THÈSE
Pour obtenir le grade de
Docteur

Université Montpellier

Préparée au sein de l'école doctorale
SIBAGHE – Systèmes intégrés en Biologie, Agronomie, Géosciences, Hydrosciences et Environnement

Et de l'unité de recherche UMR MARBEC

Spécialité : Biologie des populations et écologie

Présentée par Ana Renza Paola ALEGRE NORZA SIOR

TITRE DE LA THESE

Trophic ecology of jumbo squid and predatory fishes in the Northern Humboldt Current System

Soutenue le **21 mai 2015** devant le jury composé de :

M. Sébastien, JAQUEMET, MCU HDR Université de La Réunion	Rapporteur
M. Marc, PAGANO, Directeur de Recherche IRD	Rapporteur
M. Frédéric MENARD, Directeur de Recherche IRD	Directeur de thèse
M. Arnaud BERTRAND, Directeur de Recherche IRD	co-Directeur de thèse
M. Yves, CHEREL, Directeur de Recherche CNRS	Examinateur
M. Nicolas BEZ, Directeur de Recherche IRD	Examinateur
Mme. Monique Simier, Ingénieure de Recherche	Invitée

IN MEMORIAM

A mi profesor Dr. Juan Leonidas Tarazona Barboza, quien partió de este mundo pocos días antes de la sustentación de esta tesis doctoral, por ser un gran ejemplo de entrega y pasión por la ciencia.

DEDICATORIA

A mis padres Mario† y Angélica† que son mi fuente de inspiración, a mis hijos Paula y Salvador quienes son el motor que me impulsa a seguir adelante y a mi esposo Flavio por su gran amor y su apoyo incondicional.

Abstract

This work provides a contribution to a better understanding of the trophic ecology of important predators in the Northern Humboldt Current System, the jack mackerel (*Trachurus murphyi*), the chub mackerel (*Scomber japonicus*) and the jumbo squid (*Dosidicus gigas*) by the characterization of the highly variable feeding patterns of these species at different spatiotemporal scales. We provided new knowledge on the comparative trophic behaviour of these species, defined as opportunistic in previous investigations. For that purpose we applied a variety of statistical methods to an extensive dataset of 27,188 non-empty stomachs. We defined the spatial organization of the forage fauna of these predators and documented changes in prey composition according to predators' size and spatiotemporal features of environment. Our results highligh the key role played by the dissolved oxygen. We also deciphered an important paradox on the jumbo squid diet: why do they hardly forage on the huge anchovy (*Engraulis ringens*) biomass distributed of coastal Peru? We showed that the shallow oxygen minimum zone present off coastal Peru could hamper the co-occurrence of jumbo squids and anchovies. In addition, we proposed a conceptual model on jumbo squid trophic ecology including the ontogenetic cycle, oxygen and prey availability. Moreover we showed that the trophic behaviour of jack mackerel and chub mackerel is adapted to forage on more accessible species such as for example the squat lobster *Pleurocondes monodon* and Zoea larvae. Besides, both predators present a trophic overlap. But jack mackerel was not as voracious as chub mackerel, contradictorily to what was observed by others authors. Fish diet presented a high spatiotemporal variability, and the shelf break appeared as a strong biogeographical frontier. Diet composition of our fish predators was not necessarily a consistent indicator of changes in prey biomass. El Niño events had a weak effect on the stomach fullness and diet composition of chub mackerel and jack mackerel. Moreover, decadal changes in diet diversity challenged the classic paradigm of positive correlation between species richness and temperature. Finally, the global patterns that we described in this work, illustrated the opportunistic foraging behaviour, life strategies and the high degree of plasticity of these species. Such behaviour allows adaptation to changes in the environment.

Key words: *Dosidicus gigas, Trachurus murphyi, Scomber japonicus,* trophic behaviour, Northern Humboldt Current system, Peru.

Résumé

Ce travail est une contribution à l'étude de l'écologie trophique d'importants prédateurs de la partie Nord du système du Courant de Humboldt (NSCH), le chinchard (*Trachurus murphyi*), le maquereau (*Scomber japonicus*) et le calmar géant (*Dosidicus gigas*). Nous avons caractérisé la variabilité des modes d'alimentation de ces espèces à différentes échelles spatiotemporelles et fourni de nouvelles connaissances sur le comportement alimentaire de ces espèces, définies comme opportunistes par des travaux antérieurs. Pour ce faire, nous avons appliqué une variété de méthodes statistiques à un vaste jeu de données comprenant 27188 estomacs non vides. Sur cette base nous avons décri l'organisation spatiale de la faune fourrage de ces prédateurs et documenté les changements dans la composition des proies en fonction de la taille de prédateurs et des conditions environnementales. Nos résultats indiquent que l'oxygène dissous jour un rôle clef dans ces processus. Nous avons également résolu un paradoxe sur l'alimentation du calmar géant: pourquoi ils ne se nourrissent guère sur l'immense biomasse d'anchois (*Engraulis ringens*) présente le long de la côte du Pérou? Nous avons montré que la présence d'une zone de minimum d'oxygène (ZMO) superficielle devant le Pérou pourrait limiter la cooccurrence entre calmars géant et anchois. Pour synthétiser ces résultats, nous avons proposé un modèle conceptuel de l'écologie trophique du calmar géant tenant compte du cycle ontogénétique, de l'oxygène et de la disponibilité des proies. Par ailleurs, nous avons montré que le chinchard et le maquereau se nourrissent des espèces les plus accessibles comme par exemple la galathée *Pleurocondes monodon* ou les larves zoea. Ces deux prédateurs présentent un chevauchement trophique mais, contrairement à ce qui avait été décrit dans d'autres études, le chinchard n'est pas aussi vorace que le maquereau. Le régime alimentaire de ces poissons est caractérisé par une forte variabilité spatio-temporelle et le talus continental s'avère être une importante frontière biogéographique. La composition du régime alimentaire des poissons prédateurs étudiés n'est pas nécessairement un indicateur cohérent de l'évolution de la biomasse des proies. Les événements El Niño ont eu un faible effet sur le taux de remplissage des estomacs et sur le régime alimentaire du chinchard et du maquereau. Par ailleurs les changes en diversité des proies à échelle décennale contredisent le classique paradigme de corrélation positive entre diversité et la température. Finalement, les patrons globaux décrits dans ce travail, illustrent le comportement alimentaire opportuniste les stratégies de vie et le haut degré de plasticité de ces espèces. Un tel comportement permet de s'adapter aux changements de l'environnement.

Mots clefs: *Dosidicus gigas, Trachurus murphyi, Scomber japonicus,* comportement alimentaire, Nord du système du Courant de Humboldt, Pérou.

Acknowledgements

It took a long time before these lines, perhaps because it is difficult to summarize in a few paragraphs feelings, emotions, stories I've shared with great friends, the way of this thesis was accompanied by people who managed with my make this dream a reality. When I studied the undergraduate a great friend gave me a wise counsel: "Surround yourself with good friends and copy the best of each person"; that phrase was coined in my mind and I began to highlight the best of each person I met on my way, trying to inspire in those qualities. This road was very difficult for me, I had to overcome many obstacles, but good examples from great people who showed up my life, taught me to have the courage and perseverance to finish what I started with great enthusiasm.

I starting with my advisor Frédéric Ménard, with whom I shared long discussions, hours of work and who thoroughly revised this thesis, always being very diligent in their criticism; but also for his patience, his good nature and support to do a good job. I also want to thank Dr. Arnaud Bertrand (IRD - France), for their unconditional support and wise counsel, for giving me the strength to go on the road and not lose heart, for being a friend and partner in this struggle without your vote confidence could not finish this stage of my career, in your hands I supported all these years of struggle that began in 2008, was a long way without truce, with difficulties that without their support I would not have been able to save. A Monique Simier engineer who not only actively contributed to the development of this thesis, also showed great professionalism in reviewing scripts, text and references; she was also a great friend and companion during the time of my stay in France.

I want to thank the L'Institut de recherche pour le développement IRD of France, who gave me the scholarship for my doctorate in three years, also I am very gratefully to the IRD in Peru, his representative Jean-Loup Guyot, by performing a valuable management in my country providing facilities to Peruvians to study for a doctorate. To the administrative staff, to Liliana Lalonde, who supported me a lot especially when I had to take my kids to France, to Alain Corde and Miriam Soto, by administrative arrangements for my travel; and especially my dear friend Lourdes Valdivia who not only supported me with the registration process to the university, but also for his valuable friendship.

I want to thank to Laboratory UMR MARBEC, especially Dr. Philippe Cury and Dr. Capucine Mellon for giving me logistical support for the development of my thesis during my stay in France. I would also like to thank my fellow PhD Alexandra who supported me in difficult times, Lauriane and Andrea who they gave me their trust, Mariana, Fabian, Robert, Elizabeth, Lysel, Camille, Antonia, Angelie, Edgard, Justin and Arnaud. How I forget the friends of IFREMER, starting by Ghislaine who was my support in the most hard times, she especially wants to thank you for her affection and selfless support. To Liliana with her I shared many experiences, also her daughter Manuelita who cheered me and supplied a little lack of my children. Marta and Jeroen, who with their encouragement, cheered many of my evenings. To Isabelle Terrier who with her sweetness, always she made me feel at home. Ainhoa and Phillipe, who spread me joy, and for their pleasant conversations. To my friend Maria Grazia, she is collaborator, always giving selflessly her help. Bastien for his help, especially with the formalities documents at the university. Catherina Gilles, They very kindly opened me the doors of your home and heart. To Pierre Freon, my great friend of many years, especially by the great dear, for allowing me to come home and meet your beautiful family, for the wise counsel and representing the great example for me; his wife Martine for their joy and great affection. Sophie Bertrand, who was always concerned for my family and with whom I shared pleasant evenings, Nicolas, Alexis, Jean, Jeremie, Alex. I also want to thank the administrative staff of IFREMER, starting with Mrs. Laurence Vicens, for supporting me in the documentary efforts during my stay in France, as well as the arrangements for the trip of my children; to Isabelle Vidal Ayouba and Anne-Catherine Gandrillon who supported me with administrative formalities during my stay in the IFREMER. And finally to all my friends of IFREMER.

I am not forget the friends Sète Daniel Gonzales and Manu, with whom I shared evenings music and talks about Latin American politics, George and Solange Botet gentlemen who with whom I developed a lasting friendship, friends of Nicole and Frank Gravy, the happy times we had.

I am very gratefully to the Marine Institute of Peru for giving me the opportunity to realize this thesis, to their chairman Admiral Germán Vásquez Solís for believing in me as a prospect for the development of science in IMARPE, to the administrative personnel who conducted the negotiations efficiently for my stay in France. To Andrés Chipollini without their important support would not be possible the completion of this thesis, Marilu Bouchon who opened the doors of the Directorate General of Pelagic Resources, Teobaldo Dioses, Miguel Ñiquen and

Marco Espino, that his experience gave a great contribution to my work, to Ricardo Oliveros for his friendship and help with some aspects of my work; my fellow Functional Area Research Invertebrates and macroalgae, Carmen Yamashiro gave me the opportunity to work with the jumbo squid, to Juan Arguelles and Ricardo Tafur who contributed their knowledge in this work, Anatolio and Maria Nelly for their good wishes. To my colleagues in the Laboratory of trophic ecology, Pepe Espinoza, who served as an example for me to move on, Ivan Navarro who analyzed many of the samples and who gave me the wise counsel to move forward, to Rosario Cisneros for his unconditional friendship, Cesar Fernandez and David Castillo for their support. Jorge Tam and Michelle Graco, for their comments and contributions to my thesis. To my friends Pilar Aponte, Julio Mori, Sonia Arrieta, Yachi Febres and Carmen Moreno. To Mariano Gutierrez, who was a key element in my decision to development a doctorate, for giving me three great advices that changed the course of my story.

I cannot pass up the opportunity to thank a great master who is no longer among us, he represented the greatest example in my career, I had the great opportunity of working with him for several years and learn from him. Dr. Juan Tarazona Barboza, for his advice, his teachings and his brilliant passing through the science of Peru, he left us a few days before of sustaining this work, I would have loved to return to Peru and personally hand this thesis; Unfortunately, he depart from this world before, now I can only give a fitting tribute through these lines "To my great teacher thanks for inspiring me to follow the path of science ", to give me, the example to work hard for the dreams and translate them into reality. I also want to thank Dr. Jaime Mendo for their teachings in the field and for his friendship.

I also want to thank my great friends Gerardo, Sandro, Manuel, Carola and Claudia, they always gave me courage and his trust. My chicks friends, Rocío Joo and Daniel Grados, for the working dawns, the *soirées* with wine, cheese and Peruvian food, for their good company in the lonely moments away from home; and especially grateful to my dear Giannina who was my stand for the happy and sad moments we share, for the patience of my many manias, for her joy and zest for life and commitment of unconditional friendship.

To my cousin Ivan Alegre and his beautiful family: Isabel, Paula and Julio for his great affection despite years of estrangement, also Fernando Alegre and his wife Nancy. For all, thanks for having opened the doors of their houses in Seville and they have been always aware of my progress. To my dear friend from the school: Hokulani (Star), with whom I shared beautiful days in France for his great example of life.

