January 2000 with a Phleger extractor and a Picard dredge (for a full description see Fernández et al. 2003, 2005). Bottom water samples were collected in January 2000 with a CTD SBE (BE-BIRD electronic I model XIX) with a Seapoint Chlorophyll Fluorometer and a Niskin bottle. Epifauna data has been collected in January 2000 (Fig. 1, *INIDEP* stations) with an epibenthic trawl (for a full description see Fernández 2006) during a standard trawl duration of 10 min at a speed of two knots, a sampled surface of approximately 356 m^2 by station. Organisms were identified to the lowest possible taxonomic level and counted by INIDEP researchers.

MARES data. In addition, data from 13 stations ranging in depth from 39 m to 100 m sampled during MARES mission in February 2014 on the R/V Coriolis II were analyzed (Fig. 1 and TS1, *MARES* stations). Sediment samples were taken with a box corer and analyzed in the Coastal Development Institute (Comodoro Rivadavia, Argentina), following Buchanan (1984) and Sargent et al. (1983) methods. Bottom water samples in MARES mission were collected with a Rosette-CTD (Seabird Caroussel SBE-32 CTD SBE-911plus). Then, maximal average velocities for bottom current during January 2014 were included, estimated with a model grid with a spatial resolution of 1/60 degree, which is ~1.3km that that latitude, it has 40 vertical levels and is forced by the ERA_interim atmospheric model at the surface, developed by Combes and Matano (unpublished). Infauna data has been additionally acquired with a box corer (50 x 50 x 60 cm). The half of the box corer sample was analysed (0.125 m^2 cross-sectional area). Organisms were identified to the lowest possible taxonomic level and counted by Coastal Development Institute and Patagonia National Center researchers.

1.4.3 BENTHIC ENVIRONMENT

SPATIAL DISTRIBUTION OF ENVIRONMENTAL VARIABLES

The spatial distribution of sediments and bottom water variables were explored with data from INIDEP and MARES missions together to create a general picture of benthic environment. To choose the method of interpolation that describes best their distribution (*Inverse distance weighted* or *Ordinary Spherical Kriging*), a cross validation was followed by the Spatial Analyst extension on ArcMap (version 10.3.1, ESRI, inc). The interpolation was estimated with 29 stations and then the values were extracted for the other 10 stations. After a comparison between the estimated and measured values, the *Ordinary Spherical Kriging* method was chosen because this method adjusted better the estimated and measured values in the cross validation procedure. The interpolation was estimated with the Spatial Analyst extension on ArcMap (version 10.3.1, ESRI, inc) to build raster maps covering the SJG with the continuous distribution for sediment variables as grain size, total organic matter (TOM), total organic carbon (TOC), total nitrogen (TN) and for bottom water variables as temperature, salinity, oxygen % saturation and chlorophyll *a*.

CORRELATION BETWEEN ENVIRONMENTAL VARIABLES

A principal component analysis (PCA) was used to determine the influence of the environmental variables on the ordination of stations in a multidimensional space (Anderson et al. 2008). The PCA was estimated considering data for INIDEP and MARES stations separately because these results will be used to analyse the relation between environmental variables with epifauna and infauna data (see section 1.4.4 Relation between benthic environment and benthic diversity). The environmental variables included in the analysis were depth, sediment variables as TOM, TOC, TN and size grain, and bottom water variables as bottom current, temperature, salinity, oxygen % saturation and chlorophyll *a*. Prior to PCA, data was standardized using the "normalise" routine using the PRIMER 6 statistical package (PRIMER-E, Plymouth Marine Laboratory, UK). Results from PCA, the draftsman plot and the correlation matrix were used to evaluate collinearity (Anderson et al. 2008).

1.4.3 BENTHIC DIVERSITY

TAXONOMIC DIVERSITY

The description of the structure of the benthic community in the SJG was achieved with cluster and ordination analyses performed separately for epifauna and infauna data. Bray-Curtis similarity measure was estimated on the taxonomic abundance data representing the number of individuals identified by station, previously treated with square root transformation. This similarity matrix was explored with group average cluster method to identify the presence of assemblages. Every group of stations identified corresponded to a specific assemblage following the approach of Moritz et al. (2013). This method considers composition and abundance of species in every station when identifying assemblages. Statistical differences between assemblages were verified using the SIMPROF test (Clarke and Gorley 2006) with a significance level of 5%. A SIMPER analysis was followed to describe differences contribution of species to dissimilarity among assemblages and similarity within them. Data were analyzed using the PRIMER 6 statistical package with PERMANOVA+ (PRIMER-E, Plymouth Marine Laboratory, UK). Geographical distribution of assemblages in the SJG was mapped using ArcMap (version

10.3.1, ESRI, inc). Scientific names were verified using the Integrated Taxonomic Information System (www.itis.gov) and the World Register of Marine Species (www.marinespecies.org).

Then, in order to describe the community characteristic considering diversity attributes, different indices were estimated (Gray 2001, Cusson et al. 2007). The species richness by station is represent by **alpha diversity** (α). The average of alpha diversity by assemblage represent **alpha mean diversity** ($\alpha_{assemblage}$). The total number of taxa at the assemblage scale is the **gamma assemblage diversity** ($\gamma_{assemblage}$) while the total number of taxa at the gulf scale is estimated as **gamma gulf diversity** (γ_{gulf}). To estimate the turnover diversity, two beta indices are proposed at different scales. **Beta assemblage diversity** expressed as $\beta_{assemblage} = \gamma_{assemblage} / \alpha_{assemblage}$ represents the variation within assemblages and **beta gulf diversity** expressed as $\beta_{gulf} = \gamma / \gamma_{assemblage}$ represents the variation between assemblages throughout the SJG (Anderson et al. 2011).

FUNCTIONAL DIVERSITY

Taxonomic data was described based on functional traits, including feeding strategy, size, mobility, adult life and bioturbation (Pearson 2001, Bremner et al. 2003, Link et al. 2013; Table 1). Taxa were allowed more than one trait in the case of feeding strategy, adult life trait and bioturbation. Functional traits were classified with the best resources available considering adult stage. When species information was not available, traits were classified according to the taxa's Family, Order (Echiurida), Class (Holothuroidea, Hydrozoa, Priapulida) or Phylum (Bryozoa, Nemertea). The combination of all levels of traits resulted in a functional group, following Link et al. (2013). Then, all the analysis on the species matrix (subsection Taxonomic diversity) were done on the functional matrix.

Table 1: List of functional traits used for functional classification of taxa.

Feeding	Deposit Subsurface feeder (S) Deposit Surface feeder (D) Deposit Subsurface and Surface feeder (A) Filter/Suspension feeder (F) Opportunist (O) Predator (P)
Size	0.5 mm < Little (S) < 5 mm 5 mm < Medium (M) < 10 mm 10 mm < Large (L) < 50 mm X-Large (X) > 50 mm
Mobility	Sessile (S) Hemimobile (H) Mobile (M)
Adult life	Burrow (B) Crawl (C) Sessile (S) Swim (W)
Bioturbation	Active burrower (diffusive) (B) Gallery burrower (G) Surface dweller (S) Tube burrower (T)

* Examples for functional groups :
OXMCS = Opportunist + X-Large + Mobile +Crawl + Surface dweller
S.FLSBB = Deposit Subsurface or Filter + Large + Sessile + Burrower + Active burrower

REGRESSION MODEL FOR LOCAL DIVERSITY

A simple lineal regression has been estimated to explore the relationship between the number of taxa (taxonomic richness) and the number of functional groups (functional richness) at the local scale, in the statistical package RStudio (version 3.3.1, R Core Team, 2016). This regression was built considering epifauna and infauna data by station together. The application conditions for regression model (normal distribution of residuals and homogeneity of variance of residuals) were verified visually and met (Quinn and Keough 2002).

1.4.4 RELATION BETWEEN BENTHIC ENVIRONMENT AND BENTHIC DIVERSITY

A distance-based linear model permutation test (DistLM) was performed to identify which set of environmental variables explained best the multivariate variation of benthic assemblages. The resemblance matrix was calculated based on Bray-Curtis dissimilarity. Benthic environmental data was previously normalised. The best-fit model was estimated considering the AICc (Akaike's information criterion corrected) selection criterion and a minimum of two variables with PRIMER 6 statistical package with PERMANOVA+ (PRIMER-E, Plymouth Marine Laboratory, UK) using 9999 permutations. Results were visualized with a distance-based redundancy analysis (dbRDA).

1.4.5 BIODIVERSITY DISTRIBUTION MODEL FOR THE SAN JORGE GULF

The habitat suitability of assemblages was analysed at the gulf scale. First, a generalized linear model (GLM) was applied to relate the presence of a given assemblage with the local environmental variables at stations. Given that assemblages were identified only for taxonomic and functional epifauna data (see Results), the GLMs were applied only on these assemblages. The presence-absence of a given assemblage was used as response variable. Environmental variables identified in the DistLM and dbRDA were used as predictors. Considering the results, a second set of GLMs was applied only with significant variables. The GLMs were performed in the statistical package RStudio (version 3.3.1, R Core Team, 2016) assuming a binomial distribution with a logit-link function. The estimates values were included in the inverse logit function in the Raster Calculator (Spatial Analyst tools) to relate the model to the distribution of environmental variables at the gulf scale and to built continuous raster maps describing the probability of presence of assemblages using ArcMap (version 10.3.1, ESRI, inc).

1.5 RESULTS

1.5.1 BENTHIC ENVIRONMENT

SPATIAL DISTRIBUTION OF ENVIRONMENTAL VARIABLES

Grain size distribution in San Jorge Gulf (Fig. 2) showed that close to headlands coarse sediments predominated while in the central region fine sediments were present. This distribution pattern of environmental variables followed the spatial variation in depths. In this context, total organic matter, total organic carbon and total nitrogen presented higher proportions associated with fine sediment in the central region while they radially decreased towards the headlands.

Considering bottom water variables distribution in San Jorge Gulf, a depth-related spatial pattern was also observed (Fig. 3). In the central region, temperatures presented low values that increased towards the headlands, while salinity followed the opposite pattern. Particularly, bottom water in the South close to Cape Tres Puntas showed higher temperature and lower salinity. The mouth of the SJG also presented lower salinity values. Oxygen concentrations were highest close to headland in the South and decreased with depths. Chlorophyll *a* presented the highest concentrations close to Cape Tres Puntas.

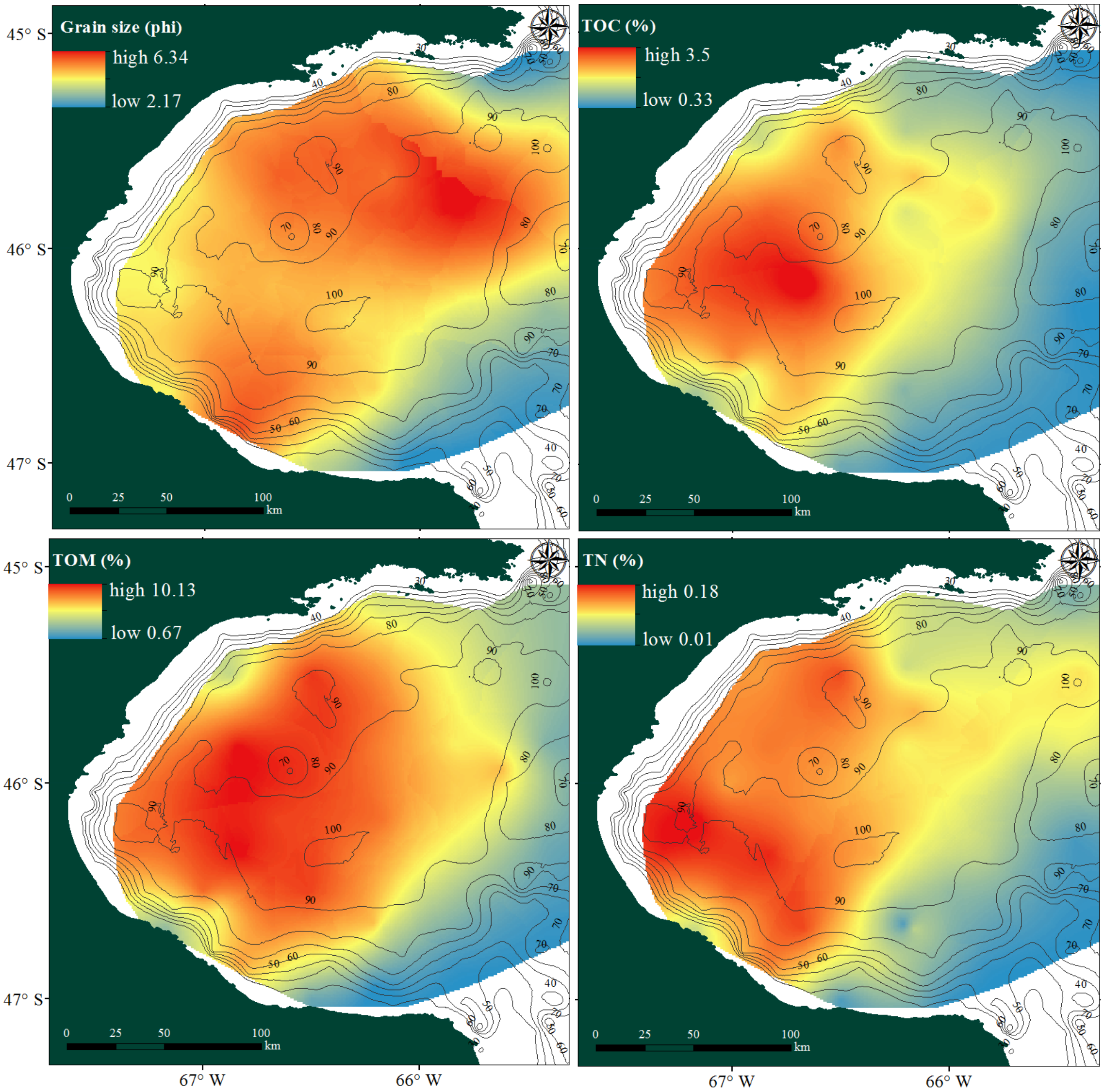

Figure 2 : Spatial distribution of sediment variables: gran size, total organic matter (TOM), total organic carbon (TOC) and total nitrogen (TN). Bathymetry is indicated by isolines.

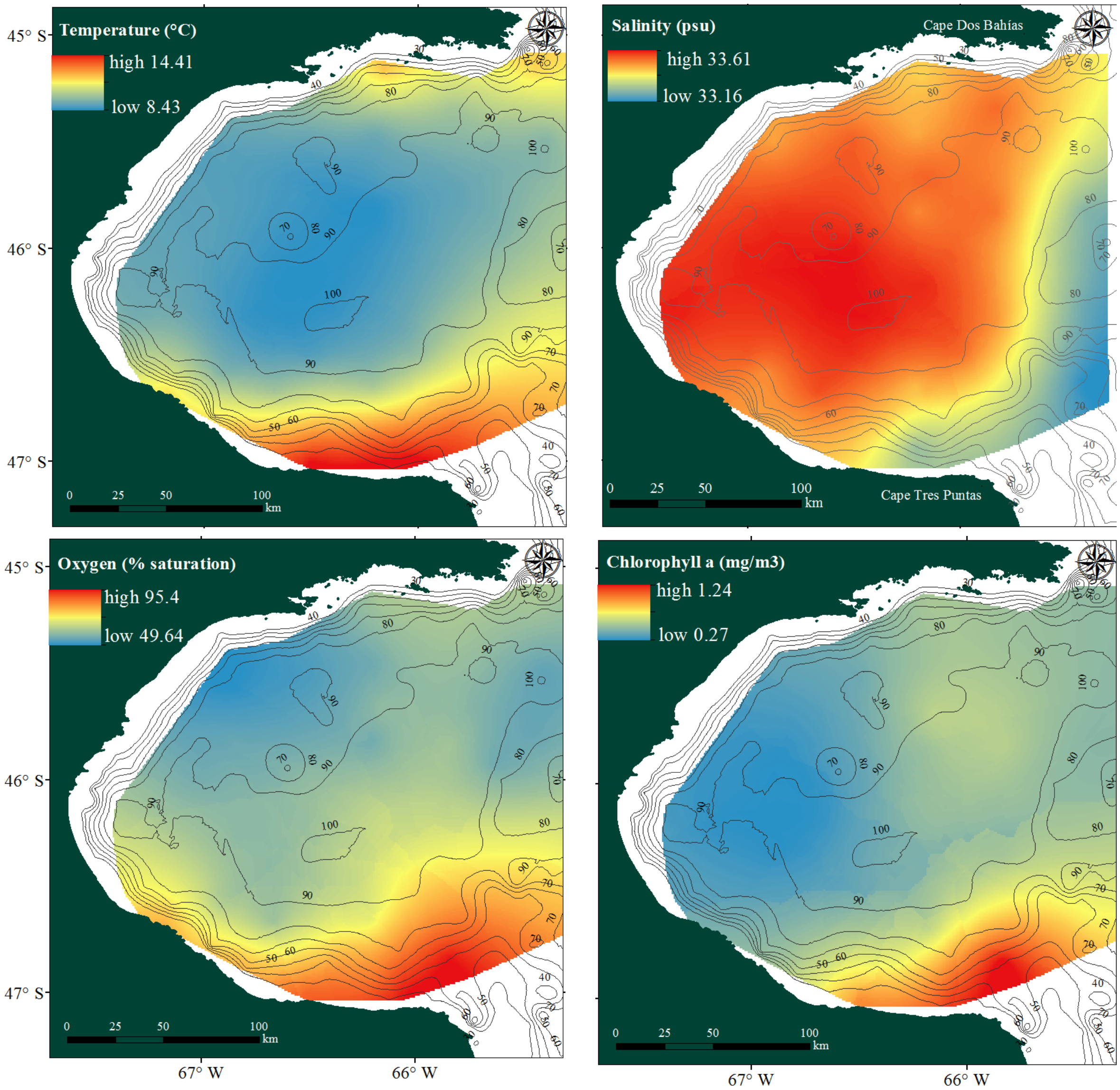

Figure 3 : Spatial distribution of bottom water variables: temperature, salinity, oxygen availability and chlorophyll *a*. Bathymetry is indicated by isolines.

CORRELATION BETWEEN ENVIRONMENTAL VARIABLES

The PCA for INIDEP data highlighted two dimensions that might explain together 81.6% of the total variability (Fig. 4 and Table 2). The PC1 axis explained 71.7% while the second dimension explained 9.9% of the variability. Oxygen, chlorophyll *a* and TOM were associated with the first PCA axis, while temperature, depth, bottom current, TN, salinity, grain size and TOC showed a closer association with the second PCA axis. Particularly, TOC and TN showed similar direction as descriptors. These variables might be highly correlated.