I want to give a very special place to my immediate family; especially my brother Mario, who showed in me the curiosity for knowledge, his long conversations in my childhood opened a door that led me to a totally fascinating way. My sister Fanny who showed me that with perseverance comes success, and encouraged me not to leave the path he had traced me. My sister Angelica that taught me to can talk with the public and give opinions and not just I hiding behind a book. To my brother in law Juan, who was always attentive and applauded my achievements. To my nephews Luis Felipe that despite the great difficulties he faced was able to overcome and follow their dreams, to Rodrigo, for his great personality, Adriano by his intelligence and Mateo for their occurrences. My niece Fanny by her great affection, complicity and her determination that characterizes by always encourage me and accompany me through thick and thin. My niece Monica made me see that should move forward in my career, for his great dear, and their mettle to conquer your goals. I also want to thank my political family to my in-laws Freddy and Luz, to my brothers in law, Joel, Gisella and Mariela and my nephews Camila, Josué, Aaron and Joel, for to give value to my husband to support me and wait me for the time I was far.

I want to thank Mrs. Sonia Zambrano, who took care of my children during my absence, without his support at home this would not have been possible. My husband Flavio Mendoza, who encouraged me to pursue this adventure, for their unconditional support, for his admiration that commits me to give the best of me, who accompanied my children during the time of my absence, always talking to my children's for that the mother figure is not erased from his thoughts, for his great love. To my two beautiful children Paula and Salvador, for understanding me, for waiting me, for joining me, for all these years, for to have the patience to see me study for hours without being able to play with them, for not make noise while I studied and for welcoming me with joy after my long absences; they are the engine that drives me to achieve my goals. I would not forget two people who left me when I was just beginning to study the undergraduate, my parents Mario and Angelica; him for teaching me that knowledge is the greatest wealth that can carry a human being and my mother who always trusted in my ability and whose last wish was to be consistent with my choices and end the race had begun; to them, wherever they are thank you very much. Finally, I want to thank God for keep me in good health to be able to realize this dream and taking care of my family during my absence.

To all, my sincere thanks.

Agradecimientos

Me tomó mucho tiempo comenzar estas líneas, tal vez porque es difícil sintetizar en pocos párrafos los sentimientos, emociones, anécdotas que he compartido junto a grandes amigos, el camino de esta tesis estuvo acompañado de personas que lograron junto a mi hacer de este sueño una realidad. Cuando estudiaba el pregrado un gran amigo me dio un sabio consejo: "rodéate de buenos amigos y copia lo bueno"; esa frase se acuñó en mi mente y comencé a destacar lo mejor de cada persona que encontré en mi camino, tratando de inspirarme en esas cualidades. Este camino fue muy difícil para mí, tuve que salvar muchos obstáculos, pero los buenos ejemplos tomados de grandes personas que se presentaron mi vida, me enseñaron a tener el temple y la perseverancia para finalizar lo que con mucha ilusión empecé.

Comenzando por mi asesor Frédéric Ménard, con quien compartí largas discusiones, horas de trabajo y quien minuciosamente revisó esta tesis, siendo siempre muy acucioso en sus críticas; pero también por su paciencia, su buen carácter y su apoyo para realizar un buen trabajo. También quiero dar las gracias al Dr. Arnaud Bertrand (IRD - Francia), por su apoyo incondicional y sabios consejos, por darme el ánimo para seguir en el camino y no desfallecer, por ser amigo y compañero en esta lucha, sin su voto de confianza no hubiera podido culminar esta etapa de mi carrera, en sus manos apoyé todos estos años de lucha que comenzaron en el 2008, fue un largo camino sin tregua lleno de dificultades y que sin su apoyo no hubiera podido salvar. A la ingeniera Monique Simier que no sólo contribuyó activamente al desarrollo de esta tesis, también demostró gran profesionalismo en la revisión de los scripts, el texto y las referencias bibliográficas; además fue una gran amiga y compañera durante el tiempo de mi estadía en Francia.

Quiero dar las gracias al L'Institut de recherche pour le développement IRD de Francia, quienes me brindaron la beca para realizar mi doctorado durante 3 años, también al IRD en Perú, a su representante Jean-Loup Guyot, por tan valiosa gestión que realiza en mi país brindando facilidades a peruanos para realizar estudios de doctorado, al personal administrativo a la señora Liliana Lalonde, que me apoyó mucho especialmente cuando tuve que llevar a mis hijos a Francia, a Miriam Soto a Alain Corde, por las gestiones administrativas para mis viajes; y especialmente a mi querida amiga Lourdes Valdivia quien no sólo me apoyó con los trámites de inscripción a la universidad, sino también por su valiosa amistad.

Asimismo, quiero agradecer al Laboratorio UMR MARBEC especialmente al Dr. Phillipe Cury y la Dra. Capucine Mellon por brindarme el apoyo logístico para el desarrollo de mi tesis durante mi estadía en Francia. También a mis compañeros del doctorado Alexandra quien me apoyó en momentos difíciles, Lauriane y Andrea quienes me brindaron su confianza, Mariana, Fabian, Robert, Elizabeth, Lysel, Camille, Antonia, Angelie, Edgard, Justin, Arnaud. Como olvidar a los amigos del IFREMER, comenzando por Ghislaine quien fue mi soporte en los momentos más duros, a ella especialmente quiero dar las gracias por su cariño y apoyo desinteresado. A Liliana con quien compartí muchas experiencias, a su hijita Manuelita quien me alegró y suplió un poco la ausencia de mis hijos. A Marta y Jeroen quienes con su ánimo, alegraron muchas de mis tardes. A Isabelle Terrier que con su dulzura me hizo siempre sentir en casa. A Ahinoa y Phillipe que me contagiaron con su alegría y sus amenas conversaciones. A mi querida amiga Maria Grazia, tan colaboradora, siempre ayudándonos desinteresadamente, a Bastien por su ayuda, especialmente con los trámites en la universidad, a Gilles y Catherina que muy gentilmente me abrieron las puertas de su casa y su corazón. A Pierre Freón, mi gran amigo de tantos años, especialmente por el gran cariño, por haberme permitido entrar a su hogar y conocer a su hermosa familia, por los sabios consejos y el gran ejemplo que representa para mí; a su esposa Martine por su alegría y gran cariño. A Sophie Bertrand, que se preocupó siempre por mi familia y con quien compartí amenas veladas, a Nicolas, Alexis, Jean, Jeremie, Alex. También quiero dar las gracias al personal administrativo del IFREMER, comenzando por la señora Laurence Vicens, por apoyarme en las gestiones documentarias durante mi estadía en Francia, así como en los trámites para el viaje de mis hijos; a Isabelle Vidal Ayouba y Anne-Catherine Gandrillon quienes me apoyaron en las gestiones administrativas durante mis estadías en el IFREMER. Y Finalmente a todos mis amigos de IFREMER.

Tampoco olvidar a los amigos de Sète Daniel y Manu, con quienes compartí tardes de música y conversaciones sobre la política latinoamericana, a los señores George y Solange Botet quienes con quienes desarrollé una duradera amistad, a los amigos de la salsa Nicole y Frank, por los momentos alegres que pasamos.

Al Instituto del Mar del Perú por haberme brindado la oportunidad de realizar esta tesis, a su presidente Contralmirante Germán Vásquez Solís por creer en mi como prospecto para el desarrollo de la ciencia en IMARPE, al personal administrativo que realizó con eficiencia las gestiones para mis estadías en Francia. A mis compañeros de IMARPE, a Andrés Chipollini, sin su importante apoyo no hubiera sido posible la culminación de este trabajo de tesis, a Marilú Bouchon quien me abrió las puertas de la Dirección General de Recursos Pelágicos, a Teobaldo Dioses, Miguel Ñiquen y Marco Espino que con su experiencia brindaron un gran aporte a mi trabajo, a Ricardo Oliveros por su amistad y ayuda con algunos aspectos de mi trabajo; a mis compañeros del Área Funcional de Investigaciones en Invertebrados y Macroalgas, Carmen Yamashiro que me dio la oportunidad de trabajar con el calamar gigante, a Juan Argüelles y Ricardo Tafur que contribuyeron con sus conocimientos en este trabajo, a Anatolio y María Nelly por sus buenos deseos. A mis compañeros del Laboratorio de Ecología Trófica, Pepe Espinoza, quien me sirvió de ejemplo para seguir adelante, Iván Navarro que analizó gran parte de las muestras y quien me dio los más sabios consejos para seguir avanzando, a Rosario Cisneros por su incondicional amistad, a César Fernández y David Castillo por su apoyo. A Jorge Tam y Michelle Graco, por sus observaciones y aportes a mi trabajo de tesis. A mis amigos Pilar Aponte, Julio Mori, Sonia Arrieta, Yachi Febres y Carmen Moreno. A Mariano Gutiérrez, quien fue un elemento clave en mi decisión de realizar el doctorado, por darme tres grandes consejos que cambiaron el curso de mi historia.

No puedo dejar pasar la oportunidad para agradecer a un gran maestro que ya no se encuentra entre nosotros, él representó el mayor ejemplo en mi carrera, tuve la gran oportunidad de trabajar a su lado por varios años y aprender mucho de él. Al Doctor Juan Tarazona Barboza, por sus consejos, sus enseñanzas y su brillante paso por la ciencia del Perú, se fue pocos días antes de sustentar este trabajo, me hubiera encantado regresar al Perú y entregarle personalmente esta tesis; lamentablemente, su partida de este mundo se adelantó, ahora sólo me queda otorgarle un merecido homenaje a través de estas líneas "A mi gran maestro gracias por haberme inspirado a seguir por el camino de la ciencia, a no rendirme, a trabajar duro por los sueños y a plasmarlos en realidad". También quiero agradecer al Doctor Jaime Mendo por sus enseñanzas en el campo y por su gran amistad.

Quiero también dar las gracias a mis grandes amigos Gerardo, Sandro, Manuel, Carola y Claudia que siempre me dieron ánimo y toda su confianza. A mis amigos los pollitos, Rocío Joo y Daniel Grados, por las amanecidas trabajando, las *soirées* con vino, queso y comida peruana, por la buena compañía en los momentos solitarios lejos de casa y muy especialmente agradeceré a mi querida Giannina quien fue mi soporte, por los momentos alegres y tristes que compartimos, por la paciencia a mis múltiples manías, por su alegría y ganas de vivir y por su compromiso de amistad incondicional.

A mi primo Iván Alegre y su hermosa familia Isabel, Paula y Julio por su gran cariño a pesar de los años de distanciamiento, igualmente a Fernando Alegre y su esposa Nancy, a todos ellos gracias por haberme abierto las puertas de sus casas en Sevilla y haber estado siempre pendientes de mis avances. A mí querida amiga del colegio Hokulani (Estrella), con quien compartí hermosos días en Francia, por su gran ejemplo de vida.

Quiero dar un espacio muy especial a mi familia más cercana, especialmente a mi hermano Mario, quien sembró en mí la curiosidad por el conocimiento, sus largas conversaciones en mi infancia abrieron una puerta que me llevó a un camino totalmente fascinante. A mi hermana Fanny quien me mostró que con la perseverancia se llega al éxito, me animó a no dejar el camino que me había trazado. A mi hermana Angélica que me enseñó a desenvolverme en público y dar opiniones y no sólo esconderme detrás de un libro. A mi cuñado Juan, quien siempre estuvo atento y aplaudió mis logros. A mis sobrinos Luis Felipe que a pesar de las grandes dificultades que tuvo que afrontar supo sobreponerse y seguir sus sueños, A Rodrigo, por su gran personalidad, A Adriano por su inteligencia y a Mateo por sus ocurrencias. A mi sobrina Fanny por su gran cariño, complicidad y esa determinación que la caracteriza, por darme siempre ánimo y acompañarme en las buenas y las malas. A mi sobrina Mónica que me hizo ver que debía seguir avanzando en mi carrera, por su gran cariño, y su temple para conquistar sus metas. También quiero agradecer a mi familia política a mis suegros Freddy y Luz, a mis cuñados, Gisella, Mariela y Joel y a mis sobrinos Camila, Josué, Aarón y Joel, por darle el valor a mi esposo de apoyarme y esperarme durante el tiempo que estuve lejos.

Quiero agradecer también a la señora Sonia Zambrano, quien cuidó a mis hijos durante mi ausencia, sin su apoyo en la casa esto no hubiera sido posible. A mi esposo Flavio Mendoza, quien me animó a seguir esta aventura, por su apoyo incondicional, su admiración que me compromete a dar lo mejor de mí, quien acompañó a mis hijos durante el tiempo de mi ausencia, hablándoles siempre para que la figura de mamá no se borre de sus pensamientos, por su gran amor. A mis dos hermosos hijos Paula y Salvador, por entenderme, por esperarme, por acompañarme durante todos estos años, por tener la paciencia de verme estudiar horas de horas sin poder jugar con ellos, por no hacer ruido mientras estudiaba y por recibirme con alegría después de mis largas ausencias; ellos son el motor que me impulsa a lograr mis metas. No quiero olvidar a dos seres que partieron cuando apenas comenzaba a estudiar el pregrado, a mis padres Mario y Angélica, a él por enseñarme que el conocimiento es la mayor riqueza que puede portar un ser humano y a mi madre quien siempre confió en mi capacidad y cuyo último deseo fue que sea consecuente con mis elecciones y que termine la carrera que ya había comenzado; a ellos, donde quiera que estén muchas gracias. Finalmente, quiero dar gracias a Dios por conservarme con buena salud para poder realizar este sueño y también cuidar de mi familia durante mi ausencia.

A todos, mi más sincero agradecimiento.

Contents

List of Figures

List of Tables

List of Appendix

Appendix A 121

Appendix B 124

THÈSE

Pour obtenir le grade de
Docteur

Université Montpellier

Préparée au sein de l'école doctorale
SIBAGHE – Systèmes intégrés en Biologie, Agronomie, Géosciences, Hydrosciences et Environnement

Et de l'unité de recherche UMR MARBEC

Spécialité : Biologie des populations et écologie

Présentée par Ana Renza Paola ALEGRE NORZA SIOR

TITRE DE LA THESE

Trophic ecology of jumbo squid and predatory fishes in the Northern Humboldt Current System

Soutenue le **21 mai 2015** devant le jury composé de :

M. Sébastien, JAQUEMET, MCU HDR Université de La Réunion	Rapporteur
M. Marc, PAGANO, Directeur de Recherche IRD	Rapporteur
M. Frédéric MENARD, Directeur de Recherche IRD	Directeur de thèse
M. Arnaud BERTRAND, Directeur de Recherche IRD	co-Directeur de thèse
M. Yves, CHEREL, Directeur de Recherche CNRS	Examinateur
M. Nicolas BEZ, Directeur de Recherche IRD	Examinateur
Mme. Monique Simier, Ingénieure de Recherche	Invitée

IN MEMORIAM

A mi profesor Dr. Juan Leonidas Tarazona Barboza, quien partió de este mundo pocos días antes de la sustentación de esta tesis doctoral, por ser un gran ejemplo de entrega y pasión por la ciencia.

DEDICATORIA

A mis padres Mario† y Angélica† que son mi fuente de inspiración, a mis hijos Paula y Salvador quienes son el motor que me impulsa a seguir adelante y a mi esposo Flavio por su gran amor y su apoyo incondicional.

Abstract

This work provides a contribution to a better understanding of the trophic ecology of important predators in the Northern Humboldt Current System, the jack mackerel (*Trachurus murphyi*), the chub mackerel (*Scomber japonicus*) and the jumbo squid (*Dosidicus gigas*) by the characterization of the highly variable feeding patterns of these species at different spatiotemporal scales. We provided new knowledge on the comparative trophic behaviour of these species, defined as opportunistic in previous investigations. For that purpose we applied a variety of statistical methods to an extensive dataset of 27,188 non-empty stomachs. We defined the spatial organization of the forage fauna of these predators and documented changes in prey composition according to predators' size and spatiotemporal features of environment. Our results highligh the key role played by the dissolved oxygen. We also deciphered an important paradox on the jumbo squid diet: why do they hardly forage on the huge anchovy (*Engraulis ringens*) biomass distributed of coastal Peru? We showed that the shallow oxygen minimum zone present off coastal Peru could hamper the co-occurrence of jumbo squids and anchovies. In addition, we proposed a conceptual model on jumbo squid trophic ecology including the ontogenetic cycle, oxygen and prey availability. Moreover we showed that the trophic behaviour of jack mackerel and chub mackerel is adapted to forage on more accessible species such as for example the squat lobster *Pleurocondes monodon* and Zoea larvae. Besides, both predators present a trophic overlap. But jack mackerel was not as voracious as chub mackerel, contradictorily to what was observed by others authors. Fish diet presented a high spatiotemporal variability, and the shelf break appeared as a strong biogeographical frontier. Diet composition of our fish predators was not necessarily a consistent indicator of changes in prey biomass. El Niño events had a weak effect on the stomach fullness and diet composition of chub mackerel and jack mackerel. Moreover, decadal changes in diet diversity challenged the classic paradigm of positive correlation between species richness and temperature. Finally, the global patterns that we described in this work, illustrated the opportunistic foraging behaviour, life strategies and the high degree of plasticity of these species. Such behaviour allows adaptation to changes in the environment.

Key words: *Dosidicus gigas, Trachurus murphyi, Scomber japonicus,* trophic behaviour, Northern Humboldt Current system, Peru.

Résumé

Ce travail est une contribution à l'étude de l'écologie trophique d'importants prédateurs de la partie Nord du système du Courant de Humboldt (NSCH), le chinchard (*Trachurus murphyi*), le maquereau (*Scomber japonicus*) et le calmar géant (*Dosidicus gigas*). Nous avons caractérisé la variabilité des modes d'alimentation de ces espèces à différentes échelles spatiotemporelles et fourni de nouvelles connaissances sur le comportement alimentaire de ces espèces, définies comme opportunistes par des travaux antérieurs. Pour ce faire, nous avons appliqué une variété de méthodes statistiques à un vaste jeu de données comprenant 27188 estomacs non vides. Sur cette base nous avons décri l'organisation spatiale de la faune fourrage de ces prédateurs et documenté les changements dans la composition des proies en fonction de la taille de prédateurs et des conditions environnementales. Nos résultats indiquent que l'oxygène dissous jour un rôle clef dans ces processus. Nous avons également résolu un paradoxe sur l'alimentation du calmar géant: pourquoi ils ne se nourrissent guère sur l'immense biomasse d'anchois (*Engraulis ringens*) présente le long de la côte du Pérou? Nous avons montré que la présence d'une zone de minimum d'oxygène (ZMO) superficielle devant le Pérou pourrait limiter la cooccurrence entre calmars géant et anchois. Pour synthétiser ces résultats, nous avons proposé un modèle conceptuel de l'écologie trophique du calmar géant tenant compte du cycle ontogénétique, de l'oxygène et de la disponibilité des proies. Par ailleurs, nous avons montré que le chinchard et le maquereau se nourrissent des espèces les plus accessibles comme par exemple la galathée *Pleurocondes monodon* ou les larves zoea. Ces deux prédateurs présentent un chevauchement trophique mais, contrairement à ce qui avait été décrit dans d'autres études, le chinchard n'est pas aussi vorace que le maquereau. Le régime alimentaire de ces poissons est caractérisé par une forte variabilité spatio-temporelle et le talus continental s'avère être une importante frontière biogéographique. La composition du régime alimentaire des poissons prédateurs étudiés n'est pas nécessairement un indicateur cohérent de l'évolution de la biomasse des proies. Les événements El Niño ont eu un faible effet sur le taux de remplissage des estomacs et sur le régime alimentaire du chinchard et du maquereau. Par ailleurs les changes en diversité des proies à échelle décennale contredisent le classique paradigme de corrélation positive entre diversité et la température. Finalement, les patrons globaux décrits dans ce travail, illustrent le comportement alimentaire opportuniste les stratégies de vie et le haut degré de plasticité de ces espèces. Un tel comportement permet de s'adapter aux changements de l'environnement.

Mots clefs: *Dosidicus gigas, Trachurus murphyi, Scomber japonicus,* comportement alimentaire, Nord du système du Courant de Humboldt, Pérou.

Acknowledgements

It took a long time before these lines, perhaps because it is difficult to summarize in a few paragraphs feelings, emotions, stories I've shared with great friends, the way of this thesis was accompanied by people who managed with my make this dream a reality. When I studied the undergraduate a great friend gave me a wise counsel: "Surround yourself with good friends and copy the best of each person"; that phrase was coined in my mind and I began to highlight the best of each person I met on my way, trying to inspire in those qualities. This road was very difficult for me, I had to overcome many obstacles, but good examples from great people who showed up my life, taught me to have the courage and perseverance to finish what I started with great enthusiasm.

I starting with my advisor Frédéric Ménard, with whom I shared long discussions, hours of work and who thoroughly revised this thesis, always being very diligent in their criticism; but also for his patience, his good nature and support to do a good job. I also want to thank Dr. Arnaud Bertrand (IRD - France), for their unconditional support and wise counsel, for giving me the strength to go on the road and not lose heart, for being a friend and partner in this struggle without your vote confidence could not finish this stage of my career, in your hands I supported all these years of struggle that began in 2008, was a long way without truce, with difficulties that without their support I would not have been able to save. A Monique Simier engineer who not only actively contributed to the development of this thesis, also showed great professionalism in reviewing scripts, text and references; she was also a great friend and companion during the time of my stay in France.

I would also like to thank my fellow PhD Alexandra who supported me in difficult times, Lauriane and Andrea who they gave me their trust, Mariana, Fabian, Robert, Elizabeth, Lysel, Camille, Antonia, Angelie, Edgard, Justin and Arnaud. How I forget the friends of IFREMER, starting by Ghislaine who was my support in the most hard times, she especially wants to thank you for her affection and selfless support. To Liliana with her I shared many experiences, also her daughter Manuelita who cheered me and supplied a little lack of my children. Marta and Jeroen, who with their encouragement, cheered many of my evenings. To Isabelle Terrier who with her sweetness, always she made me feel at home. Ainhoa and Phillipe, who spread me joy, and for their pleasant conversations. To my friend Maria Grazia, she is collaborator, always giving selflessly her help. Bastien for his help, especially with the formalities documents at the

university. Catherina Gilles, They very kindly opened me the doors of your home and heart. To Pierre Freon, my great friend of many years, especially by the great dear, for allowing me to come home and meet your beautiful family, for the wise counsel and representing the great example for me; his wife Martine for their joy and great affection. Sophie Bertrand, who was always concerned for my family and with whom I shared pleasant evenings, Nicolas, Alexis, Jean, Jeremie, Alex.

I am not forget the friends Sète Daniel Gonzales and Manu, with whom I shared evenings music and talks about Latin American politics, George and Solange Botet gentlemen who with whom I developed a lasting friendship, friends of Nicole and Frank Gravy, the happy times we had.

To my fellow IMARPE, Andrew Chipollini without their important support would not be possible the completion of this thesis, Marilu Bouchon who opened the doors of the Directorate General of Pelagic Resources, Teobaldo Dioses, Miguel Ñiquen and Marco Espino, that his experience gave a great contribution to my work, to Ricardo Oliveros for his friendship and help with some aspects of my work; my fellow Functional Area Research Invertebrates and macroalgae, Carmen Yamashiro gave me the opportunity to work with the jumbo squid, to Juan Arguelles and Ricardo Tafur who contributed their knowledge in this work, Anatolio and Maria Nelly for their good wishes. To my colleagues in the Laboratory of trophic ecology, Pepe Espinoza, who served as an example for me to move on, Ivan Navarro who analyzed many of the samples and who gave me the wise counsel to move forward, to Rosario Cisneros for his unconditional friendship, Cesar Fernandez and David Castillo for their support. Jorge Tam and Michelle Graco, for their comments and contributions to my thesis.

I cannot pass up the opportunity to thank a great master who is no longer among us, he represented the greatest example in my career, I had the great opportunity of working with him for several years and learn from him. Dr. Juan Tarazona Barboza, for his advice, his teachings and his brilliant passing through the science of Peru, he left us a few days before of sustaining this work, I would have loved to return to Peru and personally hand this thesis; Unfortunately, he depart from this world before, now I can only give a fitting tribute through these lines "To my great teacher thanks for inspiring me to follow the path of science ", to give me, the example to work hard for the dreams and translate them into reality. I also want to thank Dr. Jaime Mendo for their teachings in the field and for his friendship.

I also want to thank my great friends Gerardo, Sandro, Manuel, Carola and Claudia, they always gave me courage and his trust. My chicks friends, Rocío Joo and Daniel Grados, for the working dawns, the *soirées* with wine, cheese and Peruvian food, for their good company in the lonely moments away from home; and especially grateful to my dear Giannina who was my stand for the happy and sad moments we share, for the patience of my many manias, for her joy and zest for life and commitment of unconditional friendship.

To my cousin Ivan Alegre and his beautiful family: Isabel, Paula and Julio for his great affection despite years of estrangement, also Fernando Alegre and his wife Nancy. For all, thanks for having opened the doors of their houses in Seville and they have been always aware of my progress. To my dear friend from the school: Hokulani (Star), with whom I shared beautiful days in France for his great example of life.

I want to give a very special place to my immediate family; especially my brother Mario, who showed in me the curiosity for knowledge, his long conversations in my childhood opened a door that led me to a totally fascinating way. My sister Fanny who showed me that with perseverance comes success, and encouraged me not to leave the path he had traced me. My sister Angelica that taught me to can talk with the public and give opinions and not just I hiding behind a book. To my brother in law Juan, who was always attentive and applauded my achievements. To my nephews Luis Felipe that despite the great difficulties he faced was able to overcome and follow their dreams, to Rodrigo, for his great personality, Adriano by his intelligence and Mateo for their occurrences. My niece Fanny by her great affection, complicity and her determination that characterizes by always encourage me and accompany me through thick and thin. My niece Monica made me see that should move forward in my career, for his great dear, and their mettle to conquer your goals. I also want to thank my political family to my in-laws Freddy and Luz, to my brothers in law, Joel, Gisella and Mariela and my nephews Camila, Josué, Aaron and Joel, for to give value to my husband to support me and wait me for the time I was far.