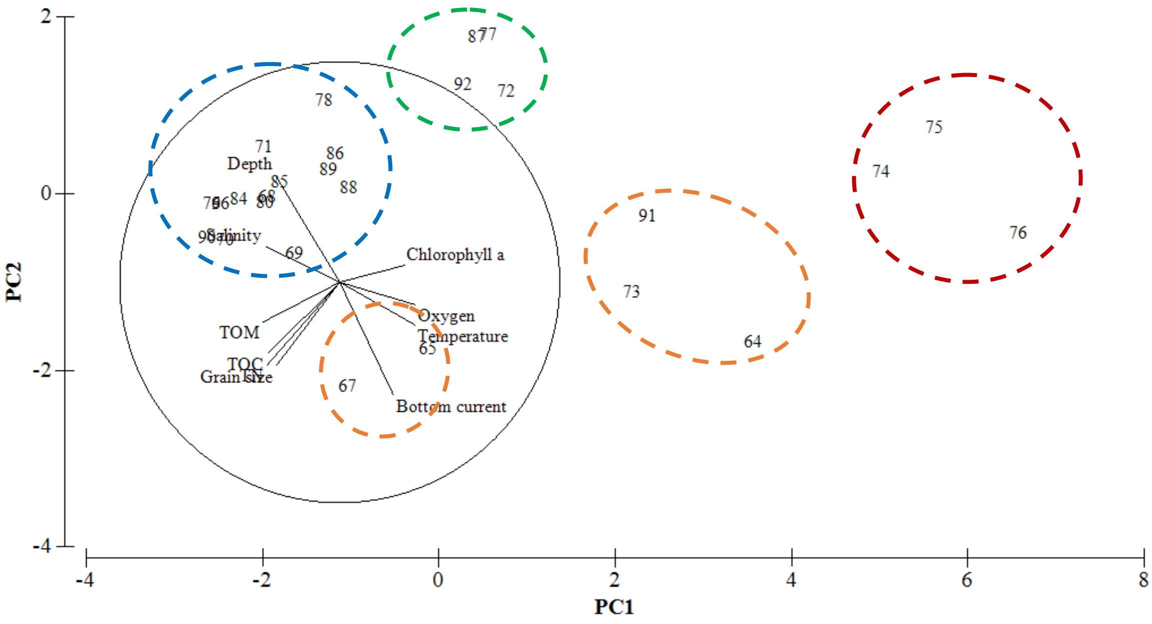

Figure 4 : Principal component analyses plots with the first two axes for INIDEP data. Stations (objects) and environmental variables (descriptors) are represented. Vectors indicate the direction and strength of environmental variables.

Regarding stations (objects) and environmental variables (descriptors), it was possible to observe that stations close to Cape Tres Puntas (indicated with red circle) showed coarse sediments and lower concentrations of TOM and TOC (Fig. 4). In turn, these stations presented higher concentrations of oxygen and chlorophyll *a*. Stations close to the coast in the inner part of the gulf (indicated with orange circles) presented fine sediments, high TOM and TOC concentrations, temperature and oxygen availability. Stations offshore (indicated with green circle) were positively associated with depths and salinity. Stations in the central region (indicated with blue circle) present fine sediments, high concentrations of TOM, TOC and TN, and bottom water is cold with low availability of oxygen and chlorophyll *a* concentration (Fig. 4).

Table 2 : Results from PCA considering INIDEP environmental data.

	PC 1	**PC 2**
Eigenvalues	7.17	0.991
Variance explained (%)	71.7	9.9
Eigenvectors		
Depth	-0.293	0.487
TOM	-0.349	-0.181
TOC	-0.325	-0.322
TN	-0.330	-0.375
Temperature	0.343	-0.194
Salinity	-0.336	0.161
Oxygen	0.343	-0.102
Chlorophyll *a*	0.294	0.076
Grain size	-0.289	-0.379
Bottom current	0.244	-0.512

The PCA for MARES data highlighted two dimensions that explained together 78.9% of the variability (Fig. 5 and Table 3). The PC1 axis explained 65.4% while the second axis explained 13.5% of the variability. Oxygen, temperature and grain size were associated with the first PCA axis while TN, TOC, depth, chlorophyll *a*, bottom current and TOM were associated with the second PCA axis. Particularly, salinity and TOM showed similar direction as descriptors. These variables might be highly correlated.

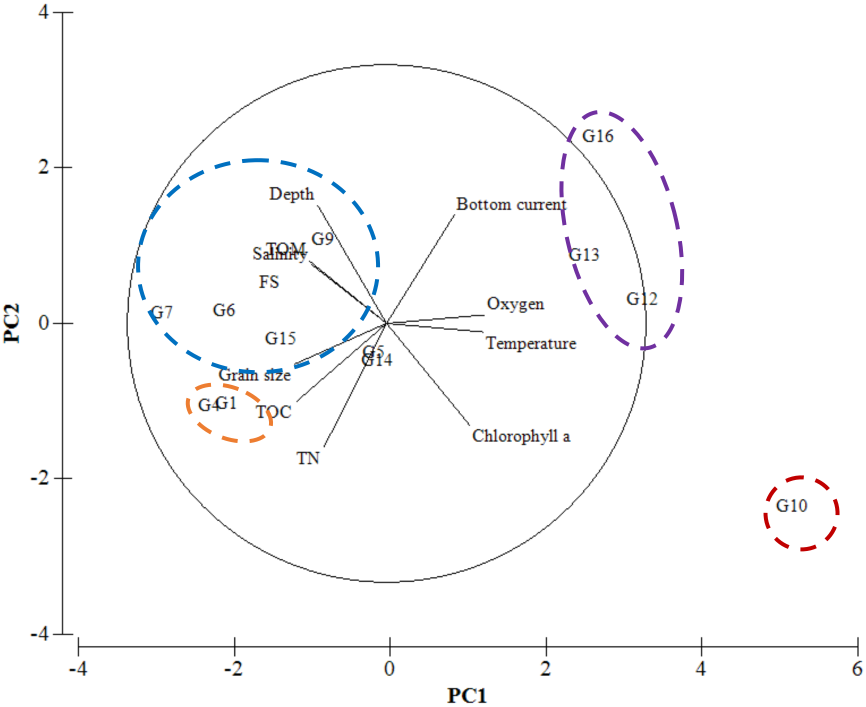

Figure 5 : Principal component analyses plots with the first two axes for MARES data. Stations (objects) and environmental variables (descriptors) are represented. Vectors indicate the direction and strength of environmental variables.

Regarding stations (objects) and environmental variables (descriptors), higher heterogeneity was observed among stations from MARES mission than from the INIDEP data. The station close to Cape Tres Puntas (indicated in red circle) presented coarse sediments, high concentrations of chlorophyll *a* and high temperature (Fig. 5), following the pattern described for stations in this area in Figure 4. Stations in the mouth (indicated purple circle) appeared to be related with bottom current and oxygen concentrations. The rest of the stations were associated with fine sediments and cold bottom waters with less availability of chlorophyll *a*, but they showed high heterogeneity (Fig. 5). Stations close to coasts (indicated with orange circles) were associated with similar gran size and TOC conditions. Stations in the central region (indicated with blue circle) present fine sediments, high concentrations of TOM, and bottom water is cold with low availability of oxygen and chlorophyll *a* concentration (Fig. 5).

Table 3 : Results from PCA considering MARES environmental data.

	PC 1	PC 2
Eigenvalues	6.54	1.35
Variance explained (%)	65.4	13.5
Eigenvectors		
Depth	-0.266	0.457
TOM	-0.298	0.241
TOC	-0.347	-0.302
TN	-0.243	-0.480
Temperature	0.373	-0.033
Salinity	-0.289	0.227
Oxygen	0.377	0.033
Chlorophyll *a*	0.322	-0.395
Grain size	-0.353	-0.157
Bottom current	0.261	0.419

1.5.2 BENTHIC DIVERSITY AND RELATIONS WITH BENTHIC ENVIRONMENT

Results are presented for epifauna taxonomic and functional diversity, and then for infauna taxonomic and functional diversity. In addition, the relations between assemblages and environmental variables are indicated in each section.

TAXONOMIC EPIFAUNA DIVERSITY

Cluster and SIMPROF analysis on epifauna data identified four groups (Fig. 6). Assemblage a has been identified with data from only one station, at the southern coast (Fig. 7). Assemblage b was found close to Cape Tres Puntas. Assemblage c was present in the central and western area. Assemblage d was found in the North, close to the mouth and southern coastal area (Mazarredo). The γ_{gulf} diversity identified 51 epifauna taxa (Table 4; see Table S3 for assemblages' composition). Differences between assemblages were mainly explained by presence or abundance of *Pseudechinus magellanicus*, *Neilonella sulculata*, *Ennucula puelcha*, *Munida gregaria*, *Renilla sp.*, *Austropandalus grayi*, *Mytilus edulis* and *Diplasterias brandti* (Table S4).

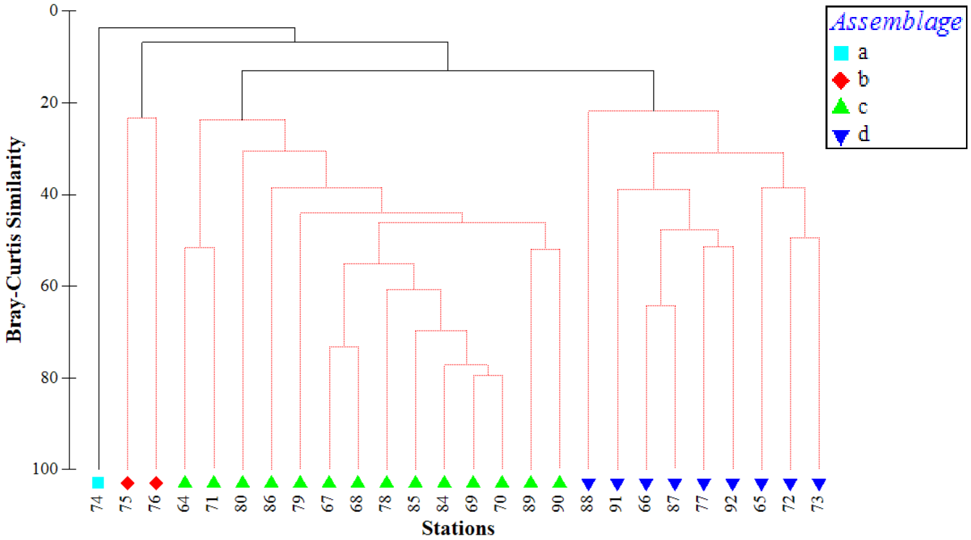

Figure 6 : Taxonomic cluster based on Bray-Curtis Similarity matrix using epifauna taxonomic abundance by station. The taxonomic epifauna assemblages are represented with different colors.

Assemblage a showed the lowest diversity, with only two taxa, Echiurida and *Renilla* sp. (Table 4). Assemblage b presented the highest $\alpha_{assemblage}$. However, the $\beta_{assemblage}$ indicated that the variation between stations from this assemblage was high. Assemblage b was characterised by *A. grayi*, *D. brandti*, *M. edulis, Molgula* sp. and *Alpheus puapeba*. The SIMPER analyses indicated that *D. brandti, A. grayi, Cirolana* sp., *Hemioedema spectabilis*, *Carolesia blakei* and *Boltenia* sp. contributed 93.62% to the average similarity of 23.29 (Table S4).

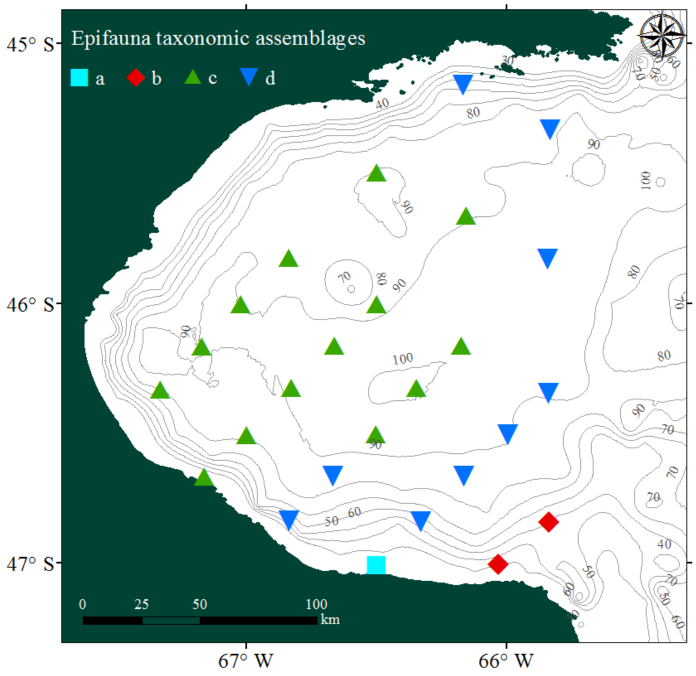

Figure 7 : Location of epifauna taxonomic assemblages in the SJG.

Assemblage c was characterised by high abundances of *P. magellanicus, M. gregaria*, Pectinariidae sp., *Ophiura* sp. and *A. grayi*. The SIMPER analyses indicated that *P. magellanicus, M. gregaria*, Pectinariidae, *Notiax brachyophthalma* and *Pterysgosquilla armata armata* contributed 90.68% to the average similarity of 41.22 (Table S4).

Assemblage d presented the highest $\gamma_{\text{assemblage}}$. This assemblage was characterised by high abundances of *N. sulculata*, *Ophiura* sp., *E. puelcha*, *Molgula* sp. and Pectinariidae. The SIMPER analyses indicated that *N. sulculata*, *E. puelcha*, *Molgula* sp., *M. gregaria*, *P. armata armata*, *Pandora cistula*, *N. brachyophthalma* and *Peachia* sp. contributed 90.49% to the average similarity of 34.15 (Table S4).

Table 4 : Taxonomic diversity indices for epifauna data by assemblage. The five dominant taxa in terms of total abundance of individuals by assemblage are presented.

Assemblage	**$\alpha_{assemblage}$**	**$\gamma_{assemblage}$**	**$\beta_{assemblage}$**	**β_{gulf}**	**Dominant taxa**
a	2	2	1	25.5	*Renilla* sp. Echiurida
b	16	25	1.56	2.04	*Austropandalus grayi* *Diplasterias brandti* *Mytilus edulis* *Molgula* sp. *Alpheus puapeba*
c	8.5	25	2.94	2.04	*Pseudechinus magellanicus* *Munida gregaria* Pectinariidae *Ophiura* sp. *Austropandalus grayi*
d	14.11	38	2.7	1.34	*Neilonella sulculata* *Ophiura* sp. *Ennucula puelcha* *Molgula* sp. Pectinariidae

* The $\alpha_{assemblage}$ represents the average of alpha diversity by assemblage. The $\gamma_{assemblage}$ is the total number of taxa at the assemblage scale. The $\beta_{assemblage} = \gamma_{assemblage} / \alpha_{assemblage}$ represents the variation within assemblages while the $\beta_{gulf} = \gamma / \gamma_{assemblage}$ represents the variation between assemblages throughout the SJG.

The distance-based linear model identified TOM and oxygen as the environmental variables that better explained the distribution of epifauna taxonomic assemblages (Table 5). The dbRDA plot presents the correlation between these environmental variables and epifauna taxonomic assemblages on the first two dimensions of the ordination (Fig. 8). The most important variable contributing to the first axis of the dbRDA plot explaining 73.3% of fitted variation was TOM, while oxygen was correlated with the second axis explaining 26.7% of variation. Considering the distribution of assemblages in the dbRDA plot, it was possible to observe that assemblages' a and b close to Cape Tres Puntas were correlated with high concentrations of oxygen and low TOM availability. Assemblage c was strongly correlated with high concentrations of TOM but low oxygen availability. Assemblage d was correlated with low concentrations of TOM and oxygen availability (Fig. 8).

Table 5 : DistLM of epifauna taxonomic assemblages against environmental variables (Best-fit model with 9999 permutations, AICc = 208.1, $R^2 = 0.269$).

Percentage of variation explained by individual axes				
	% explained variation out of fitted model		**% explained variation out of total model**	
Axis	**Individual**	**Cumulative**	**Individual**	**Cumulative**
1	73.33	73.33	19.72	19.72
2	26.67	100	7.17	26.9

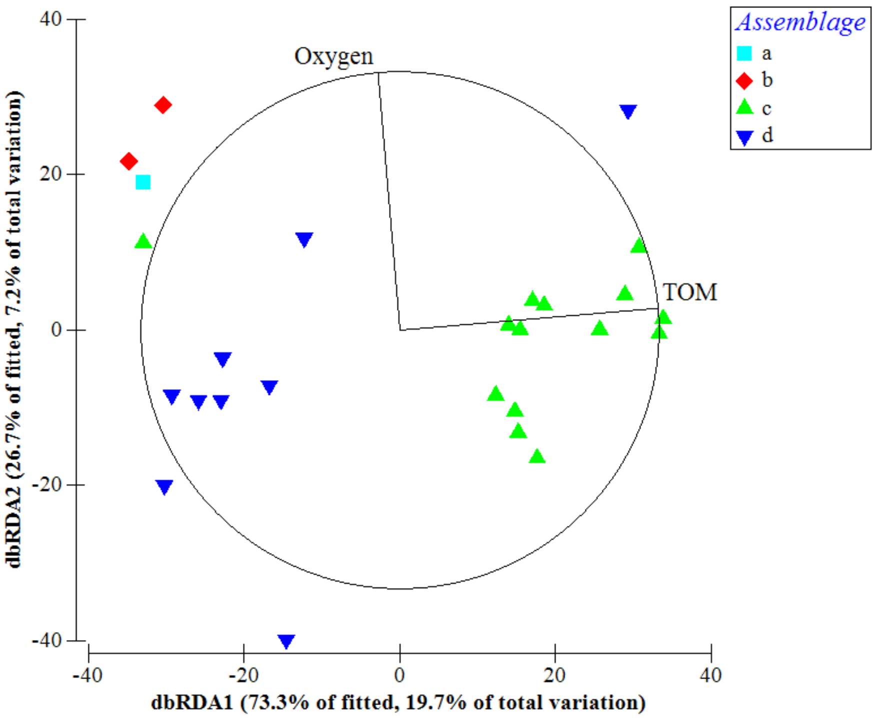

Figure 8 : Distance-based redundancy analysis (dbRDA) plot of the DistLM based on the environmental variables best-fitted to the variation in epifauna taxonomic assemblages. Vectors indicate direction of the environmental variable in the ordination plot.

The GLM models highlighted that taxonomic epifauna assemblages' c and d were correlated with TOM or with TOM and Oxygen, respectively (Table 6). However, it was not possible to estimated the GML model for assemblages' a and b, probably because of the low number of stations. The probability of presence of assemblages' c and d is projected in the habitat suitability maps (Fig. 9). The assemblage c has high probabilities to occur in the central are of the SJG where TOM concentrations are high. On the contrary, assemblage d is predicted to occur at low TOM and high oxygen close to headlands and offshore (Fig. 9).

Table 6 : Results for the second set of GLMs predicting the presence of taxonomic assemblages.

	Taxonomic epifauna assemblage c			
	Estimate	**Std. error**	**z value**	**p**
Intercept	-5.2791	2.0527	-2.572	0.01012 *
TOM	0.7872	0.2721	2.893	0.00382 **
	Taxonomic epifauna assemblage d			
	Estimate	**Std. error**	**z value**	**p**
Intercept	15.77791	7.12044	2.216	0.0267 *
TOM	-0.94591	0.38657	-2.447	0.0144 *
Oxygen	-0.14556	0.06777	-2.148	0.0317 *

Significant codes : '*' = 0.01, '**' = 0.001.