I want to thank Mrs. Sonia Zambrano, who took care of my children during my absence, without his support at home this would not have been possible. My husband Flavio Mendoza, who encouraged me to pursue this adventure, for their unconditional support, for his admiration that commits me to give the best of me, who accompanied my children during the time of my absence, always talking to my children's for that the mother figure is not erased from his thoughts, for his great love. To my two beautiful children Paula and Salvador, for understanding me, for waiting me, for joining me, for all these years, for to have the patience to see me study for hours without being able to play with them, for not make noise while I studied and for welcoming me with joy after my long absences; they are the engine that drives me to achieve my goals. I would not forget two people who left me when I was just beginning to study the undergraduate, my parents Mario and Angelica; him for teaching me that knowledge is the greatest wealth that can carry a human being and my mother who always trusted in my ability and whose last wish was to be consistent with my choices and end the race had begun; to them, wherever they are thank you very much. Finally, I want to thank God for keep me in good health to be able to realize this dream and taking care of my family during my absence.

To all, my sincere thanks.

Agradecimientos

Me tomó mucho tiempo comenzar estas líneas, tal vez porque es difícil sintetizar en pocos párrafos los sentimientos, emociones, anécdotas que he compartido junto a grandes amigos, el camino de esta tesis estuvo acompañado de personas que lograron junto a mi hacer de este sueño una realidad. Cuando estudiaba el pregrado un gran amigo me dio un sabio consejo: "rodéate de buenos amigos y copia lo bueno"; esa frase se acuñó en mi mente y comencé a destacar lo mejor de cada persona que encontré en mi camino, tratando de inspirarme en esas cualidades. Este camino fue muy difícil para mí, tuve que salvar muchos obstáculos, pero los buenos ejemplos tomados de grandes personas que se presentaron mi vida, me enseñaron a tener el temple y la perseverancia para finalizar lo que con mucha ilusión empecé.

Comenzando por mi asesor Frédéric Ménard, con quien compartí largas discusiones, horas de trabajo y quien minuciosamente revisó esta tesis, siendo siempre muy acucioso en sus críticas; pero también por su paciencia, su buen carácter y su apoyo para realizar un buen trabajo. También quiero dar las gracias al Dr. Arnaud Bertrand (IRD - Francia), por su apoyo incondicional y sabios consejos, por darme el ánimo para seguir en el camino y no desfallecer, por ser amigo y compañero en esta lucha, sin su voto de confianza no hubiera podido culminar esta etapa de mi carrera, en sus manos apoyé todos estos años de lucha que comenzaron en el 2008, fue un largo camino sin tregua lleno de dificultades y que sin su apoyo no hubiera podido salvar. A la ingeniera Monique Simier que no sólo contribuyó activamente al desarrollo de esta tesis, también demostró gran profesionalismo en la revisión de los scripts, el texto y las referencias bibliográficas; además fue una gran amiga y compañera durante el tiempo de mi estadía en Francia.

Asimismo, quiero agradecer a mis compañeros del doctorado Alexandra quien me apoyó en momentos difíciles, Lauriane y Andrea quienes me brindaron su confianza, Mariana, Fabian, Robert, Elizabeth, Lysel, Camille, Antonia, Angelie, Edgard, Justin, Arnaud. Como olvidar a los amigos del IFREMER, comenzando por Ghislaine quien fue mi soporte en los momentos más duros, a ella especialmente quiero dar las gracias por su cariño y apoyo desinteresado. A Liliana con quien compartí muchas experiencias, a su hijita Manuelita quien me alegró y suplió un poco la ausencia de mis hijos. A Marta y Jeroen quienes con su ánimo, alegraron muchas de mis tardes. A Isabelle Terrier que con su dulzura me hizo siempre sentir en casa. A Ahinoa y Phillipe que me contagiaron con su alegría y sus amenas conversaciones. A mi querida amiga Maria Grazia, tan colaboradora, siempre ayudándonos desinteresadamente, a Bastien por su ayuda, especialmente con los trámites en la universidad, a Gilles y Catherina que muy gentilmente me abrieron las puertas de su casa y su corazón. A Pierre Freón, mi gran amigo de tantos años, especialmente por el gran cariño, por haberme permitido entrar a su hogar y conocer a su hermosa familia, por los sabios consejos y el gran ejemplo que representa para mí; a su esposa Martine por su alegría y gran cariño. A Sophie Bertrand, que se preocupó siempre por mi familia y con quien compartí amenas veladas, a Nicolas, Alexis, Jean, Jeremie, Alex.

Tampoco olvidar a los amigos de Sète Daniel y Manu, con quienes compartí tardes de música y conversaciones sobre la política latinoamericana, a los señores George y Solange Botet quienes con quienes desarrollé una duradera amistad, a los amigos de la salsa Nicole y Frank, por los momentos alegres que pasamos.

A mis compañeros de IMARPE, a Andrés Chipollini, sin su importante apoyo no hubiera sido posible la culminación de este trabajo de tesis, a Marilú Bouchon quien me abrió las puertas de la Dirección General de Recursos Pelágicos, a Teobaldo Dioses, Miguel Ñiquen y Marco Espino que con su experiencia brindaron un gran aporte a mi trabajo, a Ricardo Oliveros por su amistad y ayuda con algunos aspectos de mi trabajo; a mis compañeros del Área Funcional de Investigaciones en Invertebrados y Macroalgas, Carmen Yamashiro que me dio la oportunidad de trabajar con el calamar gigante, a Juan Argüelles y Ricardo Tafur que contribuyeron con sus conocimientos en este trabajo, a Anatolio y María Nelly por sus buenos deseos. A mis compañeros del Laboratorio de Ecología Trófica, Pepe Espinoza, quien me sirvió de ejemplo para seguir adelante, Iván Navarro que analizó gran parte de las muestras y quien me dio los más sabios consejos para seguir avanzando, a Rosario Cisneros por su incondicional amistad, a César Fernández y David Castillo por su apoyo. A Jorge Tam y Michelle Graco, por sus observaciones y aportes a mi trabajo de tesis.

No puedo dejar pasar la oportunidad para agradecer a un gran maestro que ya no se encuentra entre nosotros, él representó el mayor ejemplo en mi carrera, tuve la gran oportunidad de trabajar a su lado por varios años y aprender mucho de él. Al Doctor Juan Tarazona Barboza, por sus consejos, sus enseñanzas y su brillante paso por la ciencia del Perú, se fue pocos días antes de sustentar este trabajo, me hubiera encantado regresar al Perú y entregarle personalmente esta tesis; lamentablemente, su partida de este mundo se adelantó, ahora sólo me queda otorgarle un merecido homenaje a través de estas líneas "A mi gran maestro gracias por haberme inspirado a seguir por el camino de la ciencia, a no rendirme, a trabajar duro por los sueños y a plasmarlos en realidad". También quiero agradecer al Doctor Jaime Mendo por sus enseñanzas en el campo y por su gran amistad.

Quiero también dar las gracias a mis grandes amigos Gerardo, Sandro, Manuel, Carola y Claudia que siempre me dieron ánimo y toda su confianza. A mis amigos los pollitos, Rocío Joo y Daniel Grados, por las amanecidas trabajando, las *soirées* con vino, queso y comida peruana, por la buena compañía en los momentos solitarios lejos de casa y muy especialmente agradeceré a mi querida Giannina quien fue mi soporte, por los momentos alegres y tristes que compartimos, por la paciencia a mis múltiples manías, por su alegría y ganas de vivir y por su compromiso de amistad incondicional.

A mi primo Iván Alegre y su hermosa familia Isabel, Paula y Julio por su gran cariño a pesar de los años de distanciamiento, igualmente a Fernando Alegre y su esposa Nancy, a todos ellos gracias por haberme abierto las puertas de sus casas en Sevilla y haber estado siempre pendientes de mis avances. A mí querida amiga del colegio Hokulani (Estrella), con quien compartí hermosos días en Francia, por su gran ejemplo de vida.

Quiero dar un espacio muy especial a mi familia más cercana, especialmente a mi hermano Mario, quien sembró en mí la curiosidad por el conocimiento, sus largas conversaciones en mi infancia abrieron una puerta que me llevó a un camino totalmente fascinante. A mi hermana Fanny quien me mostró que con la perseverancia se llega al éxito, me animó a no dejar el camino que me había trazado. A mi hermana Angélica que me enseñó a desenvolverme en público y dar opiniones y no sólo esconderme detrás de un libro. A mi cuñado Juan, quien siempre estuvo atento y aplaudió mis logros. A mis sobrinos Luis Felipe que a pesar de las grandes dificultades que tuvo que afrontar supo sobreponerse y seguir sus sueños, A Rodrigo, por su gran personalidad, A Adriano por su inteligencia y a Mateo por sus ocurrencias. A mi sobrina Fanny por su gran cariño, complicidad y esa determinación que la caracteriza, por darme siempre ánimo y acompañarme en las buenas y las malas. A mi sobrina Mónica que me hizo ver que debía seguir avanzando en mi carrera, por su gran cariño, y su temple para conquistar sus metas. También quiero agradecer a mi familia política a mis suegros Freddy y Luz, a mis cuñados, Gisella, Mariela y Joel y a mis sobrinos Camila, Josué, Aarón y Joel, por darle el valor a mi esposo de apoyarme y esperarme durante el tiempo que estuve lejos.

Quiero agradecer también a la señora Sonia Zambrano, quien cuidó a mis hijos durante mi ausencia, sin su apoyo en la casa esto no hubiera sido posible. A mi esposo Flavio Mendoza, quien me animó a seguir esta aventura, por su apoyo incondicional, su admiración que me compromete a dar lo mejor de mí, quien acompañó a mis hijos durante el tiempo de mi ausencia, hablándoles siempre para que la figura de mamá no se borre de sus pensamientos, por su gran amor. A mis dos hermosos hijos Paula y Salvador, por entenderme, por esperarme, por acompañarme durante todos estos años, por tener la paciencia de verme estudiar horas de horas sin poder jugar con ellos, por no hacer ruido mientras estudiaba y por recibirme con alegría después de mis largas ausencias; ellos son el motor que me impulsa a lograr mis metas. No quiero olvidar a dos seres que partieron cuando apenas comenzaba a estudiar el pregrado, a mis padres Mario y Angélica, a él por enseñarme que el conocimiento es la mayor riqueza que puede portar un ser humano y a mi madre quien siempre confió en mi capacidad y cuyo último deseo fue que sea consecuente con mis elecciones y que termine la carrera que ya había comenzado; a ellos, donde quiera que estén muchas gracias. Finalmente, quiero dar gracias a Dios por conservarme con buena salud para poder realizar este sueño y también cuidar de mi familia durante mi ausencia.

A todos, mi más sincero agradecimiento.

Contents

List of Figures

List of Tables

List of Appendix

Appendix A 121

Appendix B 124

Chapter I

General Introduction

Eastern Boundary Upwelling systems (EBUS) including the Humboldt, Canary, Benguela, and California Current systems (Figure 1.1), are among the most productive marine ecosystems in the world (Chavez and Messié, 2009; Fréon *et al.*, 2009). In their near shore upwelling zones, high primary and secondary productivity support large biomasses of small planktivorous pelagic fishes, or ‘’small pelagics”, which through predator-prey interactions can influence both higher and lower trophic levels through trophic controls (Cury *et al.*, 2000). Those four EBUS represent ~0.3% of the world surface oceans (Carr and Kearns, 2003) but produce about 20% of the world’s fish catches, contributing to securing food and livelihood strategies in many developing countries (Fréon *et al.*, 2009). Among EBUS Northern Humboldt Current system (NHCS) located off the Peruvian coast has stood as the ‘’world’s champion” producer, by far, of exploitable fish biomass (Chavez *et al.*, 2008). It represents less than 0.1% of the world ocean surface but presently sustains about 10% of the world fish catch. It produces more fish landings than the other EBUSs both total and on a per area basis (Chavez *et al.*, 2008). However, remote sensing-based estimates of primary production rank the NHCS third only (Figure 1.2), behind the Benguela and Canary Current systems (Carr, 2002; Chavez *et al.*, 2008). Between 1950 and 2012, more than 275 millions of tonnes of anchovy have been landed in Peru (FAO, 2014a). The fisheries sector is a key component of Peruvian economy, mainly as a significant source of foreign currency, after mining. The marine fisheries sector generates directly and indirectly more than 145,000 employments with an export value of 2.432 billion US dollars in 2008 (FAO, 2014b). Catches are traditionally based on marine pelagic resources, mainly anchovy and other species such as jack mackerel and chub mackerel. But other resources including dolphinfish (perico) (*Coryphaena hippurus*; Linnaeus, 1758) and invertebrates such as the jumbo squid are now exploited (FAO, 2014b).

In a way, this apparent paradox of a high fish productivity with a median primary productivity in the NHCS supports the hypothesis of a greater food chain efficiency for that EBUS (Cury and Roy, 1989; Taylor *et al.*, 2008). Indeed the NHCS proximity to the equator and large Rossby radius results in strong and sustained upwelling under relatively mild wind forcing (Cury and Roy, 1989; Bakun, 1996). Thus the large scale wind and circulation patterns provide, respectively, the driving force for upwelling and the optimal nutrient concentration for significant biological production (Carr and Kearns, 2003). These conditions create a ‘‘particularly rich, non-turbulent, benign environment” by which rich coastal plankton communities develop and persist, in turn supporting abundant populations of small pelagics (Bakun and Weeks, 2008).

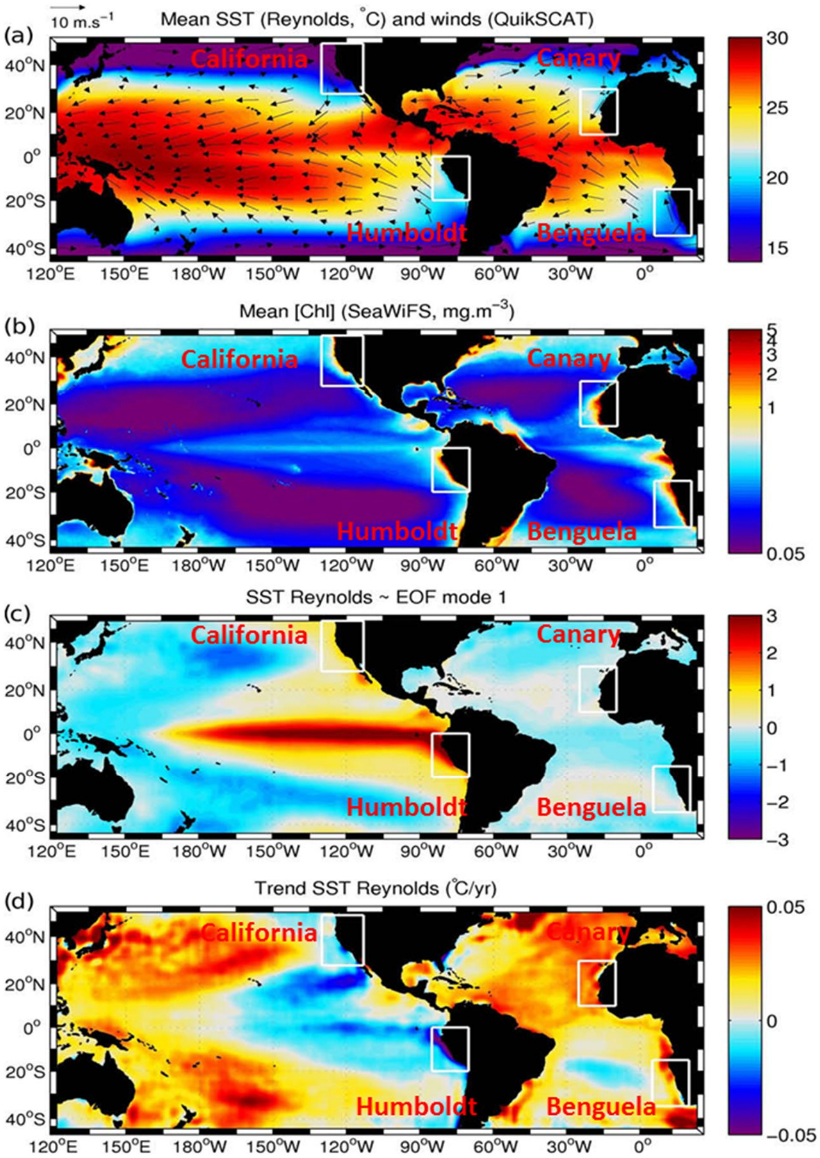

Figure 1.1. Basin-scale maps of mean sea surface temperature (SST) and winds (a). Chlorophyll (b), first empirical orthogonal function of SST (c), and trend in SST from 1981 to 2008 (d) showing the location of the Eastern Boundary Upwelling Systems (EBUS). SST is Reynolds et al. (2007) monthly averaged from October 1981 to February 2007; winds are QuikSCAT monthly averaged from July 1999 to April 2008; chlorophyll is SeaWiFS monthly climatology averaged over the year. The EOF analysis uses the same methodology as produces the Pacific Decadal Oscillation (PDO; Mantua et al., 1997), first removing the global trend and then seasonal cycle at each pixel, but in this case for the Atlantic and Pacific basins (and globally in Chavez et al., 2008) rather than just the North Pacific (Source: Chavez and Messié, 2009).

On the other hand, the NHCS is the region where El Niño Southern Oscillation (ENSO) and climatic variability in general are most notable. The NHCS and its living resources are therefore directly impacted by an intense and highly variable climate forcing at different spatiotemporal scales (e.g., climate change, secular, decadal, inter-annual, seasonal and intra seasonal variabilities) (Chavez *et al.*, 2008).

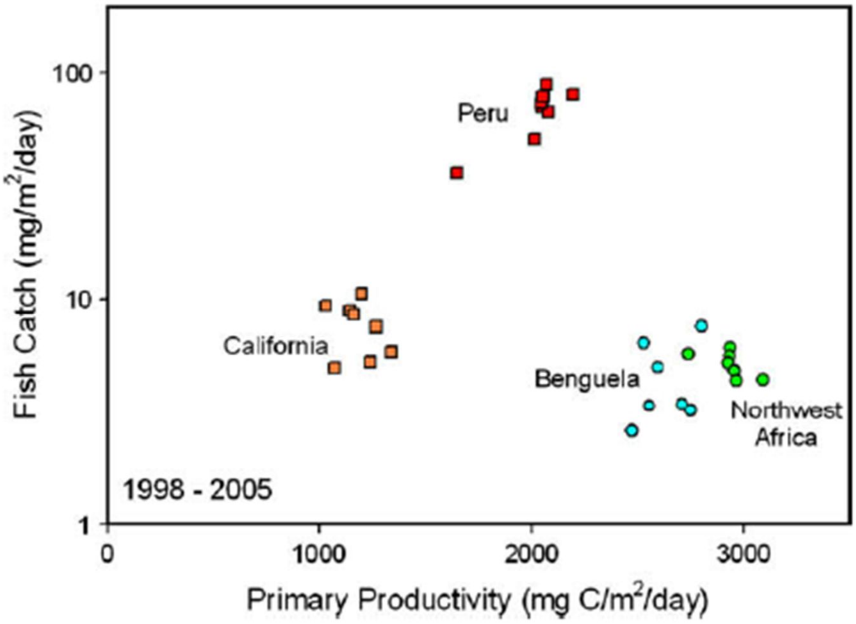

Figure 1.2. Fish catch versus primary productivity for the four main eastern boundary coastal upwelling ecosystems for the years 1998-2005. Source: Chavez et al. (2008).

Earlier studies have shown an overwhelming numerical dominance of phytoplankton in forage fish stomach contents (Rojas de Mendiola *et al.*, 1969; Pauly et al., 1989) and led to the belief that the large populations of small pelagic fish in the NHCS were fuelled by an unusually short and efficient food chain (Ryther, 1969). However, recent works (Espinoza and Bertrand, 2014, 2008; Espinoza, 2014; Espinoza *et al.*, 2009) demonstrated that the most important source of calories for anchovy and sardine (*Sardinops sagax*; Jenyns, 1842) is indeed zooplankton (primarily euphausiids and large copepods), refuting the former paradigm on the trophic pathways in the NHCS. Considering the importance of forage fish in the ecosystem, these results impose revisiting trophic flows and more generally ecosystem functioning in the NHCS. The efficient energetic transfer from one trophic level to another in the NHCS suggests that zooplankton production could be higher in the NHCS than in other upwelling systems. This higher secondary production could be related to a more efficient use of primary production by zooplankton and/or a strong connection between the coastal and the offshore pelagic ecosystems, this last argument may particularly apply to the euphausiids (Espinoza and Bertrand, 2008).

In this context the main objective of this study is to better understand the trophic behavior of important predators in the NHCS, namely the jack mackerel (*Trachurus murphyi*), the chub mackerel (*Scomber japonicus*) and the jumbo squid (*Dosidicus gigas*). For that purpose, this study is organized in the following chapters:

Chapter II provides an outline of the main characteristics of NHCS in order to help the lector to contextualize and interpret the following chapters. We first describe the physical and chemical oceanography, the primary and secondary production, and the main resources from pelagic fishes to squid. Second, we synthesize the main temporal dynamics affecting the NHCS and propose general description of each studied species.

Chapter III addresses the spatiotemporal patterns of the jumbo squid trophic ecology in the NHCS. We investigate the ontogenetic and spatiotemporal variability of the diet composition of jumbo squid in the northern Humboldt Current system. For that purpose we apply several statistical methods and here, we used an extensive dataset of 3,618 jumbo squid non empty stomachs collected off Peru from 2004 to 2011. A total of 55 prey taxa was identified that we aggregated into eleven groups to provide new insight on the size-related and spatiotemporal variability of feeding habits of *D. gigas*. We also decipher one paradox in the jumbo squid diet: why do they hardly forage on the tremendous anchovy (*Engraulis ringens*) biomass distributed of coastal Peru.

Chapter IV addresses the spatiotemporal patterns of Jack mackerel *Trachurus murphyi* (JM) and chub mackerel *Scomber japonicus* (CM) diet composition using a large dataset of stomach samples collected from 1973 to 2013 along the Peruvian coast. In total 47,535 stomachs (18,377 CM and 29,158 JM). were analysed, of which 23,570 (12,476 CM and 11,094 JM) were non-empty; and provided new insight in the variability in space and time of feeding habits and prey diversity of JM and CM in the northern Humboldt Current system (NHCS).

Chapter V consists in a section of general conclusions where, on the base of the results, we discuss how these findings allows for an improved vision of the functioning of the NHCS and what are the main following steps. To do so we will use information from studies (Rosas *et al.*, 2011; Lorrain *et al.*, 2011; Argüelles *et al.*, 2012; Alegre *et al.*, 2013, 2015) and what are the key next steps.

Chapter II

The Northern Humboldt Current system

In this chapter we briefly describe the most important physical and biological features of the NHCS. Then we describe the temporal dynamics of the NHCS and finally we propose a general description of each species studied, in order to contextualize and interpret the following chapters.

2.1. Atmospheric forcing of the NHCS

The marine climate off the west coast of South America results from the interaction of basin-scale atmospheric systems, combined with regional and local effects caused bay the land-sea boundary. Of these systems, the most influential is the South-Eastern Pacific Subtropical Anticyclone (SEPSA), which is an area of high atmospheric pressures triggering equatorward winds along the coast of Chile and Peru. This forcing generates winds rotating counterclockwise around the South Pacific. This wind system carries the surface waters by friction, giving rise to an anticyclonic ocean circulation, known as the South Pacific subtropical gyre. The SEPSA is bounded in the north by the Inter-Tropical Convergence Zone (ITCZ) and to the south by the polar front and disturbances along the front. Associated with the anticyclone is a subsidence inversion at the top of marine boundary layer, which slopes downward from west to east, creating onshore-offshore gradients in wind stress and cloudiness. The intersection of the inversion and coastal mountains supports the alongshore poleward propagation of coastally trapped atmospheric waves (coastal lows). The alongshore winds are also modified by regional effects, such as the baroclinicity created by onshore-offshore horizontal temperature gradients across upwelling fronts, the coastline and mountain slopes. Local effects are added to the basin and regional scale factors by local topography and coastline orientation, especially those created by bays and headlands. These atmospheric factors affect local surface fluxes of momentum (wind stress and buoyancy (precipitation, freshwater runoff and surface heat flux) over the coastal ocean. (Strub *et al.*, 1998) (Figure 2.1).