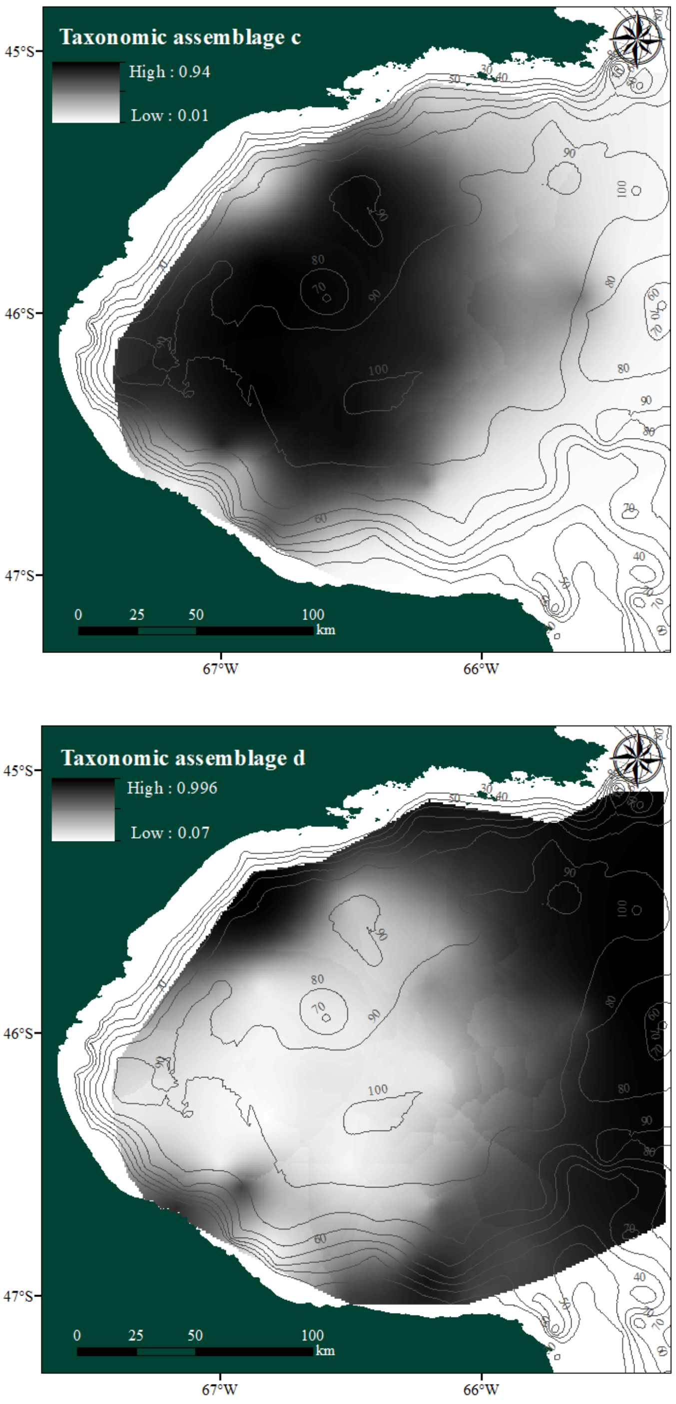

Figure 9 : Habitat suitability maps representing the probability of presence for taxonomic epifauna assemblages' c and d in the SJG.

FUNCTIONAL EPIFAUNA DIVERSITY

Cluster and SIMPROF analysis on epifauna functional data identified four groups (Fig. 10). Regarding the spatial distribution, functional assemblages' a and b were found close to Cape Tres Puntas (Fig. 11). Functional assemblage c was present in the central area and close to the coasts in the west. Functional assemblage d was found in northern and southern coastal areas and close to the mouth of the SJG. The γ_{gulf} diversity identified 38 epifauna functional groups considering feeding strategy, size, mobility, adult life traits and bioturbation (Table 7; see Table S5 for the taxa classified by functional traits and Table S6 for functional assemblages' composition). Differences between assemblages were explained by OXMCS, S.FLMBB, S.FLSBB, FXSSS, PLMWS and PXMCS in most of the cases (Table S7).

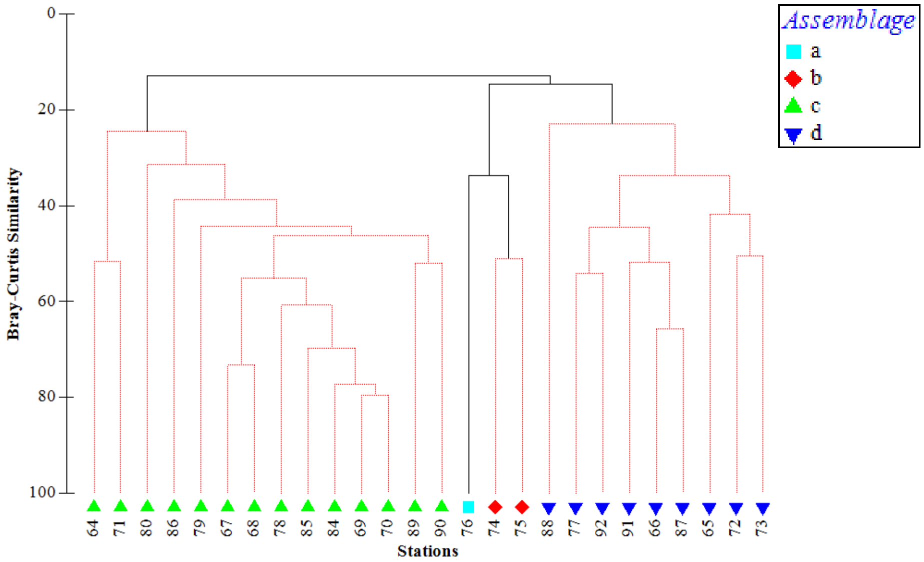

Figure 10 : Functional cluster based on Bray-Curtis Similarity matrix using epifauna functional groups abundance by station. The functional epifauna assemblages are represented with different colors.

Functional assemblage a was identified with data from only one station, at the southern coast. This assemblage was characterised by high abundances of PLMWS, PXMCS, PLMCS, OXMCS, FXSSS (Table 7).

Functional assemblage b was characterised by high abundances of functional groups FXSSS, PXMCS, PLMWS, ASHBB, PLMCS. The SIMPER analysis indicated that FXSSS and ASHBB contributed 100% to the average similarity of 50.97 (SIMPER, Table S7) of this assemblage.

Functional assemblage c presented high $\gamma_{\text{assemblage}}$ (Table 7). This assemblage was characterised by OXMCS, OXMC.WS, SLSBT, OLMCS, PLMWS. However, the variation between stations from this assemblage was also high ($\beta_{\text{assemblage}}$). The SIMPER analysis indicated that OXMCS, OXMC.WS, SLSBT, DXMBG, PXMCB contributed to 90.01% to the average similarity of 41.52 (Table S7).

Functional assemblage d presented the highest $\gamma_{\text{assemblage}}$ (Table 7). This assemblage was characterised by S.FLMBB, OLMCS, S.FLSBB, FXSSS, SLSBT. However, the variation between stations from this assemblage was also high ($\beta_{\text{assemblage}}$). The SIMPER analysis indicated that S.FLMBB, S.FLSBB, FXSSS, OXMC.WS, PXMCB, FLMBB, DXMBG contributed to 91.16% to the average similarity of 36.51 (Table S7).

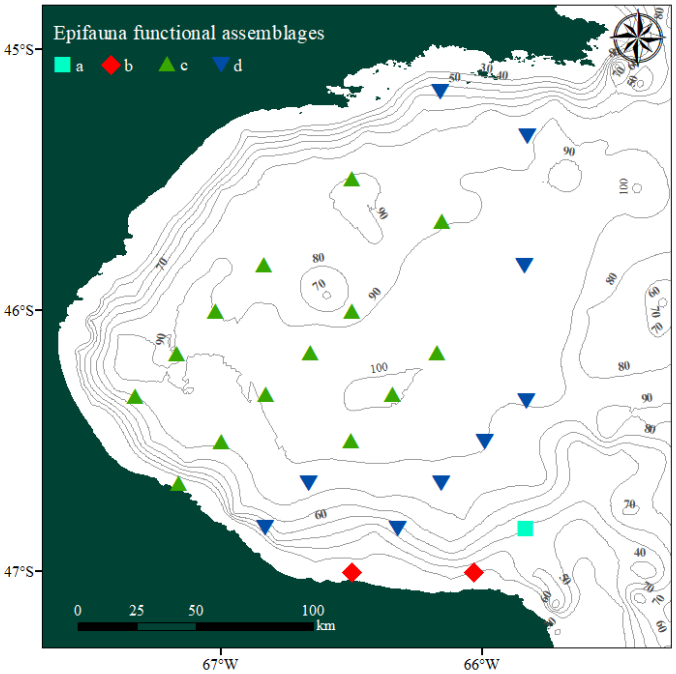

Figure 11 : Location of epifauna functional assemblages in the SJG.

The distance-based linear model identified TOM and oxygen as the environmental variables that better explained the distribution of epifauna functional assemblages (Table 8). The dbRDA plot presents the correlation between environmental variables and epifauna functional assemblages on the first two dimensions of the ordination (Fig. 12). The most important variables contributing to the first axis of the dbRDA plot explaining 76.8% of fitted variation was TOM, while oxygen was more correlated with the second axis explaining 23.2% of variation. Functional assemblages' a and b were correlated with high concentrations of oxygen and low TOM. Functional assemblage c presented high concentrations of TOM and low oxygen availability. Functional assemblage d presented low concentrations of TOM and oxygen availability (Fig. 12).

Table 7 : Functional diversity indices for epifauna data by assemblage. The five dominant functional groups in terms of total abundance of individuals by assemblage are presented.

Feeding habit	**Size**	**Mobility**	**Adult life**	**Bioturbation**
S :Deposit subsurface feeder	S :0,5 mm < Little < 5 mm	S :Sessile	B :Burrow	B :Active burrower (diffusive)
D :Deposit surface feeder	M :5 mm < Medium <10 mm	H :Hemimobile	C :Crawl	G :Gallery burrower
A :Deposit surface and subsurface feeder	L :10 mm < Large < 50 mm	M :Mobile	S :Sessile	S :Surface dweller
F :Filter/suspension feeder	X :X-Large > 50 mm		W :Swim	T :Tube burrow
O :Opportunist				
P :Predator				
H :Herbivores				

Assemblage	$\alpha_{assemblage}$	$\gamma_{assemblage}$	$\beta_{assemblage}$	β_{gulf}	**Dominant functional groups**
a	13	13	1	2.92	PLMWS PXMCS PLMCS OXMCS FXSSS
b	8	14	1.75	2.71	FXSSS PXMCS PLMWS ASHBB PLMCS
c	8.5	23	2.71	1.65	OXMCS OXMC.WS SLSBT OLMCS PLMWS
d	13	30	2.31	1.27	S.FLMBB OLMCS S.FLSBB FXSSS SLSBT

* The $\alpha_{assemblage}$ represents the average of alpha functional group diversity by assemblage. The $\gamma_{assemblage}$ is the total number of functional groups at the assemblage scale. The $\beta_{assemblage} = \gamma_{assemblage} / \alpha_{assemblage}$ represents the variation within assemblages while the $\beta_{gulf} = \gamma / \gamma_{assemblage}$ represents the variation between assemblages throughout the SJG.

Table 8 : DistLM of functional epifauna assemblages against environmental variables (Best-fit model with 9999 permutations, AICc = 205.3, $R^2 = 0.305$).

Percentage of variation explained by individual axes				
	% explained variation out of fitted model		**% explained variation out of total model**	
Axis	**Individual**	**Cumulative**	**Individual**	**Cumulative**
1	76.79	76.79	23.4	23.4
2	23.21	100	7.08	30.48

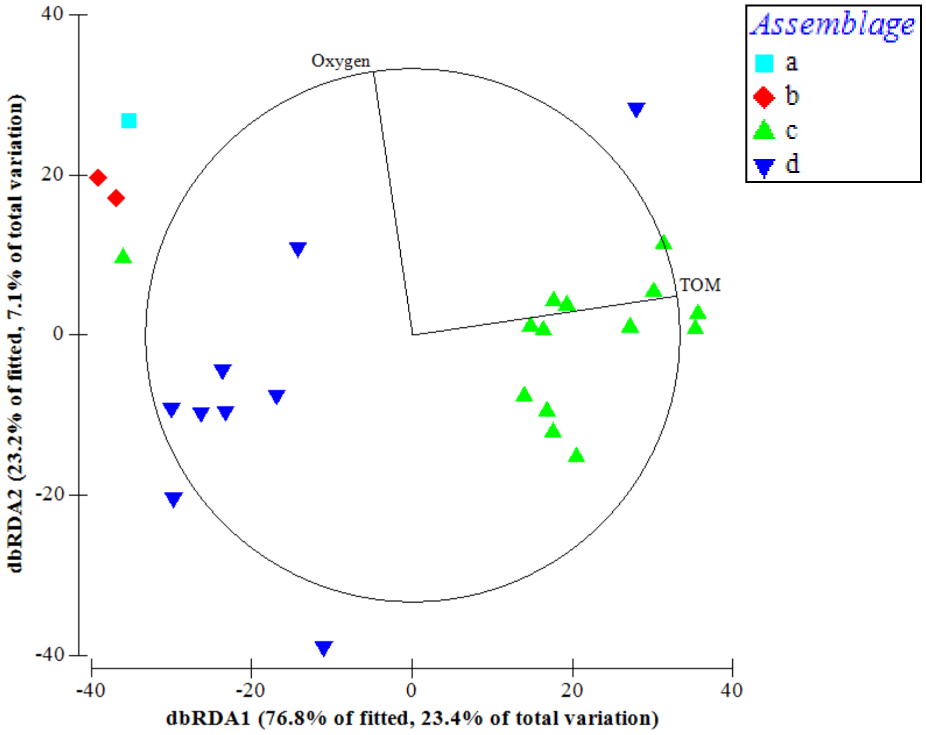

Figure 12 : Distance-based redundancy analysis (dbRDA) plot of the DistLM based on the best environmental variables fitted to the variation in epifauna functional assemblages. Vectors indicate direction of the environmental variable in the ordination plot.

The GLM models highlighted that functional epifauna assemblages' c and d were correlated with TOM or with TOM and Oxygen, respectively (Table 9). However, it was not possible to estimated the GML model for assemblages' a and b, probably again because of the low number of stations. The probability of presence of assemblages' c and d is projected in the habitat suitability maps (Fig. 13). The assemblage c has high probabilities to occur in the central are of the SJG where TOM concentrations are high. On the contrary, assemblage d is predicted to occur at low TOM and high oxygen close to headlands and offshore (Fig. 13).

Table 9 : Results for the second set of GLMs predicting the presence of functional assemblages.

Functional epifauna assemblage c				
	Estimate	**Std. error**	**z value**	**p**
Intercept	-5.2791	2.0527	-2.572	0.01012 *
TOM	0.7872	0.2721	2.893	0.00382 **
Functional epifauna assemblage d				
	Estimate	**Std. error**	**z value**	**p**
Intercept	15.77791	7.12044	2.216	0.0267 *
TOM	-0.94591	0.38657	-2.447	0.0144 *
Oxygen	-0.14556	0.06777	-2.148	0.0317 *

Significant codes : '*' = 0.01, '**' = 0.001.

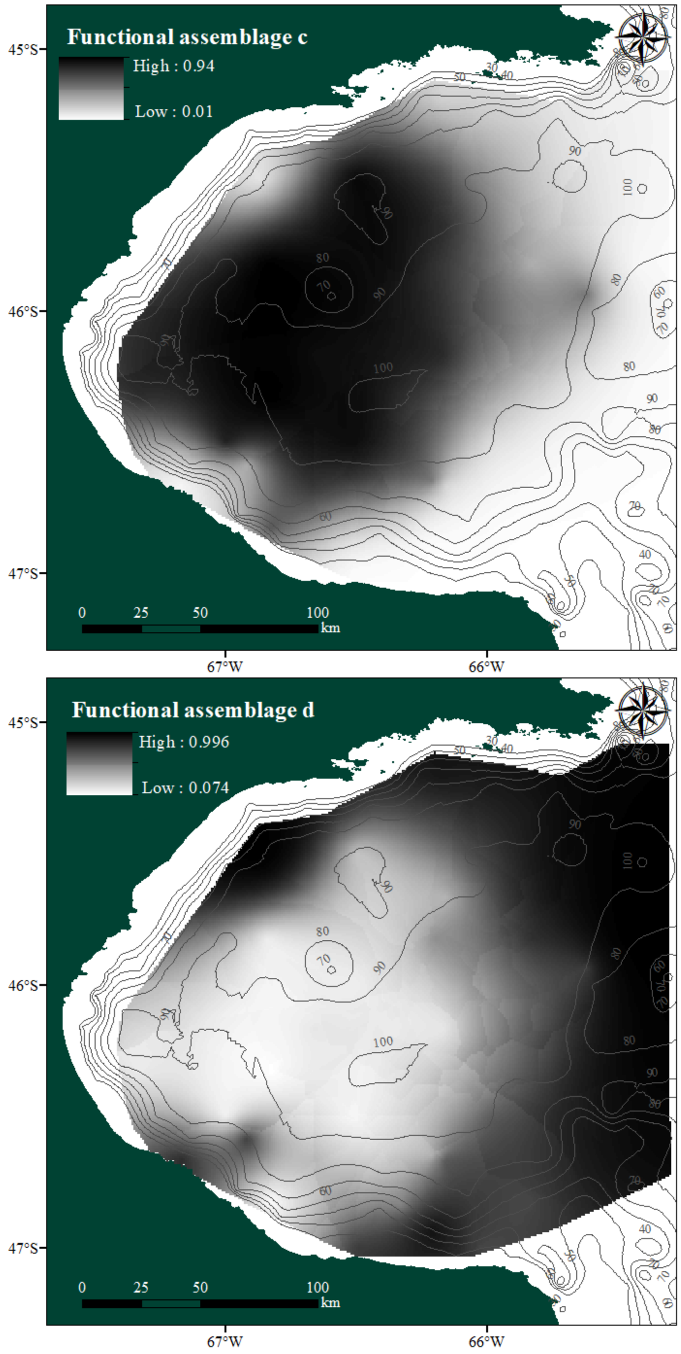

Figure 13 : Habitat suitability maps representing the presence for epifauna functional assemblages' c and d in the SJG.

TAXONOMIC INFAUNA DIVERSITY

Cluster and SIMPROF analysis on infauna data identified that there were no significant differences between stations that allowed to determine the presence of assemblages (Fig. 14). The γ_{gulf} diversity identified 23 infauna taxa. High abundances of infauna taxa were represented by *Neilonella sulculata*, *Ennucula puelcha*, Maldanidae, *Stylatula* sp. and *Notiax brachyophthalma*. However, the composition presented high variation among infauna sampled stations. The SIMPER analyses indicated that *N. sulculata*, *N. brachyophthalma*, Maldanidae, *E. puelcha* and *Tripylaster philippii* contributed 91.44% to the average similarity of 22.68 (Table S8).

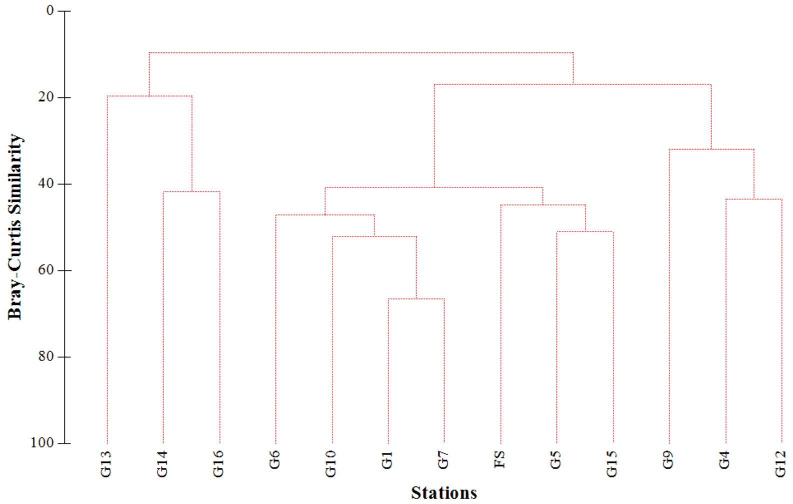

Figure 14 : Taxonomic cluster based on Bray-Curtis Similarity matrix using infauna taxonomic abundances by station. No assemblages were identified.

The distance-based linear model identified bottom current and grain size as the environmental variables that better explained the distribution of infauna taxonomic data (Table 10). The dbRDA plot presents the correlation between environmental variables and infauna stations, explaining 100% of fitted variation on the first two dimensions of the ordination (Fig. 15).