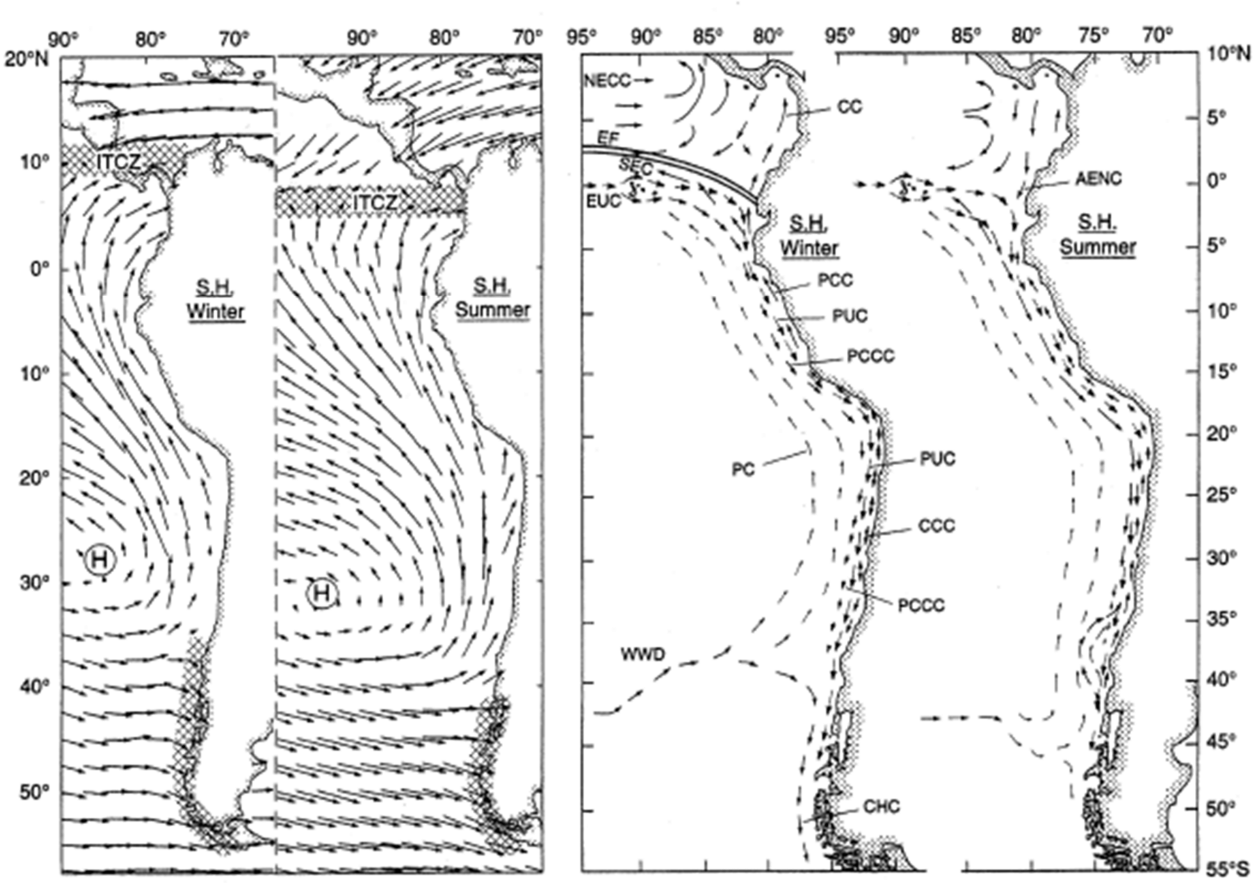

Figure 2.1. Climatologically winds and currents during austral winter and summer. Peru Current (PC), Peru Coastal Current (PCC), Poleward Undercurrent (PUC), Peru-Chile Countercurrent (PCCC), Chile Current (CC), Chile Coastal Current (CCC), Cape Horn Current (CHC), West Wind Drift (WWD) . Source: Strub *et al.* (1998).

At the northern boundary of the region, the ITCZ displays annual latitudinal displacements, moving from ~10°N with the seasonal maximum occurring in austral autumn and winter (June to September) to 2-5°N and in austral summer (December-March). The equatorward winds resulting from the land-sea temperature gradient produce coastal upwelling reinforcing the difference in temperature and pressure across the coastline.

2.2. Oceanography and physicochemical properties of the NHCS

2.2.1. Oceanic circulation

In the NHCS, the ocean circulation is mostly wind-driven by the South Pacific subtropical anticyclone forcing the South Pacific gyre whose eastern flank comprises the equatorward Peru Oceanic Current (POC) (Chaigneau *et al.*, 2013). The South Pacific subtropical anticyclone generates surface winds rotating counterclockwise around the South Pacific. The combined effect of wind force and earth rotation (Coriolis force) creates a natural pump system, the Ekman transport, advecting coastal surface waters offshore; those are replaced close to coast by colder nutrient rich waters upwelled from the bottom (Bakun, 1996).

Near the equator, the POC flows westward and feeds the South Equatorial Current (SEC) in the offshore surface layers (Strub *et al.*, 1998; Kessler, 2006). The SEC is forced by the easterlies toward the western equatorial Pacific creating an eastward pressure gradient force that drives, in subsurface layers, the eastward flowing Equatorial Undercurrent (EUC) centered along the equator (Philander, 1973). East of the Galapagos archipelago, the EUC separates into two branches, one branch flowing southeastward to reach the Peruvian coast at 5°S, while the other branch remains trapped along the equator (Kessler, 2006; Collins *et al.*, 2013). Below the thermocline and further South, the primary and secondary Southern Subsurface Countercurrents (SSCCs) flow eastward and enter the NHCS along nominal latitudes of 5° S and 7° S (Stramma *et al.*, 2010; 2011).

Near the Peruvian coast, the dominant along shore equatorward winds and cyclonic wind-stress curl lead to an intense upwelling characterized by cold and highly productive water and a current system composed of equatorward surface and mainly poleward subsurface flows (Figure 2.2). The equatorward surface circulation is composed by the Peru Coastal Current (PCC) that is mainly wind-driven (Wyrtky, 1967, 1966). The subsurface poleward circulation is mainly composed by the Peru-Chile Undercurrent (PCUC) along the Peruvian continental shelf and slope and a weaker secondary poleward flow, the Peru-Chile Countercurrent (PCCC) that flows almost directly south along 80° to 85°W (Huyer *et al.*, 1991; Penven *et al.*, 2005). North of 5°S, a near-surface coastal current flowing from Ecuador to Peru and associated with the surfacing of the EUC, has been suggested (Lukas, 1986; Collins *et al.*, 2013). Close to the Ecuadorian coast, a northwestward oriented surface current can also take place (Allauca, 1990; Collins *et al.*, 2013). Among the different currents that compose the NHCS, the PCUC is a key element advecting seawater property anomalies from equatorial to extra tropical regions and playing a major role in the functioning of the NHCS ecosystem. The PCUC that has been tracked along the continental shelf and upper slope from 5°S off Peru to 45°S off Chile (Silva and Neshybat, 1979), carries a relatively warm, salty, nutrient-rich, oxygen-poor, and weakly stratified water mass of near-equatorial origin (Silva and Neshybat, 1979; Tsuchiya and Talley, 1998). This water mass, the Equatorial Subsurface Water (ESSW), flowing southward into the PCUC is the main source of the coastal upwelled waters in NHCS promoting an intense primary productivity (Albert *et al.*, 2010; Chavez *et al.*, 2008; Huyer *et al.*, 1987; Toggweiler *et al.*, 1991).

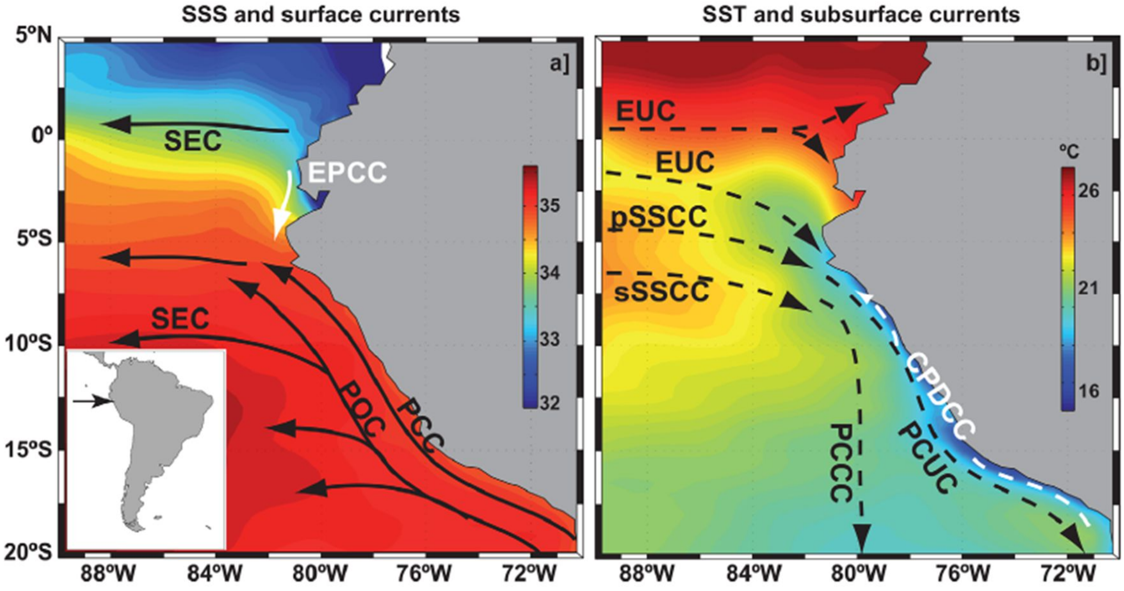

Figure 2.2. Sea surface properties and oceanic circulation scheme. (a) Sea-surface salinity (SSS, color shading) and surface circulation. (b) Sea-surface temperature (SST, color shading in °C) and subsurface circulation. SST and SSS were derived from the CARS 2009 climatology (Ridgway et al., 2002). This figure was adapted from several authors (Czeschel et al., 2011; Kessler, 2006; Mollier-Vogel et al., 2012; Montes et al., 2010; Penven et al., 2005). The newly defined Ecuador-Peru Coastal Current (EPCC) and Chile-Peru Deep Coastal Current (CPDCC) are indicated by white arrows. Surface currents: South Equatorial Current (SEC); Ecuador-Peru Coastal Current (EPCC); Peru Oceanic Current (POC); Peru Coastal Current (PCC). Subsurface currents: Equatorial Undercurrent (EUC); primary (northern branch) Southern Subsurface Countercurrent (pSSCC); secondary (southern branch) Southern Subsurface Countercurrent (sSSCC); Peru-Chile Countercurrent (PCCC); Peru-Chile Undercurrent (PCUC); Chile-Peru Deep Coastal Current (CPDCC) (Source: Chaigneau et al., 2013).

2.2.2. Water masses distribution

Four main types of water masses are observed in the NHCS: cold coastal water (CCW), subtropical surface water (SSW), equatorial surface water (ESW) and tropical surface water (TSW) (Table 2.1). Bertrand *et al.* (2004b) described extra mixed water masses: CCW–SSW and CCW–SSW–ESW. CCW are strongly influenced by coastal upwelling (Echevin *et al.*, 2004) and are very productive. The oligotrophic SSW are found offshore of the CCW. TSW are situated north of the equator and characterized by higher temperatures and lower salinities than other water masses off Peru. The mesotrophic ESW are located between the CCW and the TSW. El Niño–La Niña events strongly impact water mass distribution. For instance, during the El Niño 1997-98, most of the Peruvian EEZ was covered by oceanic water mass (SSW) until mid-1998. In the north, tropical and equatorial water masses were observed, mainly during the second flux of El Niño in March to May 1998. Close to the coast, CCW or mixed waters were always present, even if limited to restricted areas. The radical shift from El Niño to La Niña was clearly observed, first in the southern part of Peru in August to September 1998 and then along the whole coast after November 1998. The consequences were an important offshore expansion of CCW and a backflow of oceanic water (Figure 2.3). Equatorial and tropical water masses were observed north of 7°S in summer 1999 (Bertrand *et al.*, 2004b).

Table 2.1. Main characteristics of the water masses presents in the Humboldt Current System. Source: Bertrand et al. (2004b)

Water mass	Abbreviation	Temperature (°C)	Season	Salinity (‰)	Ecological Type
Cold coastal water	CCW	[15°; 17°] [15°; 19°]	winter summer	[34.80; 35.05]	coastal productive
Subtropical surface water	SSW	[17°; 25°] [20°; 25°]	winter summer	>35.10	oceanic oligotrophic
Equatorial surface water	ESW	[20°; 26°] [21°; 26°]	winter summer	[34.00; 34.80]	mesotrophic
Tropical surface water	TSW	>23° >26°	winter summer	<34.00	oligotrophic

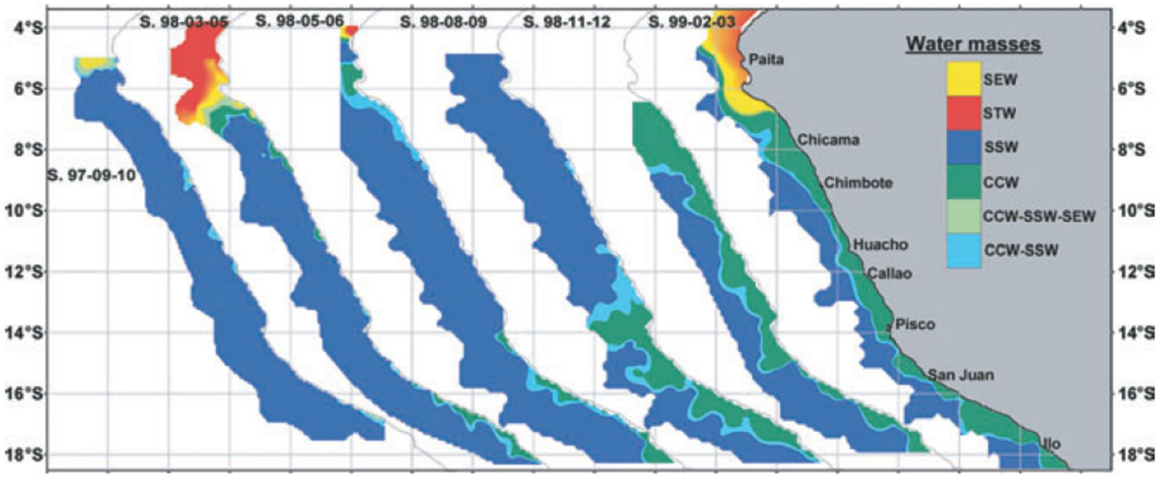

Figure 2.3. Water masses distribution for each survey (from left to right: surveys conducted in 1997-09-10, 1998-03-05, 1998-05-06, 1998-08-09, 1998-11-12 and 1999-02-03). CCW, cold coastal water; SEW, superficial equatorial waters; SSW, superficial subtropical waters; STW, superficial tropical waters (Source: Bertrand et al., 2004b).