Table 10 : DistLM of taxonomic infauna against environmental variables (Best-fit model with 9999 permutations and minimum two variables, AICc = 108.7, $R^2 = 0.250$).

	Percentage of variation explained by individual axes			
	% explained variation of fitted model		**% explained variation of total model**	
Axis	**Individual**	**Cumulative**	**Individual**	**Cumulative**
1	76.09	76.09	19.03	19.03
2	23.91	100	5.98	25.01

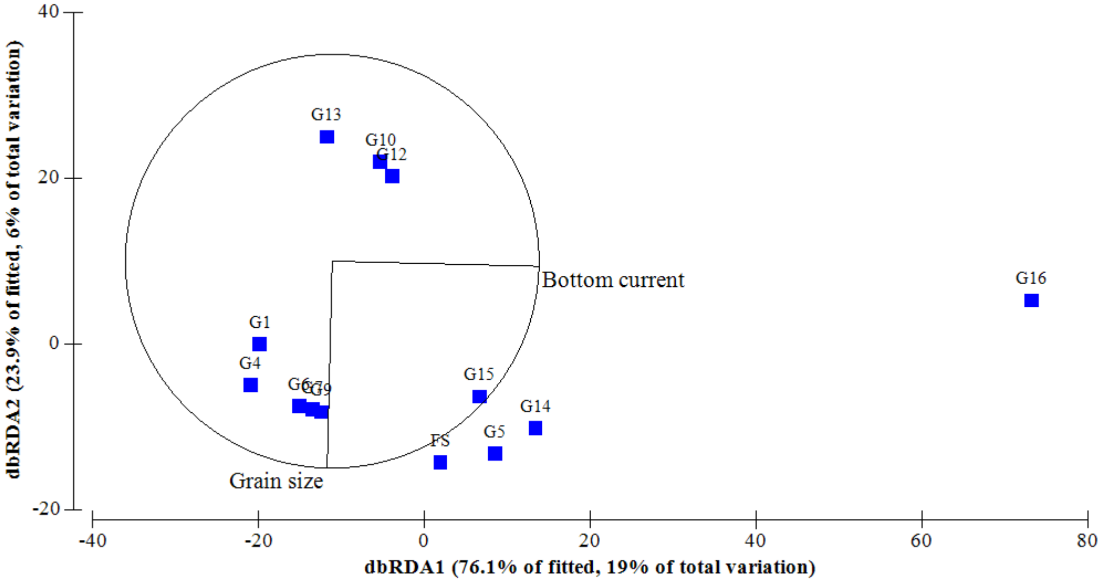

Figure 15 : Distance-based redundancy analysis (dbRDA) plot of the DistLM based on the best environmental variables fitted to the variation in infauna taxonomic stations. Vectors indicate direction of the environmental variable in the ordination plot.

Even though no assemblages were identified, a deep analyses of infauna taxonomic data and its distribution in the dbRDA allowed to observe that stations in the inner part of the SJG (1, 4, 6, 7, 9) were characterised by low bottom current velocities and fine sediments (Fig. 15). These stations were characterised by high abundances of *N. sulculata*, *E. puelcha* and *N. brachyophthalma*. On the contrary, stations offshore and close to Cape Tres Puntas presented low bottom current velocities but coarse sediments (Fig. 15). However, composition presented high variation among these stations. Finally, stations offshore and close to Cape Dos Bahías (5, 14, 15, 16, FS) presented high bottom current velocities and fine sediments. These stations were characterised by *Neilonella sulculata*, *Ennucula puelcha*, *Stylatula* sp. and Maldanidae but composition presented also high variation among these stations.

FUNCTIONAL INFAUNA DIVERSITY

Like taxonomic infauna data, cluster and SIMPROF analysis on functional infauna data did not present significant differences between stations that allowed to determine the presence of different assemblages (Fig. 16). The γ_{gulf} diversity identified 21 infauna functional groups (see Table S5 for the taxa classified by functional traits). Infauna functional groups with higher abundances were S.FLMBB, S.FLSBB, SMHBT, DXMBG, FXSSS. However, the composition presented high variation among infauna sampled stations. The SIMPER analysis indicated that S.FLMBB, DXMBG, SMHBT, S.FLSBB, SLMBS, FXSSS 91.84% to the average similarity of 23.30 (Table S9).

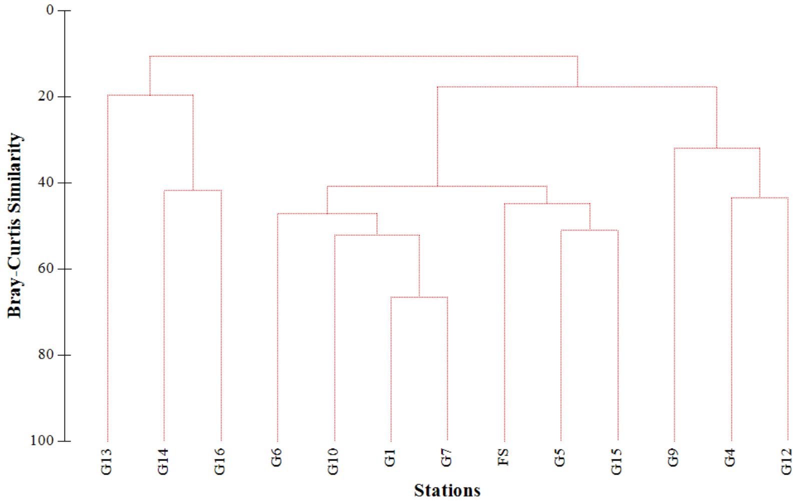

Figure 16 : Functional cluster based on Bray-Curtis Similarity matrix using infauna functional groups abundances by station. No assemblages were identified.

Table 11 : DistLM of functional infauna assemblages against environmental variables (Best-fit model with 9999 permutations, AICc = 108.14, $R^2 = 0.27$).

	Percentage of variation explained by individual axes			
	% explained variation of fitted model		**% explained variation of total model**	
Axis	**Individual**	**Cumulative**	**Individual**	**Cumulative**
1	73.08	73.08	19.7	19.7
2	26.92	100	7.26	26.95

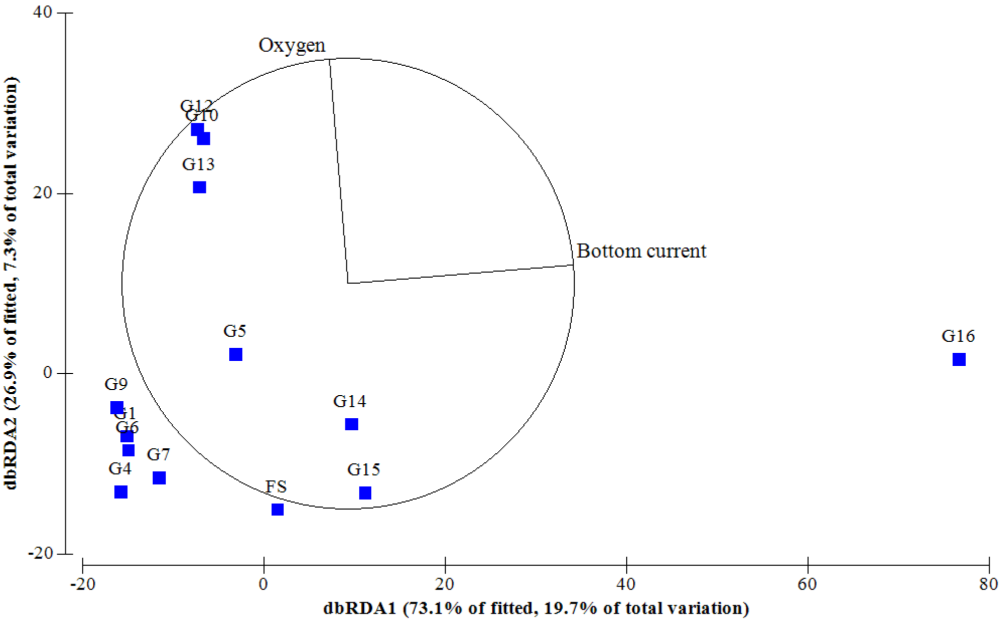

Figure 17 : Distance-based redundancy analysis (dbRDA) plot of the DistLM based on the best environmental variables fitted to the variation in functional infauna assemblages. Vectors indicate direction of the environmental variable in the ordination plot.

The distance-based linear model identified bottom current and oxygen as the environmental variables that better explained the distribution of infauna functional data (Table 11). The dbRDA plot presents the correlation between environmental variables and infauna stations on the first two dimension of the ordination, explaining 100% of fitted variation (Fig. 17). Considering the distribution of infauna functional stations in the dbRDA, it is possible to observe that most of stations are found in low bottom current velocities with low oxygen availability. However, stations in the South close to Cape Tres Puntas, presented low bottom current velocities with high oxygen availability (Fig. 17).

REGRESSION MODEL FOR LOCAL DIVERSITY

There is a positive relationship between local taxonomic diversity and local functional diversity (Fig. 18; see Table S10 for taxonomic and functional group richness by station). The lineal regression model estimated is $y = 0.79 + 0.87\ x$ (Adjusted-$R^2 = 0.98$, F-statistic = 1627, df = 1, 37, $p < 0.0001$).

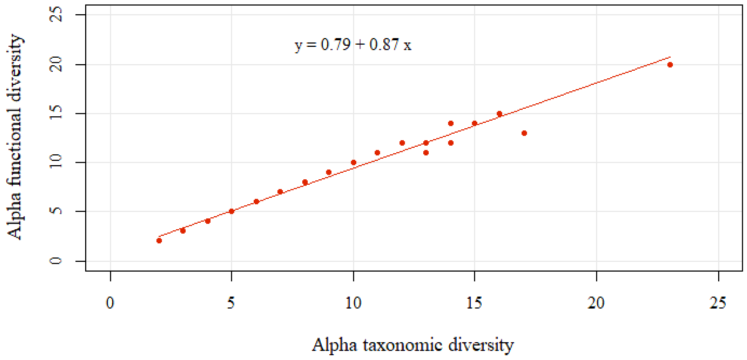

Figure 18 : Linear regression model between local taxonomic and functional richness.

1.6 DISCUSSION

This is the first study to describes the spatial variation of benthic biodiversity distribution in the San Jorge Gulf considering taxonomic and functional diversity. Epifauna assemblages were identified but contrary to our first hypothesis they were correlated with oxygen availability and organic matter concentrations. Furthermore, the assemblage with higher diversity was not associated with high organic matter concentrations as we had proposed in the second hypothesis. Instead, high taxonomic and functional epifauna diversity were presented in northern and southern coastal areas and close to the mouth of the SJG. Habitat suitability maps were estimated, describing the probability of presence for epifauna assemblages. In the case of infauna, no assemblages were identified with the available data.

DESCRIPTION OF BENTHIC ENVIRONMENT

In the present study, new data from an oceanographic mission in 2014 has been included to the spatial zonation proposed by Fernández et al. (2003, 2005) for the SJG. Particularly, the stations from MARES mission that were distributed in the mouth of the gulf completed the general picture of benthic environment in summer for the SJG. Additionally, bottom current velocities data from the model recently developed by Combes and Matano (unpublished) were included in an unprecedented way for the SJG.

Our results on bathymetry, sediment and physic-chemical features in the benthic environment mostly coincide with the spatial heterogeneity described in the zonation for the benthic environment in the SJG during the summer season (Fernández et al. 2003, 2005). The deeper zone, defined by the isobath of 80 m presented fine sediments, higher concentrations of TOM, TOC, TN and cold bottom water with low availability of oxygen and chlorophyll *a*. On the contrary, in northern and southern coastal areas and close to the mouth of the SJG, benthic environment presented a decrease in concentrations of TOM, TOC, TN in sediments and low oxygen availability. Close to Cape Tres Puntas, benthic environment was characterised by coarse sediments and low organic matter concentrations in sediments, and high temperatures, oxygen availability and chlorophyll *a* concentrations in the bottom water.

Future studies could focus on physical structures and variations in topography at a higher scale resolution (Copeland et al. 2011, Brown et al. 2012, Carvalho et al. 2017). Particularly, considering that topography in coastal ecosystems have been identified as structuring factor of benthic and pelagic biodiversity, and in the growth of sessile filterers (Archambault et al. 1998, 1999, Archambault and Bourget 1999).

BENTHIC ASSEMBLAGES DESCRIPTION

The first community-level study followed by Roux et al. (1995) in the SJG described epibenthic biodiversity and proposed that molluscs, echinoderms, crustacean and polychaetes dominate the coastal and South-East zones, while highly diverse colonies of bryozoans, hydrozoans and sponges dominate headland zones. Fainburg et al. (2012) described epibenthic communities and substrates characteristics in a small area close to Caleta Olivia. Further, studies on benthic biodiversity were principally focused on crustaceans (i.e. Vinuesa 2005, Vinuesa et al. 2011, Varisco et al. 2017), echinoderms (i.e. Brogger et al. 2013) and molluscs (i.e. Liuzzi et al. 2016, López-Gappa et al. 2016), or related with fishing grounds (i.e. Roux et al. 2009) and incidental captures of trawling fisheries (i.e. Bovcon et al. 2013). Several studies have described ecological characteristics of species, particularly related with feeding strategies (e.g. Vinuesa et al. 2013, Spath et al. 2015, Varisco et al. 2015, Liuzzi et al. 2016). Recently, organic matter recycling and trophic interactions among crustaceans were analysed considering fishing impacts close the coasts (Varisco and Vinuesa 2007, Vinuesa and Varisco 2007) and benthic fluxes were measured (oxygen and inorganic nutrients) in the National Park located in the North (Torres et al. 2016). Nonetheless, information relating biodiversity and ecosystem functioning interactions is lacking, specially for benthic biodiversity in the SJG.

In the present study, composition and structure of epifauna and infauna were explored using taxonomic and functional traits. In the case of epifauna, 51 species and 38 functional groups were identified considering size, feeding, mobility, bioturbation and adult life strategies functional traits. Four taxonomic epifauna assemblages were identified that followed mostly the same spatial distribution that the four functional epifauna assemblages. The epifauna assemblage in the deeper zone was dominated by *Pseudechinus magellanicus, Munida gregaria*, Pectinariidae sp., *Ophiura* sp. and *Austropandalus grayi*. Regarding the functional groups composition, the assemblage in this area was characterised by opportunist crawlers and deposit subsurface burrowers (OXMCS, OXMC.WS, SLSBT, OLMCS, PLMWS functional groups). In the north, close to the mouth and along the southern coastal area (Mazarredo), the epifauna assemblage was mainly composed by *Neilonella sulculata*, *Ophiura* sp., *Ennucula puelcha*, *Molgula* sp. and Pectinariidae sp.. The assemblage in this area was mostly composed by deposit subsurface feeders, filter burrowers and sessile feeders (S.FLMBB, OLMCS, S.FLSBB, FXSSS, SLSBT functional groups). Considering the zonation described by Roux et al. (1995), we expected to find a distribution for this assemblage following the coastal and South-East zones. Though, it was possible to identify stations with this assemblage in the north, very close to Cape Dos Bahías. Finally, close to Cape Tres Puntas, two assemblages were described with different spatial pattern for taxonomic and functional analyses. In the case of taxonomic assemblages, one assemblage was dominated by *A. grayi*, *Diplasterias brandti*, *Mytilus edulis, Molgula* sp. and *Alpheus puapeba* while the other was dominated by *Renilla* sp and Echiurida. These assemblages were characterised by predator swimmers, predator crawlers, opportunist crawlers and filter sessile feeders (PLMWS, PXMCS, PLMCS, OXMCS, FXSSS functional groups for assemblage a, and FXSSS, PXMCS, PLMWS, ASHBB, PLMCS for b).

Diversity indices indicated that the assemblages in the north, close to the mouth, along the southern coastal area (Mazarredo) and close to Cape Tres Puntas were more diverse in terms of species and functional groups composition. These assemblages might be proposed as *hotspots* areas in the SJG. On the contrary, the central area presented low diversity indices. Even though benthic assemblages were identified for epifauna data with significant statistical differences, it should be considered that the variation in composition between stations from the same assemblages (beta assemblage diversity) was high in most of the cases. This indicate that stations with the same assemblage did not presented always the same composition (Cusson et al. 2007). However, several species or abundances determined similarities between stations that allow to identify them with the same assemblage (Gray 2001, Anderson et al. 2011). Furthermore, the identification of an assemblage dominated by *Renilla* sp and Echiurida in only one station also close to Cape Tres Puntas could be explored in future studies to verify if this area is truly different from the surroundings or if it could be added to other described assemblages.

In the case of infauna, 23 species and 21 functional groups were found. It was not possible to identify assemblages with the available data. High variation in composition between stations was observed, *Neilonella sulculata*, *Ennucula puelcha*, Maldanidae, *Notiax brachyophthalma* and *Stylatula* sp. were the most abundant taxa. Deposit subsurface or filter feeder burrowers, deposit surface burrowers and filter sessile (S.FLMBB, S.FLSBB, SMHBT, DXMBG, FXSSS) were among the most abundant functional groups. The lack of structure could be related to the low number of stations sampled in an over large spatial extension. This might indicate that more stations from the same zone should be included to improve the description of infauna in the SJG. We believe that the inclusion of data collected as part of future missions in the context of Pampa Azul programme

(Argentina) should facilitate the description of the composition and structure of these organisms.

BIODIVERSITY DISTRIBUTION MODEL FOR THE SAN JORGE GULF

In the present study, the correlation between benthic environmental variables and benthic assemblages' distribution were analysed to build a biodiversity distribution model to predict spatial distribution and composition of the assemblages in summer. Our results highlighted that the distribution of epifauna assemblages was strongly correlated with oxygen availability in the bottom water and organic matter concentrations in sediments. On the contrary, we were also expecting a high correlation with sediments size, considered one of the strong environmental drivers in the SJG (Fernandez et al. 2003, 2005).

Our results showed high probabilities of presence for the assemblage characterised by opportunist crawlers and deposit subsurface burrowers where organic matter concentrations in sediments are high, particularly in the central zone of the gulf. Strong fishing pressure in the SJG might affects the dynamics of natural communities (Góngora et al. 2012, Bovcon et al. 2013), in ways that the discards of low commercial value species in trawling fisheries in the SJG could have an impact on the functioning of this benthic assemblage by increasing the amounts of organic material in the seabed (Varisco and Vinuesa 2007). This accumulation initially favours opportunistic species and deposit subsurface feeders, which are capable of ingesting the available organic matter. For example, *Munida gregaria* has the particularity of recycling organic matter and in turn it is strongly consumed by predators from higher trophic levels (Vinuesa and Varisco 2007). In addition, it is characterised by high mobility and plasticity so that this species does important displacements that could connect assemblages (Varisco et al. 2015). Our results mostly coincide with wide spread distribution of *M. gregaria* in the SJG. In the present study, *M. gregaria* was found in almost all stations but principally it was very abundant in the deeper zone. On the contrary, other species might be more limited in its distribution. For example, *Neilonnella sulculata* was present only in the north, close to the mouth and southern coastal area (Mazarredo). The depths and the high consumption and degradation of organic matter explains the low oxygen availability observed in this zone of the SJG (Holmer 1999).

Our model predicted high probabilities of presence for the assemblage characterised by deposit subsurface feeders, filter burrowers and sessile feeders associated with low oxygen availability in bottom water and low organic matter concentrations in sediments. The distribution of this assemblages followed the pattern of a decrease in concentrations of organic compounds in sediments found in northern and southern coastal areas and close to the mouth of the SJG. Diversity composition of this assemblage reveals a more direct dependence on primary productivity. This might be associated with the presence of frontal areas in the south and the north where the primary productivity is higher and the pelagic-benthic coupling is stronger (Rivas et al. 2006, Palma et al. 2008, Glembocki et al. 2015). Recently, Retana and Lewis (2017) identified in these areas high habitat suitability for marine mammals, principally determined by high chlorophyll *a* concentrations, bathymetry, seafloor slope, distance to the coast, distance to frontal systems and surface temperature.