2.2.3. Nutrients supply

Off Peru, primary production reaches values between 3 and 4 $g.C.m^{-2}.d^{-1}$ in the coastal strip of 100 km (Calienes *et al.*, 1985; Graco *et al.*, 2007). Nutrient availability in front of Peru is the result of coastal upwelling events, which carry from shallow depths (usually 50-100 m) waters with high levels of nitrate and low dissolved oxygen (Zuta and Guillén, 1970). Major local upwelling centers have been identified in Peru at 5°S (Paita), 6ºS (Punta Aguja), 9ºS (Chimbote), 12ºS (Callao) and 15°S (San Juan) (Rojas de Mendiola, 1981; Zuta and Guillén, 1970). The upwelling intensity increases along the coast of Peru during winter and spring, being weaker in summer and autumn (Graco *et al.*, 2007).

The highest concentrations of nutrients off Peru are located near the coast. The average surface nutrient ranges are: 0.2 to 4.0 µM for PO_4^{2-}; 0.0 to 35.0 µM for NO_3^-; 0.0 to 30.0 µM for SiO_2^{4+} (Zuta and Guillén, 1970; Calienes *et al.*, 1985). The nitrates concentration ranges between 20.0 µM and 0.5 µM from 0 to 50 miles (Zuta and Guillén, 1970), and to the north of 15°S nitrates and silicates concentrations are higher, until to 35.0 and 30.0 µM, respectively (Zuta and Guillén, 1970; Codispoti, 1981). Nitrates and silicates can be depleted during phytoplankton blooms while phosphorus is always present in excess (Graco *et al.*, 2007). The biochemical processes with the oceanographic dynamic determine the temporal variability of nutrients (Zuta and Guillén, 1970; Guillén *et al.*, 1977; Calienes *et al.*, 1985). For example silicates and nitrates have similar patterns of distribution and variability. The highest concentrations of silicates (25.0 µM) are observed in winter and spring and the lowest in summer (1.0 µM) (Calienes *et al.*, 1985).

The ratio between nitrates, phosphates and silicates (N/P/Si) are 11.0/1.0/9.0 in the layer of 0-25 m within 50 nm from the coast, and 13.0/1.0/9.0 off 55 nm from the coast (Guillén *et al.*, 1977). Silicates appear to be the main limiting nutrient for phytoplankton growth (Graco et al., 2007).

In summary, the highest concentrations of nutrients are located near the coast (Calienes *et al.*, 1985). With respect to latitude nutrient concentrations decrease from north to south (Zuta and Guillén, 1970; Codispoti, 1981), and seasonal variability is associated with the intensity of upwelling events, i.e. maximum in winter and spring, and weaker in summer and autumn (Calienes *et al.*, 1985; Graco *et al.*, 2007).

2.2.4. Oxygen Minimum Zone (OMZ)

The oceans include areas called oxygen minimum zones (OMZs) where subsurface layers are depleted in dissolved oxygen (DO) (Levin, 2003). OMZs are divided from the oxygenated surface mixed-layer by strong vertical DO gradients forming the oxycline. These OMZs contribute to 25–75% of oceanic N_2O production (Gallardo, 1977), a potent greenhouse gas, which influences the Earth's heat budget and depletes stratospheric ozone (Arntz *et al.*, 1991). The NHCS is characterized by the presence of one of the more intense and surface OMZ of the global ocean (Helly and Levin, 2004; Chavez and Messié, 2009; Paulmier and Ruiz-Pino, 2009). OMZs result from the sinking and decay of surface-derived high primary production and poor ventilation. In the NHCS, the OMZ is thickest (>600 m) off Peru between 5 and 13ºS and to about 1000 km offshore (Fuenzalida *et al.*, 2009) (Figure 2.4). Indeed the coastal upwelling lifts the coastal hypoxic layer closer to the sea surface (Fuenzalida *et al.*, 2009).

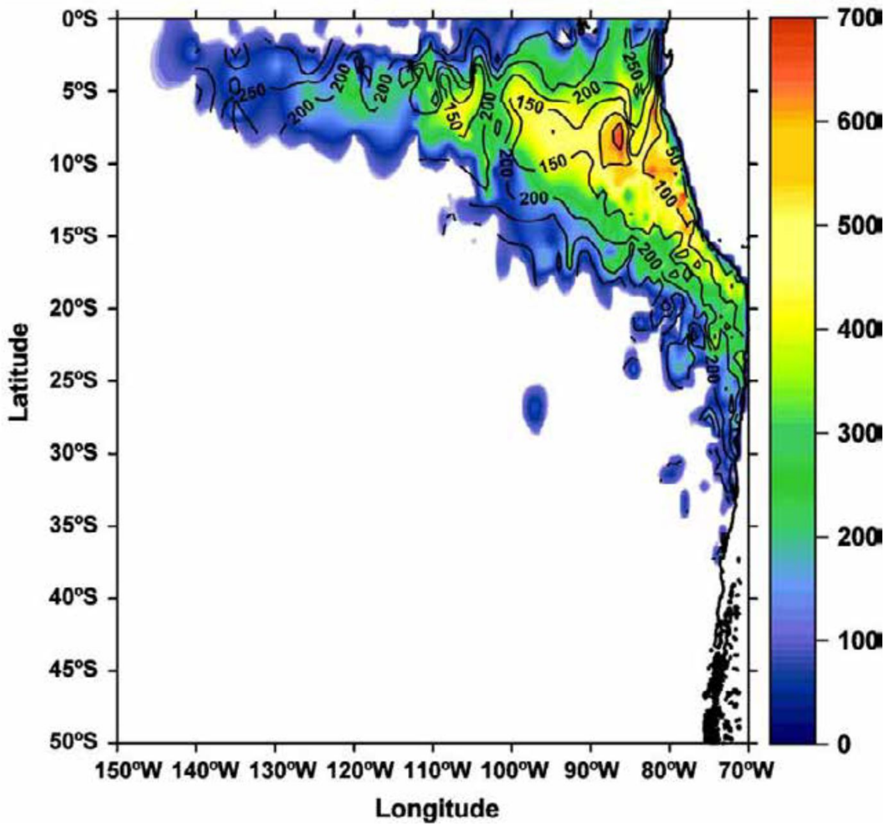

Figure 2.4. Oxygen minimum zone (OMZ) in the south-eastern Pacific. Thickness is colour-coded according to the colour bar on the right-hand side of the figure; units are in m. The upper boundary of the OMZ is shown in black contour lines with 50 m intervals. Source: Fuenzalida et al. (2009).

OMZs are generally the site of intense denitrification (Gutiérrez *et al.*, 2008a) and have notable effects on the distribution and mortality of marine organisms (Diaz and Rosenberg, 2008; Rosa and Seibel, 2008). Although some species of zooplankton, mesopelagic fish and squid have adapted their metabolism to colonize the OMZ temporarily (diel vertical migration) or permanently, the oxycline, which delimits the top of the OMZ, forms an impenetrable barrier for most marine species intolerant to hypoxia (Ayón *et al.*, 2008a; Bertrand *et al.*, 2010). In the NHCS various species of euphausiids and of copepods of the genera *Eucalanus* are adapted to hypoxia and occupy the OMZ during the day (Antezana, 2009; Escribano *et al.*, 2009). During the night, however, they migrate to the surface and become integral part of the epipelagic community (Antezana, 2009; Escribano *et al.*, 2009) (Figure 2.5). In response to global warming and anthropogenic influences, OMZs of the World Ocean are increasing (Stramma *et al.*, 2008). The upper limit of OMZs is growing and therefore, the vertical extent of the well-oxygenated surface layer contracts, constraining the vertical habitat of epipelagic organisms (Bertrand *et al.*, 2010, 2011). Upwelling regions are particularly vulnerable given that they encompass the largest OMZs (Levin, 2003).

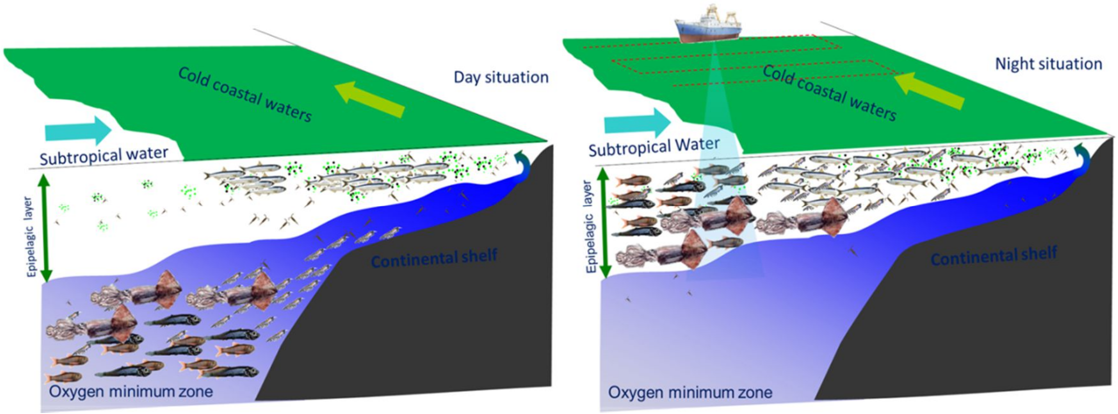

Figure 2.5. Schematic vision of the effect of Oxygen minimum zone (OMZ) in the distribution of species according to day and night periods.

2.3. The Pelagic Ecosystem

2.3.1. Primary and secondary production

In the NHCS, moderate and seasonally varying winds drive an offshore Ekman transport and an upward flux of cold, nutrient-rich waters along the coast. The presence of nutrient-rich waters and high insolation at this low latitude generates a year-long but fluctuating phytoplankton bloom which sustains a very rich ecosystem with high stocks of pelagic fish (Echevin *et al.*, 2008).

In this system, the phytoplankton community is characterized by the dominance of diatoms within coastal upwelling areas. However, phytoplankton species composition changes during the primary production cycle: from small diatoms with a high reproduction rate (*Skeletonema costatum*, *Chaetoceros debilis*) to larger diatoms species (*Thalassionema nitzchioides, Proboscia alata*) (Sánchez, 2000). While diatoms dominate phytoplankton communities within the CCW, dinoflagellates and nanoplankton dominate the offshore less turbulent water masses (Sánchez, 2000). Some species of dinoflagellates are commonly used as biological indicators of water masses (Arntz and Fahrbach, 1996; Sánchez, 2000): *Protoperidinium obtusum* for CCW; *Ceratium breve*, *Ornithocercus steinii*, *Ornithocercus thumii* and *Amphisolenia Thrinax* for ESW; and *Ceratium praelongum* and *Ceratium incisum* for SSW.

High primary production in upwelling areas fuels an elevated secondary production of herbivorous zooplankton. Among upwelling areas, the EBUS apparently show the greatest secondary production (Cushing, 1971).

In the NHCS, the secondary production is predominantly composed by several zooplankton groups, in particular copepods, euphausiids and chaetognaths (Gutiérrez *et al.*, 2005; Ayón *et al.*, 2008a). Santander (1981) defined three major mesozooplankton groups according to their spatial distribution: (i) a continental shelf group dominated by the copepods *Acartia tonsa* and *Centropages brachiatus*; (ii) a continental slope group composed by siphonophores, bivalves, foraminifera, and radiolaria; and (iii) an oceanic group composed by the copepods *Mecynocera clausi*, *Pleuromamma gracilis*, *Scolecithrix danae*, *Lucicutia flavicornis*, *Euchaeta marina*, *Euchirella bella*, *Oithona plumifera*, *Calocalanus pavo*, *Temora stylifera*, *Temora discaudata*, *Nannocalanus minor*, *Eucalanus subtenuis*, *Acrocalanus* sp., *Corycaeus* sp., *Oithona* sp., *Oncaea* sp., *Sapphirina* sp., *Corycella* sp. and *Copilia* sp..

The analysis of historical data (plankton net sampling) shows that higher mesozooplankton biovolumes are found offshore, probably due to stronger predation nearshore within the CCW (Ayón *et al.*, 2008b) and an higher vertical range of habitat allowing for vertical migration. In addition the number of tropical species greatly decreases toward the coast (Ayón *et al.*, 2008a).