Despite that it was no possible to state correlations between the assemblages' close to Cape Tres Puntas and environmental variables, it should be considered that benthic environment was particularly different in this zone of the SJG. It was characterised by coarse sediments and low organic matter concentrations, and high temperatures, oxygen availability and chlorophyll *a* concentrations in the bottom water. These areas might present higher habitat complexity as a result of coarse sediments that promote the establishment of assemblages with higher diversity (Roux et al. 1995). Further studies should evaluate more accurately the composition of benthic assemblages in this region of the SJG.

Alternative biodiversity distribution modelling approaches are developed for other coastal ecosystems worldwide (Robinson et al. 2011). Several studies focused on the distributions of fish species to promote sustainable fisheries management (Valavanis et al. 2008, Maxwell et al. 2009), on cetacean-habitat models to improve the understanding on ecological dynamics (Redfern et al. 2006). Results from models allow to determine zones with particular interest for conservation or to identify indicator species in assemblages for monitoring (Moritz et al. 2013, Sswat et al. 2015). In turn, models can be used to predict climate change impacts on habitats and biodiversity distribution (Poloczanska et al. 2008). Usually, developed models assume that physical environment exerts a strong control. Robinson et al. (2011) proposed to consider in future studies ecological characteristics, like dispersal, species interactions, ontogenetic shifts and aggregations of individuals as important ecological factors that also determine biodiversity distribution. In addition, it could be considered to integrate habitat data across multiple spatial and temporal scales, for example considering seasonal variations for SJG ecosystem (Fernández et al. 2005), to improve predictions on models. Accounting for these factors will result in more robust models SJG benthic biodiversity.

RELATION BETWEEN SPECIES RICHNESS AND FUNCTIONAL GROUPS RICHNESS

It was observed in the local diversity regression that functional groups richness increased linearly with species richness. The estimation of this function is a wide debate for ecologists (Bolam et al. 2002, Cadotte et al. 2011, Törnroos et al 2015). It is related with the niche theory, where the niche space separation allows the coexistence through lack of competition for similar resources (Hutchinson 1957). Rosenfeld (2002) proposed that functional diversity is the distribution of species in a space where the axes are functional features (Mouchet et al. 2010). In addition, as more functional traits are considered, the redundancy between species is less likely (Petchey and Gaston 2002), so the addition of species is accompanied by an increase in the probability of species with another combination of functional traits (Mouchet et al. 2010). The covariance between species richness and functional diversity is still a challenge for ecologists to interpret. Particularly, some of the questions are if species and functional groups richness can be considered a proxy for functional diversity (Cadotte et al. 2011), and if functional diversity can be a predictor for ecosystem functioning (Petchey and Gaston 2006). In turn, the relation between species richness and functional diversity is expected to change through environmental gradient (Naeem & Wright 2003, Cadotte et al. 2011).

Functional diversity still presents several limitations in the estimation, specially because available information to classify taxa is usually not enough to represent accurately functional traits for species. Additionally, it considers that species within functional groups are identical and redundant while species from different functional groups are equally different (Petchey et al. 2004). Recently, biodiversity-ecosystem function studies have manipulated species richness to deduced changes in functional diversity and in ecosystem processes (Mokany et al. 2016). Further studies in SJG could also focus to asses the performance of complementary methods to calculate functional diversity. These results will be very useful to improve predictive models on biodiversity-ecosystem functioning in the SJG.

1.7 CONCLUSION

San Jorge Gulf benthic biodiversity distribution model identified spatial patterns in benthic assemblages' distribution that are highly associated with benthic environment characteristics. We demonstrated the presence of epifauna taxonomic and functional assemblages strongly correlated with organic matter concentrations in sediments and oxygen availability on bottom water. Among the environmental variables, bottom current velocities were included in biodiversity analyses for the first time in this coastal ecosystem. Even though the classification of functional groups might be improved in the future with local information, this was the first study to classify and analyse benthic biodiversity structure considering functional groups. The perspective of preserving ecosystem functioning could be incorporated to biodiversity and habitat efforts to manage and conserve the ecosystem services provided by the San Jorge Gulf ecosystem.

CONCLUSION GÉNÉRALE

L’objectif générale de ce mémoire était de caractériser la distribution spatiale de la biodiversité benthique du golfe San Jorge, situé dans le plateau continental d'Argentine. Les résultats de cette étude montrent la présence des assemblages taxonomiques et fonctionnels pour l’épifaune qui sont fortement corrélés avec la disponibilité d’oxygène et les concentrations de matière organique dans les sédiments, contrairement à notre première hypothèse. La recherche des assemblages a permis d’identifier des espèces et des groupes fonctionnels caractéristiques pour chacun des assemblages. Notamment, notre modèle de distribution de la biodiversité benthique prédit des hautes probabilités de présence des opportunistes rampant et déposivores de subsurface creuseur dans la région centrale du golfe, corrélés avec des concentrations de matière organique plus élevées. Ensuite, notre modèle prédit la présence de déposivores de subsurface, suspensivores sessile ou creuseur dans le nord, près de l’embouchure et dans les côtes, associés avec basses concentrations d’oxygène et de matière organique. Contrairement à notre deuxième hypothèse, les analyses de diversité ont reconnu une richesse plus élevée des espèces et de groups fonctionnels dans cet assemblage, qui peut être identifié comme un *hotspots* de biodiversité benthique dans le SJG. Dans le cas de l'endofaune, aucun modèle spatial n'a été identifié, probablement en raison de l'effort d'échantillonnage.

CONTRIBUTIONS DE L'ÉTUDE

La présente étude a permis d'ajouter des données de variables physico-chimiques de l'environnement benthique de l'année 2014, principalement dans l'embouchure du SJG, au modèle de Fernández et al. (2003, 2005). En plus, des données de vitesse de courants de fond ont été traitées pour la première fois dans le cadre des analyses de biodiversité à l'échelle du golfe. Ce mémoire apporte également la première classification des espèces d'endofaune et d'épifaune selon une panoplie de traits fonctionnels. En plus, cet étude a inclue pour la première fois des données avec la composition d'endofaune qui ont été analysé en considérant la distribution spatiale et des relations avec l'environnement benthique.

Finalement, les analyses sur la distribution spatial de la biodiversité ont permis l'élaboration des cartes avec les habitats préférentiels pour l'épifaune. Ces modèles permettent de prédire la distribution des espèces et des groupes fonctionnels dans le SJG, en particulier selon la disponibilité d'oxygène dans l'eau de fond et les concentrations de la matière organique dans les sédiments. Cet information pourrait être utilisée pour surveiller des changements dans l'écosystème, par exemple liés avec les impacts des activités anthropiques, sur la composition et l'abondance dans les assemblages.

LIMITATIONS DE L'ÉTUDE

Cependant, il y a des limitations dans notre étude liées avec les méthodes d'échantillonnage et le traitement de données. Tout d'abord, les différences dans la distribution des stations a interdit la possibilité d'explorer un modèle de distribution de la biodiversité benthique avec de données d'endofaune et d'épifaune ensemble. Ensuite, l'effort d'échantillonnage d'endofaune a été très faible ce qui a fortement déterminé la puissance statistique des analyses. Notamment, la région centrale et la région près de promontoires ont été moins représentés dans ces données. En plus, le manque d'information locale sur les traits fonctionnels des espèces a déterminé la classification avec d'information décrite pour les espèces dans des autres écosystèmes.

PERSPECTIVES

À l'avenir, les études dans le SJG pourraient approfondir la description sur la complexité des habitats benthiques (Brown et al. 2012). Particulièrement pour décrire avec une résolution spatiale plus élevée la présence des structures physiques et des changements dans la topographie qui favorisent l'hétérogénéité des habitats disponibles pour la biodiversité (Archambault et al. 1998, 1999, Archambault and Bourget 1999). En plus, la description de variations saisonnières dans l'environnement benthique, spécialement liées avec la matière organique, pourrait permettre de comprendre l'importance des apports pélagiques dans les réseaux trophiques dans le SJG, principalement dans les zones de fronts (Glembocki et al. 2015) et dans les zones avec une forte pression de la pêche (Góngora et al. 2012). En considérant la présence des variations saisonnières dans l'environnement benthique décrites par Fernández et al. (2005), nous proposons que la composition des assemblages puisse varier selon la période de l'année.

Des futures études sur la diversité des organismes benthiques pourraient porter sur l'intégration des données d'épifaune et d'endofaune pour les mêmes coordonnées (ou stations) pour identifier des assemblages. Des données pour la diversité des organismes de la meiofaune, pas disponible pour cet étude, pourraient être ajouter. Finalement, des stations d'échantillonnage pourraient être choisies pour mieux comprendre la transition entre les côtes et les zones les plus profondes.

La classification des traits fonctionnels pourrait être améliorée dans le futur avec d'information pour les populations locales dans le SJG, qui incluent également l'ontogenèse et les variations phénotypiques, les stratégies de dispersion, les processus dépendant de la densité, les interactions trophiques et l'information sur les processus biogéochimiques (Duffy et al. 2007, Gamfeldt et al. 2015, Robinson et al. 2011). Par exemple, la présence d'espèces envahissantes, car le crabe vert *Carcinus maenas* (Vinuesa 2007) ou le *Pleurobranchaea maculata* (Farias et al. 2016) devrait être analysé compte tenu de leurs effets potentiels sur la dynamique de l'écosystème benthique. De plus, il reste encore à explorer en profondeur comment la diversité d'espèces favorise la provision d'un ensemble de processus écosystémiques simultanés, définie comme la *multifonctionnalité*, et comment la perte de la biodiversité peut modifier les fonctions écosystémiques (Byrnes et al. 2014).

Il serait intéressant d'explorer des autres alternatives pour décrire la diversité fonctionnelle dans le SJG (Petchey and Gaston 2006, Mouchet et al. 2010, Cadotte et al. 2011), par exemple à partir d'intégrer des études expérimentales et observationnelles (Hector et al. 2007). Des expériences sur comment la modification de la richesse taxonomique ou la richesse fonctionnelle affect des processus écosystémiques pourraient se développer (Worm et al. 2006, Stachowicz et al. 2007, Törnroos et al 2015). Ces études pourraient considérer différents niveaux trophiques pour déterminer des effets de cascades trophiques dans la dynamique d'utilisation de ressources et l'importance relative des contrôles *top-down* et *bottom-up* (Bremner et al. 2003, Cardinale et al. 2006, Gamfeldt et al. 2015).

Également, il serait intéressant de mesurer de processus écosystémiques liés avec la productivité et les cycles biogéochimiques, la stabilité et la résilience dans le SJG (en suivant Gamfeldt et al. 2015, Mokany et al. 2016) pour améliorer la compréhension de la relation entre la biodiversité et le fonctionnement. Des études pourraient mesurer par exemple le taux de dégradation de la matière organique, le taux de production d'oxygène, le taux de production de biomasse o la consommation de ressources (Norling et al. 2007, Link et al. 2013b). Ces flux doivent être étudiés en fonction de différentes échelles spatio-temporelles (Lecours et al. 2015).

Finalement, le modèle de distribution de la biodiversité pourrait aussi considérer des informations permettant de décrire les impacts des activités anthropiques, par exemple de la pêche au chalut ou l'apport de matière organique qui arrivent des captures accidentelles, des activités liées à l'extraction du pétrole et du gaz, des effluents côtiers. Ces activités pourraient être incorporées dans la zonation pour mieux décrire leurs effets sur la complexité des habitats benthiques et améliorer les stratégies de gestion. De plus, l'identification des espèces clés dans les assemblages pourrait être utilisée pour la surveillance de changements dans les assemblages benthiques.

ANNEXES

Table S1 : Geographical coordinates for stations.

Longitude	Latitude	Station	Depth (m)
-67.17	-46.67	64	31
-66.83	-46.83	65	66
-66.67	-46.67	66	80
-67	-46.5	67	40
-67.33	-46.33	68	83
-67.17	-46.17	69	86
-66.83	-46.33	70	87
-66.51	-46.5	71	92
-66.16	-46.67	72	75
-66.33	-46.84	73	58
-66.5	-47	74	21
-66.03	-47	75	53
-65.84	-46.83	76	36
-66	-46.5	77	89
-66.34	-46.33	78	93
-66.66	-46.17	79	89
-67.02	-46.01	80	88
-66.84	-45.83	84	86
-66.5	-46	85	92
-66.17	-46.17	86	95
-65.83	-46.34	87	91
-65.83	-45.83	88	92
-66.16	-45.67	89	91
-66.5	-45.5	90	87
-66.16	-45.17	91	69
-65.83	-45.34	92	87
-66.92	-46.59	G1	88
-66.87	-45.5	G4	90
-66.18	-45.2	G5	73
-66.2	-45.46	G6	90
-66.2	-45.83	G7	100
-66.21	-46.65	G9	85
-66.21	-46.94	G10	39
-65.43	-46.63	G12	86
-65.42	-46.27	G13	89
-65.42	-45.82	G14	85
-65.4	-45.49	G15	99
-65.44	-45.16	G16	86
-65.62	-45.94	SF	89

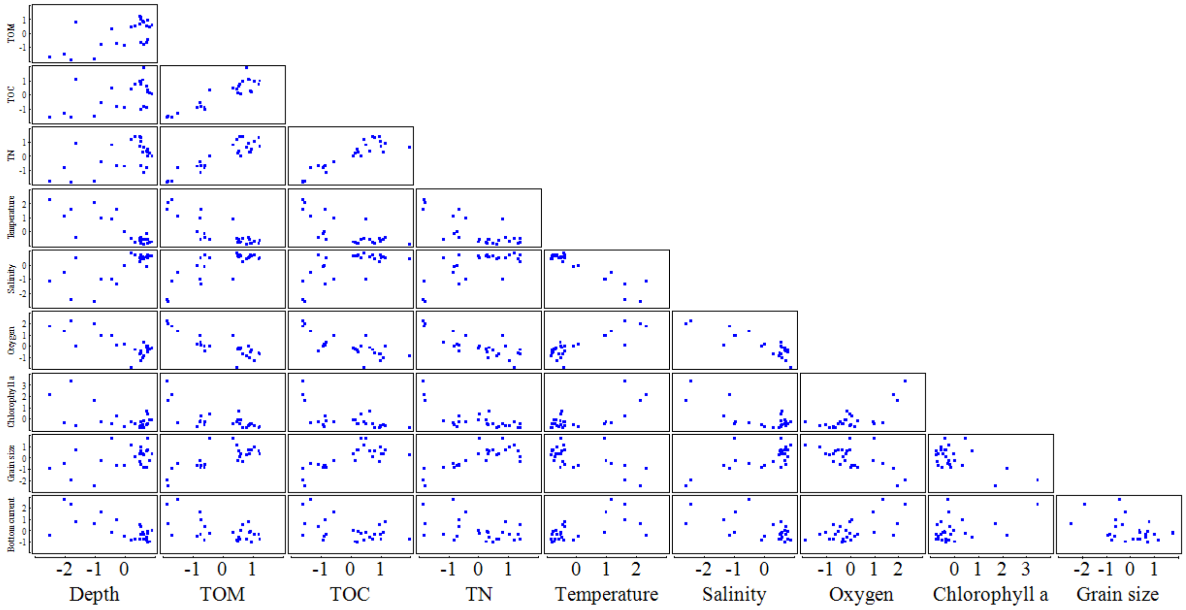

Figure S1. Draftman plot for INIDEP environmental variables.

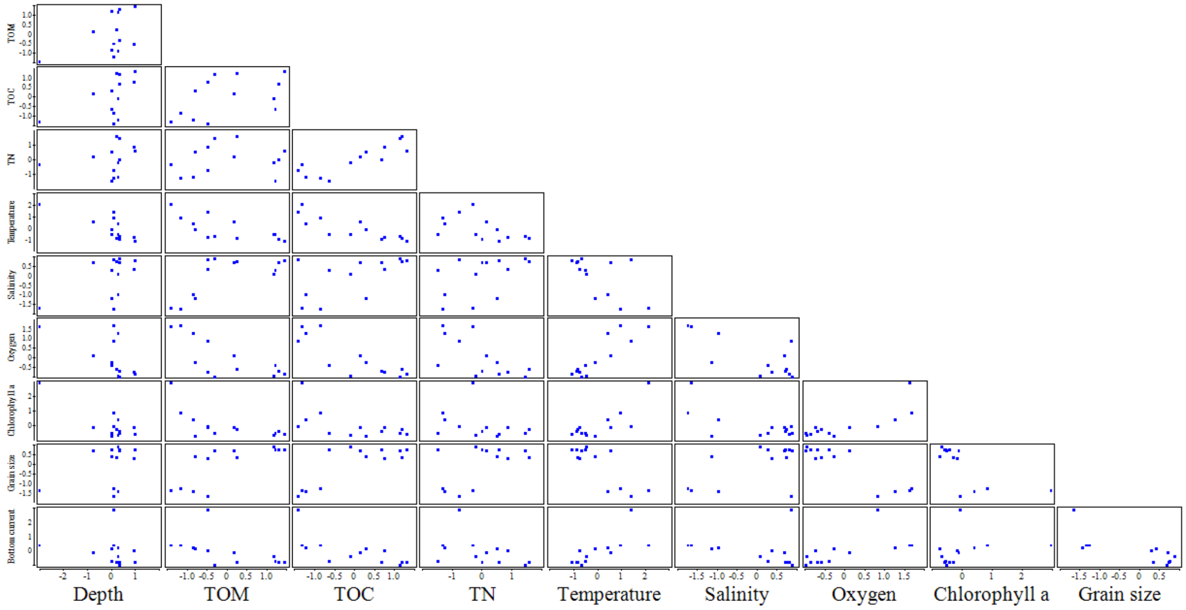

Figure S2. Draftman plot for MARES environmental variables.

Table S2. List of taxa in epifauna and infauna data.

Taxa	**Epifauna**	**Infauna**
Eunicidae	x	
Lumbrineridae	x	x
Onuphidae		x
Glyceridae	x	x
Nereididae		x
Polynoidae	x	x
Sigalionidae	x	
Pectinariidae	x	x
Terebellidae		x
Echiurida	x	x
Maldanidae	x	x
Orbiniidae		x
Amphipoda indet 1	x	x
Amphipoda indet 2		x
Gammarus sp.	x	
Alpheus puapeba	x	
Notiax brachyophthalma	x	x
Munida gregaria	x	
Lithodes santolla	x	
Austropandalus grayi	x	
Peisos petrunkevitchi	x	
Peltarion spinulosum	x	
Cirolana sp.	x	
Pterygosquilla armata armata	x	x
Scalpellidae	x	
Terebratella dorsata	x	
Bryozoa indet		x
Smittipora sp.		x
Priapulida	x	
Molgula sp. indet 1	x	
Boltenia sp.	x	
Myxine australis		x
Actinostolla crassicornis	x	
Edwardsia sp.	x	

Peachia sp.	x	
Renilla sp.	x	
Stylatula sp.		x
Diplasterias brandti	x	
Ctenodiscus australis	x	
Arbacia dufresnii	x	
Pseudechinus magellanicus	x	
Tripylaster philippii	x	x
Holothuroidea indet		x
Hemioedema spectabilis	x	
Ophiactis asperula	x	
Ophiura sp.	x	
Mytilus edulis	x	
Malletia cumingii	x	
Neilonella sulculata	x	x
Ennucula puelcha	x	x
Zygochlamys patagonica	x	
Pandora cistula	x	
Pitar rostratus	x	x
Semirossia tenera	x	
Carolesia blakei	x	
Odontocymbiola magellanica	x	
Calyptraea pileolus	x	
Falsilunatia patagonica	x	
Notocochlis isabelleana	x	
Marionia cucullata	x	
Nemertinos indet	x	

Table S3. Composition of taxonomic epifauna assemblages.

	Taxonomic epifauna assemblages			
Epifauna Taxa	a	b	c	d
Eunicidae				x
Lumbrineridae			x	x
Glyceridae		x		
Polynoidae				x
Sigalionidae			x	x
Pectinariidae			x	x
Echiurida	x	x	x	x
Maldanidae			x	x
Amphipoda indet 1				x
Gammarus sp.		x	x	
Alpheus puapeba		x		x
Notiax brachyophthalma			x	x
Munida gregaria			x	x
Lithodes santolla		x		x
Austropandalus grayi		x	x	x
Peisos petrunkevitchi			x	x
Peltarion spinulosum			x	x
Cirolana sp.		x		x
Pterygosquilla armata armata			x	x
Scalpellidae		x		
Terebratella dorsata		x		
Priapulida			x	
Molgula sp indet 1		x	x	x
Boltenia sp.		x		
Actinostolla crassicornis		x		x
Edwardsia sp.			x	x
Peachia sp.		x	x	x
Renilla sp.	x		x	x
Diplasterias brandti		x		x
Ctenodiscus australis		x		
Arbacia dufresnii		x		x
Pseudechinus magellanicus		x	x	x
Tripylaster philippii		x	x	x

Hemioedema spectabilis	x		
Ophiactis asperula	x		x
Ophiura sp.		x	x
Mytilus edulis	x		
Malletia cumingii		x	x
Neilonella sulculata			x
Ennucula puelcha		x	x
Zygochlamys patagonica		x	
Pandora cistula			x
Pitar rostratus			x
Semirossia tenera	x	x	x
Carolesia blakei	x		
Odontocymbiola magellanica			x
Calyptraea pileolus	x		
Falsilunatia patagonica			x
Notocochlis isabelleana			x
Marionia cucullata		x	x
Nemertinos indet.	x		

Table S4. Contributions from SIMPER analyses on taxonomic epifauna assemblages.

Assemblage c Average similarity = 41.22

Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Pseudechinus magellanicus	2.41	21.64	1.14	52.52	52.52
Munida gregaria	0.94	9.93	0.94	24.1	76.61
Pectinariidae	0.34	3.54	0.91	8.6	85.21
Notiax brachyophthalma	0.16	1.23	0.58	3	88.21
Pterygosquilla armata armata	0.08	1.02	0.95	2.47	90.68

Assemblage d Average similarity = 34.15

Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Neilonella sulculata	2.41	11.33	1	33.16	33.16
Ennucula puelcha	1.28	8.69	1.19	25.44	58.61
Molgula sp. indet 1	0.82	2.88	0.49	8.42	67.03
Munida gregaria	0.35	2.85	0.84	8.35	75.39
Pterygosquilla armata armata	0.39	2.72	1.55	7.97	83.35
Pandora cistula	0.24	1.04	0.63	3.04	86.39
Notiax brachyophthalma	0.19	0.77	0.45	2.26	88.65
Peachia sp.	0.09	0.63	0.52	1.84	90.49

Assemblage a

Less than 2 samples in group

Assemblage b Average similarity = 23.29

Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Diplasterias brandti	1.16	6.48	#######	27.82	27.82
Austropandalus grayi	1.7	5.56	#######	23.88	51.7
Cirolana sp.	0.37	2.97	#######	12.76	64.46
Hemioedema spectabilis	0.3	2.65	#######	11.39	75.85
Carolesia blakei	0.31	2.65	#######	11.39	87.24
Boltenia sp.	0.17	1.49	#######	6.38	93.62

Assemblages c & d Average dissimilarity = 87.00

	Group c	Group d				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Pseudechinus magellanicus	2.41	0.03	18.46	1.24	21.22	21.22
Neilonella sulculata	0	2.41	16.86	1.16	19.37	40.59
Ennucula puelcha	0.06	1.28	8.73	1.68	10.03	50.63
Munida gregaria	0.94	0.35	6.99	0.92	8.03	58.66
Molgula sp indet 1	0.02	0.82	6.44	0.85	7.4	66.06
Ophiura sp.	0.13	0.96	4.01	0.48	4.61	70.66
Pectinariidae	0.34	0.29	3.53	1.12	4.05	74.72
Pterygosquilla armata armata	0.08	0.39	2.3	1.09	2.65	77.37
Maldanidae	0.1	0.33	2.09	0.89	2.41	79.77
Pandora cistula	0	0.24	1.95	0.84	2.24	82.01
Notiax brachyophthalma	0.16	0.19	1.83	1.04	2.11	84.12
Sigalionidae	0.11	0.23	1.57	1.16	1.81	85.93
Austropandalus grayi	0.12	0.07	1.36	0.66	1.56	87.49
Renilla sp.	0.03	0.18	1.36	0.86	1.56	89.05
Edwardsia sp.	0.06	0.22	1.12	0.64	1.28	90.33

Assemblages c & a Average dissimilarity = 96.73

	Group c	Group a				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Pseudechinus magellanicus	2.41	0	31.28	1.55	32.34	32.34
Renilla sp.	0.03	1.41	23.48	2.83	24.27	56.61
Munida gregaria	0.94	0	15.29	1.03	15.81	72.42
Pectinariidae	0.34	0	5.48	1.04	5.66	78.08
Echiurida	0.07	0.27	3.48	1.69	3.6	81.68
Notiax brachyophthalma	0.16	0	2.44	0.9	2.52	84.2
Austropandalus grayi	0.12	0	2.24	0.53	2.32	86.52
Ophiura sp.	0.13	0	2	0.34	2.07	88.59
Sigalionidae	0.11	0	1.83	0.95	1.89	90.48

Assemblages d & a Average dissimilarity = 95.91

	Group d	Group a				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Neilonella sulculata	2.41	0	21.83	1.16	22.77	22.77
Renilla sp.	0.18	1.41	16.86	1.8	17.58	40.35
Ennucula puelcha	1.28	0	12.31	1.79	12.84	53.19
Molgula sp indet 1	0.82	0	8.63	0.83	8.99	62.18
Munida gregaria	0.35	0	4.74	1.1	4.94	67.12
Pterygosquilla armata armata	0.39	0	4.09	1.43	4.26	71.38
Ophiura sp.	0.96	0	3.35	0.36	3.5	74.88
Echiurida	0.05	0.27	3.07	1.64	3.2	78.08
Pandora cistula	0.24	0	2.62	0.8	2.73	80.82
Maldanidae	0.33	0	2.41	0.66	2.52	83.33
Notiax brachyophthalma	0.19	0	2.18	0.73	2.27	85.6
Peisos petrunkevitchi	0.06	0	1.35	0.33	1.41	87.01
Peachia sp.	0.09	0	1.33	0.87	1.38	88.39
Sigalionidae	0.23	0	1.31	0.71	1.36	89.76
Malletia cumingii	0.14	0	1.16	1.11	1.21	90.97

Assemblages c & b Average dissimilarity = 92.92

	Group c	Group b				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Pseudechinus magellanicus	2.41	0.31	15.81	1.22	17.01	17.01
Austropandalus grayi	0.12	1.7	10.69	1.52	11.5	28.52
Diplasterias brandti	0	1.16	8.3	2.8	8.94	37.45
Mytilus edulis	0	0.75	7.86	0.94	8.46	45.92
Munida gregaria	0.94	0	7.74	1.01	8.33	54.24
Molgula sp. indet 1	0.02	0.68	4.26	1.02	4.59	58.83
Alpheus puapeba	0	0.47	2.89	0.97	3.11	61.94
Cirolana sp.	0	0.37	2.83	5.24	3.05	64.99
Carolesia blakei	0	0.31	2.75	1.77	2.96	67.95
Pectinariidae	0.34	0	2.73	1.04	2.94	70.89
Hemioedema spectabilis	0	0.3	2.65	1.83	2.85	73.74
Ophiactis asperula	0	0.31	1.93	0.97	2.07	75.81
Lithodes santolla	0	0.29	1.8	0.97	1.94	77.75
Echiurida	0.07	0.18	1.71	1.05	1.84	79.59
Terebratella dorsata	0	0.22	1.36	0.97	1.47	81.06

Arbacia dufresnii	0	0.22	1.36	0.97	1.47	82.52
Boltenia sp.	0	0.17	1.34	5.55	1.44	83.96
Notiax brachyophthalma	0.16	0	1.25	0.91	1.35	85.31
Ophiura sp.	0.13	0	1.05	0.33	1.12	86.43
Peachia sp.	0.05	0.11	1	1.13	1.08	87.51
Nemertinos indet.	0	0.09	0.93	0.94	1	88.51
Tripylaster philippii	0	0.09	0.91	0.97	0.98	89.49
Sigalionidae	0.11	0	0.91	0.92	0.97	90.47

Assemblages d & b Average dissimilarity = 93.50

	Group d	**Group b**				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Neilonella sulculata	2.41	0	13.56	1.1	14.5	14.5
Austropandalus grayi	0.07	1.7	9.33	1.37	9.98	24.48
Ennucula puelcha	1.28	0	7.09	1.67	7.59	32.07
Diplasterias brandti	0.02	1.16	6.96	2.13	7.45	39.52
Mytilus edulis	0	0.75	6.46	0.87	6.91	46.42
Molgula sp. indet 1	0.82	0.68	5.93	1.04	6.34	52.77
Ophiura sp.	0.96	0	2.69	0.36	2.88	55.65
Munida gregaria	0.35	0	2.53	1.14	2.7	58.35
Alpheus puapeba	0.01	0.47	2.53	0.94	2.7	61.05
Pterygosquilla armata armata	0.39	0	2.32	1.37	2.48	63.53
Cirolana sp.	0.01	0.37	2.31	2.88	2.47	66
Carolesia blakei	0	0.31	2.29	1.58	2.45	68.46
Hemioedema spectabilis	0	0.3	2.21	1.63	2.36	70.82
Pseudechinus magellanicus	0.03	0.31	1.74	1.73	1.87	72.68
Ophiactis asperula	0.01	0.31	1.69	0.96	1.81	74.49
Lithodes santolla	0.01	0.29	1.59	0.98	1.7	76.19
Pandora cistula	0.24	0	1.52	0.82	1.63	77.82
Maldanidae	0.33	0	1.49	0.68	1.59	79.41
Echiurida	0.05	0.18	1.47	0.93	1.58	80.99
Notiax brachyophthalma	0.19	0	1.21	0.77	1.29	82.28
Arbacia dufresnii	0.01	0.22	1.19	0.95	1.28	83.56
Terebratella dorsata	0	0.22	1.18	0.92	1.27	84.82
Boltenia sp.	0	0.17	1.13	3.2	1.21	86.03
Renilla sp.	0.18	0	0.97	0.78	1.04	87.07
Sigalionidae	0.23	0	0.9	0.66	0.97	88.04

Pectinariidae	0.29	0	0.84	0.4	0.9	88.94
Peachia sp.	0.09	0.11	0.79	1.11	0.85	89.79
Nemertinos indet.	0	0.09	0.76	0.87	0.81	90.6

Assemblages a & b Average dissimilarity = 96.04

Species	**Group a** **Av.Abund**	**Group b** **Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Renilla sp.	1.41	0	15.77	2.15	16.42	16.42
Austropandalus grayi	0	1.7	14.48	1.35	15.07	31.49
Mytilus edulis	0	0.75	11.08	0.71	11.54	43.03
Diplasterias brandti	0	1.16	10.67	2.88	11.11	54.14
Molgula sp. indet 1	0	0.68	5.12	0.71	5.33	59.47
Carolesia blakei	0	0.31	3.75	1.27	3.91	63.38
Cirolana sp.	0	0.37	3.7	240.05	3.86	67.24
Hemioedema spectabilis	0	0.3	3.6	1.31	3.75	70.99
Alpheus puapeba	0	0.47	3.52	0.71	3.67	74.66
Pseudechinus magellanicus	0	0.31	2.78	2.1	2.9	77.55
Ophiactis asperula	0	0.31	2.35	0.71	2.45	80
Lithodes santolla	0	0.29	2.2	0.71	2.29	82.29
Boltenia sp.	0	0.17	1.75	13.39	1.83	84.11
Terebratella dorsata	0	0.22	1.66	0.71	1.73	85.84
Arbacia dufresnii	0	0.22	1.66	0.71	1.73	87.57
Echiurida	0.27	0.18	1.63	3.13	1.7	89.27
Peachia sp.	0	0.11	1.6	0.71	1.67	90.94

Table S5: Taxa classified by functional traits.

Feeding habit	**Size**	**Mobility**	**Adult life**	**Bioturbation**
S :Deposit subsurface feeder	S :0,5 mm < Little < 5 mm	S :Sessile	B :Burrow	B :Active burrower (diffusive)
D :Deposit surface feeder	M :5 mm < Medium <10 mm	H :Hemimobile	C :Crawl	G :Gallery burrower
A :Deposit surface and subsurface feeder	L :10 mm < Large < 50 mm	M :Mobile	S :Sessile	S :Surface dweller
F :Filter/suspension feeder	X :X-Large > 50 mm		W :Swim	T :Tube burrow
O :Opportunist				
P :Predator				
H :Herbivores				

Taxa	**Feeding habit**	**Size**	**Mobility**	**Adult life habit**	**Bioturbation**	**Functional groups**
Eunicidae	O	X	H	C.B	T	OXHC.BT
Lumbrineridae	O	M	M	B	T	OMMBT
Onuphidae	P	L	M	C	T	PLMCT
Glyceridae	O	X	M	B	G	OXMBG
Nereididae	P	X	M	B	T	PXMBT
Polynoidae	P	M	M	B	B	PMMBB
Sigalionidae	P	M	M	B	B	PMMBB
Pectinariidae	S	L	S	B	T	SLSBT
Terebellidae	D	M	S	B	T	DMSBT
Echiurida	A	S	H	B	B	ASHBB
Maldanidae	S	M	H	B	T	SMHBT
Orbiniidae	S	M	M	B	B	SMMBB
Amphipoda indet 1	O	L	M	C.W	S	OLMC.WS
Amphipoda indet 2	O	L	M	C.W	S	OLMC.WS
Gammarus sp	P	M	M	C.W	S	PMMC.WS
Alpheus puapeba	P	L	M	C	S	PLMCS
Notiax brachyophthalma	D	X	M	B	G	DXMBG
Munida gregaria	O	X	M	C.W	S	OXMC.WS
Lithodes santolla	O	X	M	C	S	OXMCS
Austropandalus grayi	P	L	M	W	S	PLMWS
Peisos petrunkevitchi	F	L	M	W	S	FLMWS
Peltarion spinulosum	D.O	X	M	C	S	D.OXMCS
Cirolana sp	O	M	M	W	B	OMMWB
Pterygosquilla armata armata	P	X	M	C	B	PXMCB

Scalpellidae	F	M	S	S	S	FMSSS
Terebratella dorsata	F	L	S	S	S	FLSSS
Bryozoa indet	F	X	S	S	S	FXSSS
Smittipora sp	F	L	S	S	S	FLSSS
Priapulida	P	X	H	B	B	PXHBB
Molgula sp indet 1	F	X	S	S	S	FXSSS
Boltenia sp	F	L	S	S	S	FLSSS
Myxine australis	P	X	M	C.W	S	PXMC.WS
Actinostolla crassicornis	P	X	S	S	S	PXSSS
Edwardsia sp	F	X	H	S	S	FXHSS
Peachia sp	F	X	H	B	B	FXHBB
Renilla sp	F	X	S	S	S	FXSSS
Stylatula sp	F	X	S	S	S	FXSSS
Diplasterias brandti	P	X	M	C	S	PXMCS
Ctenodiscus australis	D.P	L	M	C	S	D.PLMCS
Arbacia dufresnii	O	X	M	C	S	OXMCS
Pseudechinus magellanicus	O	X	M	C	S	OXMCS
Tripylaster philippii	S	L	M	B	S	SLMBS
Holothuroidea indet	D.F	X	M	C	B	D.FXMCB
Hemioedema spectabilis	D	X	M	C.B	B	DXMC.BB
Ophiactis asperula	F	L	M	C	S	FLMCS
Ophiura sp	O	L	M	C	S	OLMCS
Mytilus edulis	F	X	S	S	S	FXSSS
Malletia cumingii	S	L	S	B	B	SLSBB
Neilonella sulculata	S.F	L	M	B	B	S.FLMBB
Ennucula puelcha	S.F	L	S	B	B	S.FLSBB
Zygochlamys patagonica	F	X	S	S	S	FXSSS
Pandora cistula	F	L	M	B	B	FLMBB
Pitar rostratus	F	L	M	B	B	FLMBB
Semirossia tenera	P	X	M	W	S	PXMWS
Carolesia blakei	P	L	M	C	S	PLMCS
Odontocymbiola magellanica	P	X	M	C	S	PXMCS
Calyptraea pileolus	F	L	H	C	S	FLHCS
Falsilunatia patagonica	P	L	M	C	B	PLMCB
Notocochlis isabelleana	P	L	M	C	B	PLMCB
Marionia cucullata	P	X	M	C	S	PXMCS
Nemertinos indet	P	X	M	C	S	PXMCS

Table S6. Composition of functional epifauna assemblages.

Feeding habit	**Size**	**Mobility**	**Adult life**	**Bioturbation**
S :Deposit subsurface feeder	S :0,5 mm < Little < 5 mm	S :Sessile	B :Burrow	B :Active burrower (diffusive)
D :Deposit surface feeder	M :5 mm < Medium <10 mm	H :Hemimobile	C :Crawl	G :Gallery burrower
A :Deposit surface and subsurface feeder	L :10 mm < Large < 50 mm	M :Mobile	S :Sessile	S :Surface dweller
F :Filter/suspension feeder	X :X-Large > 50 mm		W :Swim	T :Tube burrow
O :Opportunist				
P :Predator				
H :Herbivores				

	Functional epifauna assemblages			
Functional group	a	b	c	d
ASHBB		x	x	x
D.OXMCS			x	x
D.PLMCS		x		
DXMBG			x	x
DXMC.BB	x	x		
FLHCS	x			
FLMBB				x
FLMCS	x			x
FLMWS			x	x
FLSSS	x	x		
FMSSS		x		
FXHBB		x	x	x
FXHSS			x	x
FXSSS	x	x	x	x
OLMC.WS				x
OLMCS			x	x
OMMBT			x	x
OMMWB	x	x		x
OXHC.BT				x
OXMBG		x		
OXMC.WS			x	x
OXMCS	x	x	x	x
PLMCB				x

PLMCS	x	x		x
PLMWS	x	x	x	x
PMMBB			x	x
PMMC.WS	x		x	
PXHBB			x	
PXMCB			x	x
PXMCS	x	x	x	x
PXMWS	x		x	x
PXSSS	x			x
S.FLMBB				x
S.FLSBB			x	x
SLMBS		x	x	x
SLSBB			x	x
SLSBT			x	x
SMHBT			x	x

Table S7 : Contributions from SIMPER analyses on epifauna functional assemblages (please see Table S4 for functional traits abbreviations).

Assemblage c Average similarity = 41.52

Functional group	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
OXMCS	2.41	21.64	1.14	52.13	52.13
OXMC.WS	0.94	9.93	0.94	23.92	76.05
SLSBT	0.34	3.54	0.91	8.53	84.58
DXMBG	0.16	1.23	0.58	2.97	87.55
PXMCB	0.08	1.02	0.95	2.45	90.01

Assemblage d Average similarity = 36.51

Functional group	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
S.FLMBB	2.41	11.44	1.00	31.33	31.33
S.FLSBB	1.28	8.78	1.19	24.05	55.37
FXSSS	0.95	5.11	0.93	13.99	69.37
OXMC.WS	0.35	2.89	0.84	7.91	77.27
PXMCB	0.39	2.75	1.56	7.52	84.80
FLMBB	0.26	1.54	1.00	4.21	89.01
DXMBG	0.19	0.79	0.44	2.15	91.16

Assemblage a

Less than 2 samples in group

Assemblage b Average similarity = 50.97

Functional group	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
FXSSS	1.45	42.87	#######	84.11	84.11
ASHBB	0.31	8.10	#######	15.89	100.00

Assemblages c & d Average dissimilarity = 85.85

	Group c	**Group d**				
Functional group	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
OXMCS	2.41	0.04	18.49	1.24	21.53	21.53
S.FLMBB	0.00	2.41	16.97	1.16	19.77	41.30
S.FLSBB	0.06	1.28	8.78	1.67	10.23	51.53

FXSSS	0.10	0.95	7.09	1.02	8.26	59.79
OXMC.WS	0.94	0.35	7.03	0.92	8.19	67.98
OLMCS	0.13	0.96	4.03	0.48	4.70	72.67
SLSBT	0.34	0.29	3.55	1.12	4.13	76.81
PXMCB	0.08	0.39	2.31	1.10	2.70	79.50
FLMBB	0.00	0.26	2.19	0.97	2.55	82.05
SMHBT	0.10	0.33	2.11	0.88	2.46	84.51
DXMBG	0.16	0.19	1.85	1.04	2.15	86.66
PMMBB	0.11	0.23	1.58	1.17	1.84	88.50
PLMWS	0.12	0.07	1.37	0.66	1.60	90.10

Assemblages c & b Average dissimilarity = 92.81

	Group c	**Group b**				
Functional group	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
OXMCS	2.41	0.06	25.91	1.42	27.91	27.91
FXSSS	0.10	1.45	18.80	2.59	20.26	48.17
OXMC.WS	0.94	0.00	12.59	1.01	13.57	61.74
SLSBT	0.34	0.00	4.48	1.02	4.83	66.57
ASHBB	0.07	0.31	3.27	1.91	3.52	70.09
PLMWS	0.12	0.23	3.21	0.99	3.45	73.55
PXMCS	0.01	0.28	3.07	0.97	3.31	76.86
PLMCS	0.00	0.20	2.11	0.94	2.27	79.13
DXMBG	0.16	0.00	2.01	0.89	2.17	81.30
DXMC.BB	0.00	0.19	2.00	0.94	2.15	83.45
OLMCS	0.13	0.00	1.66	0.34	1.79	85.25
PMMBB	0.11	0.00	1.50	0.93	1.61	86.86
FXHBB	0.05	0.11	1.36	1.21	1.46	88.32
OMMWB	0.00	0.12	1.33	0.94	1.44	89.75
SMHBT	0.10	0.00	1.10	0.73	1.19	90.94

Assemblages d & b Average dissimilarity = 83.19

	Group d	**Group b**				
Functional group	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
S.FLMBB	2.41	0.00	19.24	1.15	23.13	23.13
FXSSS	0.95	1.45	11.00	1.45	13.22	36.35
S.FLSBB	1.28	0.00	10.58	1.74	12.71	49.07

OXMC.WS	0.35	0.00	3.98	1.11	4.79	53.85
PXMCB	0.39	0.00	3.49	1.41	4.20	58.05
OLMCS	0.96	0.00	3.18	0.36	3.82	61.87
ASHBB	0.05	0.31	2.94	1.86	3.54	65.41
PXMCS	0.04	0.28	2.58	0.98	3.10	68.51
FLMBB	0.26	0.00	2.54	0.95	3.05	71.56
PLMWS	0.07	0.23	2.24	1.25	2.69	74.25
SMHBT	0.33	0.00	2.12	0.67	2.55	76.80
DXMBG	0.19	0.00	1.86	0.74	2.24	79.04
PLMCS	0.01	0.20	1.76	0.91	2.11	81.15
DXMC.BB	0.00	0.19	1.65	0.87	1.98	83.13
FXHBB	0.09	0.11	1.21	1.01	1.46	84.59
PMMBB	0.23	0.00	1.21	0.72	1.45	86.05
OMMWB	0.01	0.12	1.13	0.94	1.35	87.40
FLMWS	0.06	0.00	1.07	0.33	1.28	88.68
SLSBB	0.14	0.00	1.01	1.12	1.21	89.89
SLSBT	0.29	0.00	1.00	0.41	1.20	91.09

Assemblage c & a Average dissimilarity = 87.67

	Group c	**Group a**				
Functional group	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
PLMWS	0.12	2.94	18.43	6.31	21.03	21.03
PXMCS	0.01	1.77	11.58	6.96	13.21	34.24
OXMCS	2.41	0.89	10.74	1.18	12.25	46.49
FXSSS	0.10	1.37	8.38	4.95	9.55	56.04
PLMCS	0.00	0.97	6.33	6.91	7.22	63.27
OXMC.WS	0.94	0.00	6.12	1.07	6.98	70.24
FLMCS	0.00	0.63	4.11	6.91	4.69	74.93
FLSSS	0.00	0.50	3.25	6.91	3.71	78.64
OMMWB	0.00	0.50	3.25	6.91	3.71	82.34
SLSBT	0.34	0.00	2.16	1.11	2.47	84.81
DXMC.BB	0.00	0.22	1.45	6.91	1.66	86.47
FLHCS	0.00	0.22	1.45	6.91	1.66	88.12
PXSSS	0.00	0.22	1.45	6.91	1.66	89.78
PMMC.WS	0.00	0.22	1.42	7.38	1.62	91.40

Assemblages d & a Average dissimilarity = 89.78

Functional group	Group d Av.Abund	Group a Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
PLMWS	0.07	2.94	16.29	3.68	18.15	18.15
S.FLMBB	2.41	0.00	11.54	1.10	12.86	31.01
PXMCS	0.04	1.77	9.87	3.48	10.99	41.99
S.FLSBB	1.28	0.00	5.93	1.69	6.60	48.60
PLMCS	0.01	0.97	5.44	3.61	6.06	54.66
FXSSS	0.95	1.37	5.40	1.69	6.02	60.67
OXMCS	0.04	0.89	4.83	3.35	5.38	66.05
FLMCS	0.01	0.63	3.50	3.57	3.90	69.95
FLSSS	0.00	0.50	2.82	3.61	3.14	73.09
OMMWB	0.01	0.50	2.74	3.51	3.06	76.15
OLMCS	0.96	0.00	2.51	0.34	2.80	78.95
OXMC.WS	0.35	0.00	2.05	1.19	2.29	81.23
PXMCB	0.39	0.00	1.93	1.40	2.15	83.38
FLMBB	0.26	0.00	1.40	0.99	1.56	84.93
SMHBT	0.33	0.00	1.27	0.68	1.42	86.35
DXMC.BB	0.00	0.22	1.26	3.61	1.40	87.76
FLHCS	0.00	0.22	1.26	3.61	1.40	89.16
PMMC.WS	0.00	0.22	1.26	3.61	1.40	90.57

Assemblages b & a Average dissimilarity = 66.36

Functional group	Group b Av.Abund	Group a Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
PLMWS	0.23	2.94	19.87	3.55	29.95	29.95
PXMCS	0.28	1.77	11.06	2.36	16.66	46.61
OXMCS	0.06	0.89	6.04	3.74	9.11	55.72
PLMCS	0.20	0.97	5.76	1.96	8.68	64.39
FLMCS	0.00	0.63	4.56	6.12	6.87	71.26
FLSSS	0.06	0.50	3.20	2.78	4.83	76.08
OMMWB	0.12	0.50	2.80	1.63	4.22	80.31
ASHBB	0.31	0.00	2.21	32.03	3.33	83.64
FLHCS	0.00	0.22	1.61	6.12	2.43	86.07
PMMC.WS	0.00	0.22	1.61	6.12	2.43	88.49
PXMWS	0.00	0.22	1.61	6.12	2.43	90.92

Table S8 : Contributions from SIMPER analyses on taxonomic infauna data.

Average similarity 22.68					
Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Neilonella sulculata	2.22	7.64	0.56	33.69	33.69
Notiax brachyophthalma	1.22	5.77	0.58	25.46	59.15
Maldanidae	1.16	3.91	0.43	17.23	76.38
Ennucula puelcha	1.18	2.71	0.48	11.94	88.32
Tripylaster philippii	0.37	0.71	0.2	3.12	91.44

Table S9 : Contributions from SIMPER analyses on functional infauna data.

Average similarity = 23.30					
Functional group	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
S.FLMBB	2.22	7.64	0.56	32.80	32.80
DXMBG	1.22	5.77	0.58	24.78	57.58
SMHBT	1.16	3.91	0.43	16.77	74.36
S.FLSBB	1.18	2.71	0.48	11.63	85.99
SLMBS	0.37	0.71	0.20	3.03	89.02
FXSSS	0.43	0.66	0.20	2.82	91.84

Table S10 : Number of taxa and functional groups by station for INIDEP and MARES data.

Station	**α taxonomic**	**α functional**
64	8	8
65	12	12
66	14	14
67	11	11
68	9	9
69	5	5
70	10	10
71	5	5
72	14	12
73	15	14
74	2	2
75	15	14
76	17	13
77	23	20
78	5	5
79	7	7
80	12	12
84	8	8
85	9	9
86	9	9
87	13	12
88	16	15
89	12	12
90	9	9
91	13	11
92	7	7
G1	3	3
G4	6	6
G5	5	5
G6	4	4
G7	5	5
G9	7	7
G10	7	7
G12	4	4
G13	4	4
G14	5	5
G15	2	2
G16	2	2
SF	5	5

RÉFÉRENCES BIBLIOGRAPHIQUES

Acha EM, Mianzan HW, Guerrero RA, Favero M, Bava J (2004) Marine fronts at the continental shelves of austral South America: physical and ecological processes. *Journal of Marine Systems* 44:83–105 doi:10.1016/j.jmarsys.2003.09.005

Akselman R (1996) Estudios ecológicos en el Golfo San Jorge y adyacencias (Atlántico sudoccidental). Distribución, abundancia y variación estacional del fitoplancton en relación a factores físico-químicos y la dinámica hidrológica. PhD thesis, Universidad de Buenos Aires, Buenos Aires, Argentina

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. Plymouth, UK: PRIMER-E Ltd

Anderson MJ, Crist TO, Chase JM, Vellend M, Inouye BD, Freestone AL, Sanders NJ, Cornell HV, Comita LS, Davies KF, Harrison SP, Kraft NJB, Stegen JC, Swenson NG (2011) Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters* 14(1):19-28 doi:10.1111/j.1461-0248.2010.01552.x

Archambault P, Bourget E (1996) Scales of coastal heterogeneity and benthic intertidal species richness, diversity and abundance. *Marine Ecology Progress Series* 136:111-121 doi:10.3354/meps136111

Archambault P, Roff JC, Bourget E, Bang B, Ingram RG (1998) Nearshore abundance of zooplankton in relation to shoreline configuration and mechanisms involved. *Journal of Plankton Research* 20:671-690

Archambault P, Bourget E (1999) The influence of shoreline configuration on spatial variation of meroplanktonic larvae, recruitment and diversity of benthic subtidal communities. *Journal of Experimental Marine Biology and Ecology* 238:163-186 (voir *erratum* dans vol. 241:309-333)

Archambault P, Bourget E, McKindsey CW (1999) Large-scale shoreline configuration influences phytoplankton concentration and mussel growth. *Estuarine Coastal and Shelf Science* 49:193-208.

Balvanera P, Pfisterer AB, Buchmann N, He JS, Nakashizuka T, Raffaelli D, Schmid B (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology letters* 9:1146–1156

Bianchi AA, Bianucci L, Piola AR, Pino DR, Schloss I, Poisson A, Balestrini CF (2005) Vertical stratification and air-sea CO2 fluxes in the Patagonian shelf. *Journal of Geophysical Research: Oceans* 110, C07003 doi:10.1029/2004JC002488

Bolam SG, Fernandes TF, Huxham M (2002) Diversity, biomass, and ecosystem processes in the marine benthos. *Ecological Monographs* 72(4):599-615 doi:10.1890/0012-9615(2002)072[0599:DBAEPI]2.0.CO;2

Bovcon ND, Góngora, ME, Marinao, C, González-Zevallos D (2013) Catches composition and discards generated by hake *Merluccius hubbsi* and shrimp *Pleoticus muelleri* fisheries: a case of study in the high-sea ice trawlers of San Jorge Gulf, Chubut, Argentina. *Revista de Biología Marina y Oceanografí*a 48(2):303–319 doi:10.4067/S0718-19572013000200010

Breitburg DL, Baxter JW, Hatfield CA, Howarth RW, Jones CG, Lovett GM, Wigand C (1998) Understanding effects of multiple stressors: ideas and challenges. In: Pace ML, Groffman PM (Eds) Successes, Limitations, and Frontiers in Ecosystem Science. Springer, New York, p 416–431

Bremner J, Rogers SI, Frid CLJ (2003) Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. *Marine Ecology Progress Series* 254:11-25 doi:10.3354/meps254011

Brogger MI, Gil DG, Rubilar T, Martinez MI, Díaz de Vivar ME, Escolar M, Epherra L, Pérez AF, Tablado A (2013) Echinoderms from Argentina: Biodiversity, distribution and current state of knowledge. In: Alvarado JJ, Solís-Marín FA (Eds) Echinoderm Research and Diversity in Latin America. Springer Berlin Heidelberg, p 359-402, chapter 11 doi:10.1007/978-3-642-20051-9_11

Brown CJ, Smith SJ, Lawton P, Anderson JT (2011) Benthic habitat mapping: a review of progress towards improved understanding of the spatial ecology of the seafloor using acoustic techniques. *Estuaries, Coastal and Shelf Sciences* 92:502−520 doi:10.1016/j.ecss.2011.02.007

Brown CJ, Sameoto JA, Smith SJ (2012) Multiple methods, maps, and management applications: purpose made seafloor maps in support of ocean management. *Journal of Sea Research* 72:1-13 doi:10.1016/j.seares.2012.04.009

Buchanan JB (1984) Sediment Analysis. In: Holme NA, McIntyre AD (Eds) Methods for the Study of Marine Benthos. Blackwell Scientific Publications, p 41–64

Byrnes JEK, Gamfeldt L, Isbell F, Lefcheck JS, Griffin JN, Hector A, Cardinale BJ, Hooper DU, Dee LE, Duffy JE (2014) Investigating the relationship between biodiversity and ecosystem multifunctionality: challenges and solutions. *Methods in Ecology and Evolution* 5:111-124 doi:10.1111/2041-210X.12143

Cadotte MW, Carscadden K, Mirotchnick, N (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of applied ecology* 48(5):1079-1087

Cardinale BJ, Srivastava DS, Duffy JE, Wright JP, Downing AL, Sankaran M, Jouseau C (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443(7114):989 doi:10.1038/nature05202

Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM, Tilman D, Wardle DA, Kinzig, AP, Daily GC, Loreau M, Grace JB, Larigauderie A, Srivastava DS, Naeem S (2012) Biodiversity loss and its impact on humanity. *Nature* 486(7401):59

Carvalho LRS, Loiola M, Barros F (2017) Manipulating habitat complexity to understand its influence on benthic macrofauna. *Journal of Experimental Marine Biology and Ecology* 489:48-57 doi:10.1016/j.jembe.2017.01.014

Chapin FS, Walker BH, Hobbs RJ, Hooper DU, Lawton JH, Sala OE, Tilman D (1997) Biotic control over the functioning of ecosystems. *Science* 277(5325):500-504 doi:10.1126/science.277.5325.500

Clarke KR, Gorley RN (2006) PRIMER v6: User manual/tutorial. Plymouth, UK: PRIMER-E Ltd. p 192

Commendatore MG, Esteves, JL (2007) An assessment of oil pollution in the coastal zone of Patagonia, Argentina. *Environmental Management* 40(5):814–821 doi:10.1007/s00267-005-0221-3

Cook R, Fariñas-Franco JM, Gell FR, Holt RHF, Holt T, Lindenbaum C, Porter JS, Seed R, Skates LR, Stringell TB, Sanderson WG (2013) The substantial first impact of bottom fishing on rare biodiversity hotspots: a dilemma for evidence-based conservation. *PloS one* 8(8): e69904 doi:10.1371/journal.pone.0069904

Copeland A, Edinger E, Devillers R, Bell T, LeBlanc P, Wroblewski J (2011) Marine habitat mapping in support of Marine Protected Area management in a subarctic fjord: Gilbert Bay, Labrador, Canada. *Journal of Coastal Conservation* 17(2):225-237 doi:10.1007/s11852-011-0172-1

Crain CM, Kroeker K, Halpern BS (2008) Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters* 11(12):1304-1315 doi:10.1111/j.1461-0248.2008.01253.x

Cucchi Colleoni D, Carreto JI (2001) Variación estacional de la biomasa fitoplanctónica en el Golfo San Jorge. Resultados de las campañas de investigación OB-01/00. OB-03/00, OB-07/00, OB-10/00 y OB-12/00. Inf Téc Int DNI-INIDEP, p 49-30

Cusson M, Archambault P, Aitken A (2007) Biodiversity of benthic assemblages on the Arctic continental shelf: historical data from Canada. *Marine Ecology Progress Series* 331:291-304

D'Amen M, Dubuis A, Fernandes RF, Pottier J, Pellissier L, Guisan A (2015) Using species richness and functional traits predictions to constrain assemblage predictions from stacked species distribution models. *Journal of biogeography* 42(7):1255-1266

Díaz S, Cabido M (2001) Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in ecology & evolution* 16(11):646-655

Duffy JE, Cardinale BJ, France KE, McIntyre PB, Thébault E, Loreau M (2007) The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters* 10(6):522-538 doi:10.1111/j.1461-0248.2007.01037.x

Duffy JE (2009) Why biodiversity is important to the functioning of real-world ecosystems. *Frontiers in Ecology and the Environment* 7(8):437-444 doi:10.1890/070195

Fainburg L, Trassens M, Bastida J, Farenga M, Isla F, Bastida R (2012) Nearshore benthic communities and bioengineers from the macrotidal San Jorge gulf: patagonia, Argentina. *Thalassas* 28(2):45-56

Farias NE, Wood SA, Obenat S, Schwindt E (2016) Genetic barcoding confirms the presence of the neurotoxic sea slug *Pleurobranchaea maculata* in southwestern Atlantic coast. *New Zealand Journal of Zoology* 43(3) 292-298 doi:10.1080/03014223.2016.1159582

Fernández M, Roux A, Fernández E, Caló J, Marcos A and Aldacur H (2003) Grain-size analysis of surficial sediments from Golfo San Jorge, Argentina. *Journal of the Marine Biological Association of the United Kingdom* 83:1193–1197 doi:10.1017/S0025315403008488

Fernández M, Carreto JI, Mora J and Roux A (2005) Physico-chemical characterization of the benthic environment of the Golfo San Jorge, Argentina. *Journal of the Marine Biological Association of the United Kingdom* 85:1317–1328 doi:10.4067/S0718-19572007000200005

Fernández M (2006) Características físico-químicas de los sedimentos del Golfo San Jorge y su relación con los organismos bentónicos del sector. PhD Thesis, Universidad Nacional de Mar del Plata, Argentina

Fernández M, Hernández D, Roux A (2007) Spatial distribution of the red shrimp *Pleoticus muelleri* (Bate, 1888) and its relationship with the environmental variables, San Jorge Gulf, Argentina. *Revista de Biología Marina y Oceanografía* 42(3):335–344 doi:10.4067/S0718-19572007000300012

Field JG, Clarke KR, Warwick RM (1982) A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series* 8:37–52

Gamfeldt L, Hillebrand H, Jonsson PR (2008) Multiple functions increase the importance of biodiversity for overall ecosystem functioning. *Ecology* 89:1223–1231

Gamfeldt L, Lefcheck JS, Byrnes JEK, Cardinale BJ, Duffy JE, Griffin JN (2015) Marine biodiversity and ecosystem functioning: what's known and what's next? *Oikos* 124:252-265 doi:10.1111/oik.01549

Glembocki NG, Williams GN, Góngora ME, Gagliardini DA, Orensanz JM (Lobo) (2015) Synoptic oceanography of San Jorge Gulf (Argentina): A template for Patagonian red shrimp (*Pleoticus muelleri*) spatial dynamics. *Journal of Sea Research* 95:22–35 doi:10.1016/j.seares.2014.10.011

Góngora ME, González-Zevallos D, Pettovello A, Mendía L (2012) Characterization of the main fisheries in San Jorge Gulf, Patagonia, Argentina. *Latin American Journal of Aquatic Research* 40(1):1–11 doi:10.3856/vol40-issue1-fulltext-1

Gray J (2001) Marine diversity: the paradigms in patterns of species richness examined. *Scientia Marina* 65:41–56

Gray JS, Elliott M (2009) Ecology of marine sediments: from science to management. Oxford University Press 256p

Grabowski JH, Bachman M, Demarest C, Eayrs S, Harris BP, Malkoski V, Packer D, Stevenson D (2014) Assessing the vulnerability of marine benthos to fishing gear impacts. *Reviews in Fisheries Science & Aquaculture* 22(2):142-155 doi:10.1080/10641262.2013.846292

Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'Agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, Fujita R, Heinemann D, Lenihan HS, Madin EMP, Perry MT, Selig ER, Spalding M, Steneck R, Watson R (2008) A global map of human impact on marine ecosystems. *Science* 319: 948−952 doi:10.1126/science.1149345

Halpern BS, Longo C, Lowndes JSS, Best BD, Frazier M, Katona SK, Kleisner KM, Rosenberg AA, Scarborough C, Selig ER (2015) Patterns and emerging trends in global ocean health. *PLoS One* 10(3) e0117863

Harris PT (2012) Anthropogenic threats to benthic habitats. In: Harris PT, Baker EK (Eds) Seafloor geomorphology as benthic habitats: GeoHab atlas of seafloor geomorphic features and benthic habitats. Elsevier, Amsterdam, p 39−60 doi:10.1016/B978-0-12-385140-6.00003-7

Harvey E, Séguin A, Nozais C, Archambault P, Gravel D (2013) Identity effects dominate the impacts of multiple species extinctions on the functioning of complex food webs. *Ecology* 94:169–179 doi:10.1890/12-0414.1

Hector A, Bagchi R (2007) Biodiversity and ecosystem multifunctionality. *Nature* 448: 188–190

Hector A, Joshi J, Scherer-Lorenzen M, Schmid B, Spehn EM, Wacker L, Weilenmann M, Bazeley-White E, Beierkuhnlein C, Caldeira MC, Dimitrakopoulos PG, Finn JA, Huss-Danell K, Jumpponen A, Leadley PW, Loreau M, Mulder CPH, Nebhover C, Palmborg C, Read DJ, Siamantziouras ASD, Terry AC, Troumbis AY (2007) Biodiversity and ecosystem functioning: reconciling the results of experimental and observational studies. *Functional Ecology* 21(5):998-1002 doi:10.1111/j.1365-2435.2007.01308.x

Holmer M (1999) The effect of oxygen depletion on anaerobic organic matter degradation in marine sediments. *Estuarine, Coastal and Shelf Science* 48(3):383-390

Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75(1):3–35 doi:10.1890/04-0922

Hooper DU, Adair EC, Cardinale BJ, Byrnes JEK, Hungate BA, Matulich KL, Gonzalez A, Duffy JE, Gamfeldt L, O'Connor MI (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486(7401):105-108 doi:10.1038/nature11118

Hutchinson GE (1957) Concluding Remarks. In: Cold Spring Harbor Symposium Quantitative Biology, vol. 22 415e427

Kovalenko KE, Thomaz SM, Warfe DM (2012) Habitat complexity: approaches and future directions. *Hydrobiologia* 685(1):1-17 doi:10.1007/s10750-011-0974-z

Kristensen E, Penha-Lopes G, Delefosse M, Valdemarsen T, Quintana CO, Banta GT (2012) What is bioturbation? The need for a precise definition for fauna in aquatic sciences. *Marine Ecology Progress Series* 446:285-302 doi: 10.3354/meps09506

Lecours V, Devillers R, Schneider DC, Lucieer VL, Brown CJ, Edinger EN (2015) Spatial scale and geographic context in benthic habitat mapping: review and future directions. *Marine Ecology Progress Series* 535:259-284 doi:10.3354/meps11378

Lefcheck JS, Byrnes JEK, Isbell F, Gamfeldt L, Griffin JN, Eisenhauer N, Hensel MJS, Hector A, Cardinale BJ, Duffy JE (2015) Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. *Nature* communications 6:6936 doi:10.1038/ncomms7936

Lévesque M, Savard L, Moritz C, Archambault P (2012) Assessment of the potential impacts of northern shrimp (*Pandalus borealis*) trawl fishing on benthic habitats in the Estuary and northern Gulf of St. Lawrence. DFO Can. Sci. Advis. Sec. Res. Doc. 2012/094. ii + 28 p.

Link H, Piepenburg D, Archambault P (2013) Are hotspots always hotspots? The relationship between diversity, resource and ecosystem functions in the Arctic. *PLoS One* 8(9),e74077 doi:10.1371/journal.pone.0074077

Link H, Chaillou G, Forest A, Piepenburg D, Archambault P (2013b) Multivariate benthic ecosystem functioning in the Arctic benthic fluxes explained by environmental parameters in the southeastern Beaufort Sea. *Biogeosciences* 10:5911-5929 doi:10.5194/bg-10-5911-2013

Liuzzi MG, López-Gappa J, Olivieri V (2016) The clam *Neilonella sulculata* in San Jorge Gulf (Argentina, Southwest Atlantic): spatial distribution pattern and inverse relationship between size and density. *Marine Biology Research* 12(6): 621-630 doi:10.1080/17451000.2016.1174336

Longhurst AR (2007) Ecological geography of the sea. Academic Press 2nd ed

López-Gappa J, Liuzzi MG, Genzano G (2016) Role of the clam Neilonella sulculata as substrate for the hydroid Bougainvillia macloviana on muddy bottoms of San Jorge Gulf (Argentina, Southwest Atlantic). *Marine Biology Research* 12(8):888-893

Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, Wardle DA (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294:804–808 doi:10.1126/science.1064088

Louge E, Reta R, Santos, B, Hernandez D (2009) Distribution of the Argentine hake *Merluccius hubbsi* (Marini, 1933) in the Argentine Sea (41º- 48ºS) in relation to oceanographic parameters during winter (1996-2003). *Revista de Biología Marina y Oceanografía* 44(2):497–510 doi:10.4067/S0718-19572009000200022

Marchese C (2015) Biodiversity hotspots: A shortcut for a more complicated concept. *Global Ecology and Conservation* 3:297-309 doi:10.1016/j.gecco.2014.12.008

Marinho CH, Gil MN, Esteves JL (2013) Distribution and origin of trace metals in sediments of a marine park (Northern San Jorge Gulf) from Argentina. *Marine pollution bulletin* 72(1):260-263

Maxwell DL, Stelzenmuller V, Eastwood PD, Rogers SI (2009) Modelling the spatial distribution of plaice (*Pleuronectes platessa*), sole (*Solea solea*) and thornback ray (*Raja clavata*) in UK waters for marine management and planning. *Journal of Sea Research* 61:258–267

Mermillod-Blondin F, François-Carcaillet F, Rosenberg R (2005) Biodiversity of benthic invertebrates and organic matter processing in shallow marine sediments: An experimental study. *Journal of Experimental Marine Biology and Ecology* 315(2):187–209 doi:10.1016/j.jembe.2004.09.013

Miloslavich P, Klein E, Diaz JM, Hernandez CE, Bigatti G, Campos L, Artigas F, Castillo J, Penchaszadeh PE, Neill PE, Carranza A, Retana MV, Diaz de Astarloa JM, Lewis M, Yorio P, Piriz ML, Rodriguez D, Yoneshigue-Valentin Y, Gamboa L, Martin A (2011) Marine biodiversity in the Atlantic and Pacific coasts of South America: Knowledge and gaps. *PLoS One* 6, e14631 doi:10.1371/journal.pone.0014631

Mokany K, Ferrier S, Connolly SR, Dunstan PK, Fulton EA, Harfoot MB, Harwood TD, Richardson AJ, Roxburgh SH, Scharlermann JPW, Tittensor DP, Westcott DA, Wintle BA (2016) Integrating modelling of biodiversity composition and ecosystem function. *Oikos* 125(1):10-19 doi:10.1111/oik.02792

Moritz C, Lévesque M, Gravel D, Vaz S, Archambault D and Archambault P. 2013. Modelling spatial distribution of epibenthic communities in the Gulf of St. Lawrence (Canada). *Journal of Sea Research* 78:75–84 doi:10.1016/j.seares.2012.10.009

Mouchet MA, Villéger S, Mason NW, Mouillot D (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology* 24(4):867-876

Naeem S, Wright JP (2003) Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology* Letters 6:567‑579

Norling K, Rosenberg R, Hulth S, Grémare A, Bonsdorff E (2007) Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment. *Marine and Ecology Progress Series* 332:11–23 doi:10.3354/meps332011

Palma ED, Matano RP, Piola AR (2004) A numerical study of the Southwestern Atlantic Shelf circulation: Barotropic response to tidal and wind forcing. *Journal of Geophysical Research* 109, C08014 doi:10.1029/2004JC002315

Palma ED, Matano RP, Piola AR (2008) A numerical study of the Southwestern Atlantic Shelf circulation: Stratified ocean response to local and offshore forcing. *Journal of Geophysical Research* 113, C11010 doi:10.1029/2007JC004720

Palma ED, Matano RP (2012) A numerical study of the Magellan Plume. *Journal of Geophysical Research* 117, C05041 doi:10.1029/2011JC007750

Pearson T (2001) Functional group ecology in soft-sediment marine benthos: The role of bioturbation. *Oceanography and Marine Biology* 39:233–267

Pearson TH, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology: An Annual Review* 16: 229-311

Petchey OL, Gaston KJ (2002) Functional diversity (FD), species richness and community composition. *Ecology Letters* 5:402‑411

Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. *Ecology Letters* 9:741-758 doi:10.1111/j.1461-0248.2006.00924.x

Petchey OL, Hector A, Gaston KJ (2004) How do different measures of functional diversity perform? *Ecology* 85:847‑857

Poloczanska ES, Hawkins SJ, Southward AJ, Burrows MT (2008) Modeling the response of populations of competing species to climate change. *Ecology* 89:3138–3149

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press

Redfern JV, Ferguson MC, Becker EA, Hyrenbach KD, Good C, Barlow J, Kaschner K, Baumgartner MF, Forney KA, Ballance LT, Fauchald P, Halpin P, Hamazaki T, Pershing AJ, Qian SS, Read A, Reilly SB, Torres L, Werner F (2006) Techniques for cetacean-habitat modeling. *Marine Ecology Progress Series* 310:271–295

Reta R (1986) Aspectos oceanográficos y biológicos pesqueros del golfo San Jorge. Seminario de Grado de Licenciatura en Oceanografía. Universidad Nacional del Sur, Bahía Blanca, Argentina 135 pp.

Retana MV, Lewis MN (2017) Suitable habitat for marine mammals during austral summer in San Jorge Gulf, Argentina. *Revista de Biología Marina y Oceanografía* 52(2):275-288

Rivas AL, Dogliotti AI Gagliardini DA (2006) Seasonal variability in satellite-measured surface chlorophyll in the Patagonian Shelf. *Continental Shelf Research* 26:703–720 doi:10.1016/j.csr.2006.01.013

Robinson LM, Elith J, Hobday AJ, Pearson RG, Kendall BE, Possingham HP, Richardson AJ (2011) Pushing the limits in marine species distribution modelling: lessons from the land present challenges and opportunities. *Global Ecology and Biogeography* 20:789−802 doi:10.1111/j.1466-8238.2010.00636.x

Rosenberg R (2001) Marine benthic faunal successional stages and related sedimentary activity. *Scientia Marina* 65:107–119

Rosenfeld JS (2002) Functional redundancy in ecology and conservation. *Oikos* 98:156‑162

Roth S, Wilson JG (1998) Functional analysis by trophic guilds of macrobenthic community structure in Dublin Bay, Ireland. *Journal of Experimental Marine Biology and Ecology* 222:195–217 doi:10.1016/S0022-0981(97)00145-7

Roux AM, Fernandez M, Bremec CS (1995) Preliminary survey of the benthic communities of the Patagonian shrimp fishing grounds in San Jorge Gulf, Argentina. *Ciencias Marinas* 21:295–310

Roux A, Piñero R, Moriondo P, Fernández M (2009) Diet of the red shrimp *Pleoticus muelleri* (Bate, 1888) in Patagonian fishing grounds, Argentine. *Revista de Biología Marina y Oceanografía* 44(3):775-781 doi:10.4067/S0718-19572009000300023

Sargent JR, Hopkins CCE, Seiring JV, Youngson A (1983) Partial characterization of organic material in surface sediments from Balsfjorden, northern Norway, in relation to its origin and nutritional value for sediment-ingesting animals. *Marine Biology* 76:87–94 doi:10.1007/BF00393059

Solan M, Cardinale BJ, Downing AL, Engelhardt KAM, Ruesink JL, Srivastava DS (2004) Extinction and ecosystem function in the marine benthos. *Science* 306(5699):1177-1180

Song H, Marshall J, Follows MJ, Dutkiewicz S, Forget G (2016) Source waters for the highly productive Patagonian shelf in the southwestern Atlantic. *Journal of Marine Systems* 158:120-128 doi:10.1016/j.jmarsys.2016.02.009

Spath MC, Delpiani G, Figueroa DE (2016) Feeding ecology of the apron ray *Discopyge tschudii* (Elasmobranchii, Narcinidae) in San Jorge Gulf, Patagonia, Argentina. *Journal of the Marine Biological Association of the United Kingdom* 96(5):1093-1099

Sswat M, Gulliksen B, Menn I, Sweetman AK, Piepenburg D (2015) Distribution and composition of the epibenthic megafauna north of Svalbard (Arctic). *Polar Biology* 38(6):861-877

Stachowicz JJ, Bruno JF, Duffy JE (2007) Understanding the effects of marine biodiversity on communities and ecosystems. Annual *Review of Ecology Evolution and Systematics* 38:739-766 doi:10.1146/annurev.ecolsys.38.091206.095659

Tilman D (2001) Functional diversity. Encyclopedia of Biodiversity 3:109–120

Tokeshi M, Arakaki S (2012) Habitat complexity in aquatic systems: fractals and beyond. *Hydrobiologia* 685(1):27-47

Tonini M, Palma ED, Rivas A (2006) Modelo de alta resolución de los Golfos Patagónicos. *Mecánica Computacional* 25:1441-1460

Torn K, Herkül K, Martin G, Oganjan K (2017) Assessment of quality of three marine benthic habitat types in northern Baltic Sea. *Ecological Indicators* 73:772-783 doi:10.1016/j.ecolind.2016.10.037

Törnroos A, Bonsdorff E, Bremner J, Blomqvist M, Josefson AB, Garcia C, Warzocha J (2015) Marine benthic ecological functioning over decreasing taxonomic richness. *Journal of Sea Research* 98:49-56

Torres AI, Faleschini M, Esteves JL (2016) Benthic fluxes and nitrate reduction activity in a marine park (Northern San Jorge Gulf) from Patagonia Argentina. *Environmental Earth Sciences* 75(9):815

Valavanis VD, Pierce GJ, Zuur AF, Palialexis A, Saveliev A, Katara I, Wang JJ (2008) Modelling of essential fish habitat based on remote sensing, spatial analysis and GIS. *Hydrobiologia* 612:5–20

Varisco M, Vinuesa JH (2007) La alimentación de *Munida gregaria* (Fabricius, 1793) (Crustacea: Anomura: Galatheidae) en fondos de pesca del Golfo San Jorge, Argentina. *Revista de Biología Marina y Oceanografía* 42(3):221-229

Varisco M, Vinuesa JH, Góngora M (2015) Bycatch of the squat lobster *Munida gregaria* in bottom trawl fisheries in San Jorge Gulf, Argentina. *Revista de Biología Marina y Oceanografía* 50(2):249-259 doi:10.4067/S0718-19572015000300004

Varisco M, Cochia P, Góngora ME, Bovcon N, Balz, P, Vinuesa J (2017) Bycatch of the Southern King Crab (*Lithodes santolla*) in the Patagonian shrimp fishery in the Southwestern Atlantic Ocean. Can it contribute to the depletion of its population?. *Ocean & Coastal Management* 136 177-184

Vierod ADT, Guinotte JM, Davies AJ (2014) Predicting the distribution of vulnerable marine ecosystems in the deep sea using presence-background models. *Deep-Sea Res II: Topical Studies in Oceanography* 99:6-18 doi:10.1016/j.dsr2.2013.06.010

Vinuesa JH (2005) Distribution of decapod and stomatopod crustaceans from San Jorge Gulf, Argentina. *Revista de Biología Marina y Oceanografía* 40(1):7–21 doi:10.4067/S0718-19572005000100002

Vinuesa JH (2007) Molt and reproduction of the European green crab *Carcinus maenas* (Decapoda: Portunidae) in Patagonia, Argentina. *Revista de Biología Tropical* 55(1):49-54

Vinuesa JH, Varisco M (2007) Trophic ecology of the lobster krill *Munida gregaria* in San Jorge Gulf, Argentina. *Investigaciones Marinas* 35:25–34 doi:10.4067/S0717-71782007000200003

Vinuesa JH, Varisco M, Escriche F (2011) Settlement and recruitment of the crab *Halicarcinus planatus* (Crustacea: Decapoda: Hymenosomatidae) in Golfo San Jorge, Argentina. *Journal of the Marine Biological Association of the United Kingdom* 91(3):685-690

Vinuesa JH, Varisco MA, Balzi P (2013) Feeding strategy of early juvenile stages of the southern King crab *Lithodes santolla* in the San Jorge Gulf, Argentina. *Revista de Biología Marina y Oceanografía* 48(2):353–363 doi:10.4067/S0718-19572013000200014

Wassmann P (1997) Retention versus export food chains: processes controlling sinking loss from marine pelagic systems. *Hydrobiologia* 363(1):29-57

Williams A, Schlacher TA, Rowden AA, Althaus F, Clark MR, Bowden DA, Stewart R, Bax NJ, Consalvey M, Kloser RJ (2010) Seamount megabenthic assemblages fail to recover from trawling impacts. *Marine Ecology* 31(s1):183−199 doi:10.1111/j.1439-0485.2010.00385.x

Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, Halpern BS, Jackson BC, Lotze HK, Micheli F, Palumbi SR, Sala E, Selkoe KA, Stachowicz JJ, Watson R (2006) Impacts of biodiversity loss on ocean ecosystem services. *Science* 314(5800):787-790

Yorio P (2009) Marine protected areas, spatial scales, and governance: implications for the conservation of breeding seabirds. *Conservation Letters* 2:171–178 doi:10.1111/j.1755-263X.2009.00062.x

Zaixso HE, Boraso de Zaixso A (2015) Recursos biológicos bentónicos: la Zona Costera Patagónica Argentina. Universitaria de la Patagonia - EDUPA. Comodoro Rivadavia

Zajac RN, Vozarik JM, Gibbons BR (2013) Spatial and temporal patterns in macrofaunal diversity components relative to sea floor landscape structure. *PloS one* 8(6) e65823