The macrozooplankton biomass also increase across the continental shelf, slope and toward the offshore area Ballón *et al.* (2011) . This macrozooplankton fraction is dominated by euphausiids and large copepods in particular *Eucalanus* spp. (Ayón et al., 2008a, Escribano *et al.*, 2009). About 75% of macrozooplankton biomass, in particular euphausiids and *Eucalanus* spp. perform diel vertical migration and inhabit the OMZ during the day (Ayón *et al.*, 2008a; Escribano *et al.*, 2009; Ballón *et al.*, 2011).

Specifically *Eucalanus inermis* is the most important large copepod species (Ayón et al., 2008a). It is considered as indicator of CCW (Ayón *et al.*, 2008a) and is very common in the diet of anchovy and sardine in the NHCS (Espinoza and Bertrand, 2008; Espinoza *et al.*, 2009).

Euphausiids are most likely the most abundant zooplankton group by biomass in the NHCS. They form very dense swarms that are able to remove most of the diatoms biomass, exerting a local top-down control on primary production (Antezana 2010). In addition they contribute to two and one third of the diet (by carbon content) of anchovy (Espinoza and Bertrand, 2008) and sardine (Espinoza *et al.*, 2009), respectively. Very high concentration of euphausiids usually occurs along the shelf break when the deep flow is convergent and the upwelling very strong (Simard and Mackas, 1989; Mackas *et al.*, 1997). The shelf break play an important role in transporting and retaining zooplankton (Bakun, 1996; Genin, 2004; Zhu *et al.*, 2009). Adult euphausiids can maintain their position along the continental shelf break through diel vertical migration (Barange and Pillar, 1992; Swartzman *et al.*, 2005).

The squat lobster *Pleuroncodes monodon* has also an important role in the system, either by competing for space and food with important pelagic fish stocks, or as a food source for top predators (Gutiérrez *et al.*, 2008b). This species is mainly distributed off Chile with a demersal habitat, but has extended its distribution from northern Chile to Peru, and has considerably increased its biomass off Peru in the mid-1990s, which match with the period of colder conditions. Surprisingly, squat lobster exhibits a complete pelagic life cycle in the NHCS which is attributed to the intense and shallow OMZ off Peru, restricting demersal habitats (Gutiérrez *et al.*, 2008b).

2.3.2. Pelagic fishes

“Small pelagic fish” commonly refers to shoaling epipelagic fish characterized by high horizontal and vertical mobility in coastal areas and which, as adults, range usually in length from 10 to 30 cm. The upper limit is often debated, and some authors use the term “medium-sized pelagic fish” to designate larger fish ranging from 20 to 60 cm. The small pelagic fish includes typical forage species like sardine and anchovy mainly preying on zooplankton, while the group of medium-sized pelagic fish includes mostly species from intermediate trophic levels like jack mackerel, chub mackerel and coastal tunas (e.g., bonito). When adults, the latter species prey mainly on macrozooplankton, ichthyoplankton, and small fish or mollusks (Fréon *et al.*, 2005). These species exert a major trophic control on the dynamics of marine ecosystems, and are heavily exploited by industrial and artisanal fisheries (Cury *et al.*, 2000). Small pelagics are most abundant in upwelling areas and contribute to food security. Exploited stocks of these species are prone to large interannual and interdecadal variation of abundance as well as to collapse (Fréon *et al.*, 2005). At present, small pelagic forage fish species represent the largest landings of the world fisheries (27.3 millions of tonnes and 29.7% of total world catches). Currently, the Peruvian anchovy is the top landed species with more of 7 millions of tonnes in 2011 (FAO, 2014a).

The NHCS sustains large populations of small pelagic fish and supports the world's largest tonnage fishery for Peruvian anchovy (Bouchon *et al.*, 2000). The NHCS also supported a major sardine fishery in the past (Csirke *et al.*, 1996). However, at the end of the 1997-98 El Niño, the anchovy population was high while the sardine population was depleted (Bertrand *et al.*, 2004b, 2011; Cardenas, 2009) and currently, there is virtually no more sardine exploited in the NHCS . Pelagic resources off the coast of the Southeast Pacific are abundant and exhibit high variability over short periods of time. Their availability is directly related to the intensity and persistence of local upwelling processes and remote climatic forcing. Anchovy dominated the pelagic fishery landings in the 1960s, becoming the most important fishery in the world but landings declined drastically from 1972, (Ñiquen *et al.*, 2000). The anchovy collapse has been attributed to a combination of overfishing, an El Niño event and the decadal shift towards less productive conditions (Alheit and Niquen, 2004; Bertrand *et al.*, 2004b, 2011). The anchovy stock started giving signs of recovery in 1981 but was hit again by the El Niño 1982-83(Hilborn and Walters, 1992). Anchovy the began to recover and become highly abundant again since the 1990s (Ñiquen *et al.*, 2000; Gutiérrez *et al.*, 2007; Bertrand *et al.*, 2011).

Among the medium-sized pelagic fish, jack mackerel is one of the most important exploited fish populations in the world. Its distribution covers the sub-tropical waters of the South Pacific Ocean, from South America up to New Zealand and even Australia (Gerlotto *et al.*, 2012). In Peru records of jack mackerel landings started in 1907 (Coker, 1910) and continuous statistics are available since 1939. At the beginning of its exploitation, annual catches were low, but increased from 10 to a few hundred tonnes per year prior to 1963 (Tilic, 1963). Catches had a steep increase from 130,000 tonnes in 1974 to 500,000 tonnes in 1977. Biomass of jack mackerel were assessed by acoustics at 1.9 million of tonnes at the end of 1997, and then almost disappeared from the acoustic observations (Bertrand *et al.*, 2004b) until the late 2000s. According to Gerlotto *et al.* (2012), since the late 1990s, *T. murphyi* has suffered a strong decrease in total catches, which dropped to close to 0.5 million tonnes. During the 2002-2011 period, annual reports of *T. murphyi* landings showed a clear downward trend in the Peruvian coast with a minimum in 2010. On the opposite, 260,000 tonnes were recorded in 2011, a figure much higher than the ones obtained in 2007 and 2008 (Ñiquen *et al.*, 2013).

2.3.3. Pelagic squids

In Peru, fishery statistics register four species of squids caught along the coast: *Doryteuthis (Amerigo) gahi* (d'Orbigny,1835), *Lolliguncula (Lolliguncula) panamensis* (Berry, 1911), *Lolliguncula (Loliolopsis) diomedeae* (Hoyle, 1904) and the jumbo squid *Dosidicus gigas* (Benites and Valdivieso, 1986; Villegas, 2001).*D. gahi*, which is the one of most common and most widely distributed species in these waters (Villegas, 2001), is a neritic loliginid squid. It is distributed over the continental shelf and slope of the Eastern Pacific, from Puerto Pizarro (Peru) to southwestern Chile, and in the South Atlantic from the Gulf of San Matias (Argentina, about 42ºS) to Tierra del Fuego (Jereb and Roper, 2010). El Niño events (rise in sea temperatures) have a negative effect on *D. gahi* catches, while La Niña episodes (lower sea temperatures) have a positive effect (Villegas, 2001). *L. panamensis* commonly called "calamarete" is a coastal surface species (between 5 and 30 m depth) (Jereb and Roper, 2010). It is frequently caught with prawns in northern Peru (Benites and Valdivieso, 1986). *L. diomedae* called "squid dart" is a neritic species usually found in large schools in the Gulf of Panama. Catches of this species are usually incidental in Peru (Jereb and Roper, 2010).

The jumbo squid is one of the most abundant squids in the eastern Pacific Ocean (Nigmatullin *et al.*, 2001; Waluda *et al.*, 2004). *D. gigas* supports a major fishery in the Eastern Pacific, off the coasts of North and South America. This species has a semi oceanic pelagic habitat, and occurs at depths of up to 1200 m (Nigmatullin *et al.*, 2001). Highly labile populations exhibit large fluctuations in abundance in response to environmental variability (Waluda *et al.*, 2006). Off Peru, *D. gigas* has been targeted commercially by the artisanal fleet since 1961 (Yamashiro *et al.*, 1998), mainly in the north, and by industrial fleets since 1991 (Taipe *et al.*, 2001). In Chile, landing data of *D. gigas* are available since 1957 (Rocha and Vega, 2003) and older records of stranded individual exist before (Wilhelm, 1954). Catches of *D. gigas* were sporadic before 1970, although high abundances have been reported (Schmiede and Acuña, 1992). In the Gulf of California the artisanal fishery targeting *D. gigas* started in 1974 (Ehrhardt *et al.*, 1983; Argüelles *et al.*, 2008).

2.4. Mesopelagics fishes

Mesopelagic fishes are important components of oceanic ecosystems because of their common and abundant distribution in the world oceans (Ahlstrom, 1969; Sassa *et al.*, 2002; McClatchie and Dunford, 2003; Irigoyen *et al.*, 2014). They are main consumers of zooplankton and larval and juvenile fishes and are important prey for the top predators in the oceanic food web such as tunas, squids and dolphins (Kinzer and Schulz, 1985; Williams *et al.*, 2001; Cornejo and Koppelmann, 2006).

An important feature of mesopelagic fish, such as the lanternfish (Myctophidae) and lightfish (Phosichthyidae), is that they perform extensive vertical migrations and form dense patches. Vertical migration is one of the most widespread patterns of animal behaviour in mesopelagic zones (Frank and Widder, 2002), and influences the life histories of non-migrating and migrating fish and cephalopods (mainly the jumbo squid) and the feeding behaviour and spatial distribution patterns of predators (Konchina, 1993, 1990; Bertrand *et al.*, 2002b; Benoit-Bird and Au, 2003).

The mesopelagic community of NHCS is dominated by the fish families Phosichthyidae (*Vinciguerria lucetia*), Myctophidae (especially *Diogenichthys laternatus* and *Lampanyctus idostigma*) and Bathylagidae (especially *Leuroglossus urotranus*) accounting for 60.4, 12.8 and 3.7% of the total abundance, respectively (Figure 2.6; Cornejo and Koppelmann, 2006).

The biomass of V. *lucetia* varied from 2 to 11 million of tonnes as measured by acoustic means (Castillo *et al.*, 1998; Gutiérrez and Peraltilla, 2008). Therefore, *V. lucetia* is a significant ecosystem component in the NHCS (Cornejo and Koppelmann, 2006).

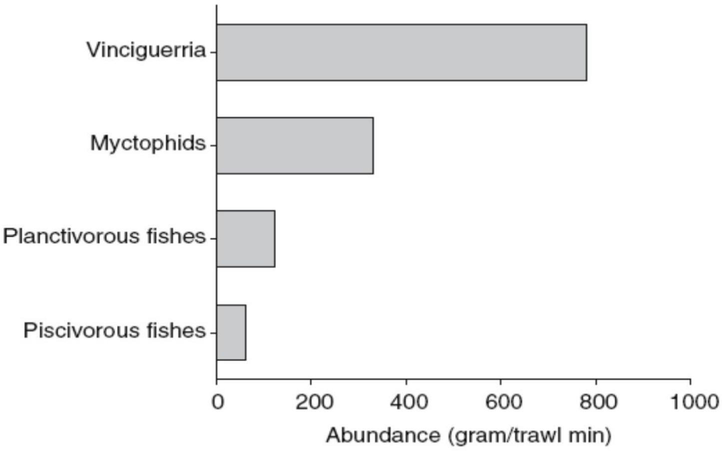

Figure 2.6. Mean abundance of functional groups of mesopelagic fishes collected in pelagic trawls (source: Cornejo and Koppelmann, 2006)

2.5. Temporal dynamics of the NHCS

The NHCS is subject to bottom-up forcing at seasonal, interannual, multidecadal, centennial scales and millennial scales (Chavez *et al.*, 2008; Salvatecci, 2013).

2.5.1. Centennial and millennial variability

Large scale variability (~ 20 000 years) in terms of environmental conditions and fish abundance proxy has been recently studied using laminated sediments retrieved off Peru (Salvatteci, 2013; Salvatteci *et al.*, 2011). Both components of the ecosystem presented very high variability at centennial and millennial scales. During the globally cold Little Ice Age period (from ~1500 to ~1850 AD), the NHCS was little productive. Then the system shifted in ca.1820 towards more productive conditions (Figure 2.7) (Sifeddine *et al.*, 2008; Gutiérrez *et al.*, 2009). Before the shift, the NHCS was characterized by lower productivity, weaker OMZ and low abundances of fish scales. In opposite the last ~150 years were characterized by an increase in export production, a strong OMZ and high fluxes of anchovy scales. A rapid expansion of the subsurface nutrient rich, oxygen depleted waters occurred in recent years with a higher biological productivity *(Valdés et al.,* 2008; Gutiérrez *et al.*, 2009; Salvatteci, 2013). Since 1900 AD, anchovy reached very high levels of productivity; actually the highest levels of productivity in the last 20 000 years (Salvatecci, 2013). In general, fish productivity modulation appears to be strongly linked to primary productivity and oxygen.

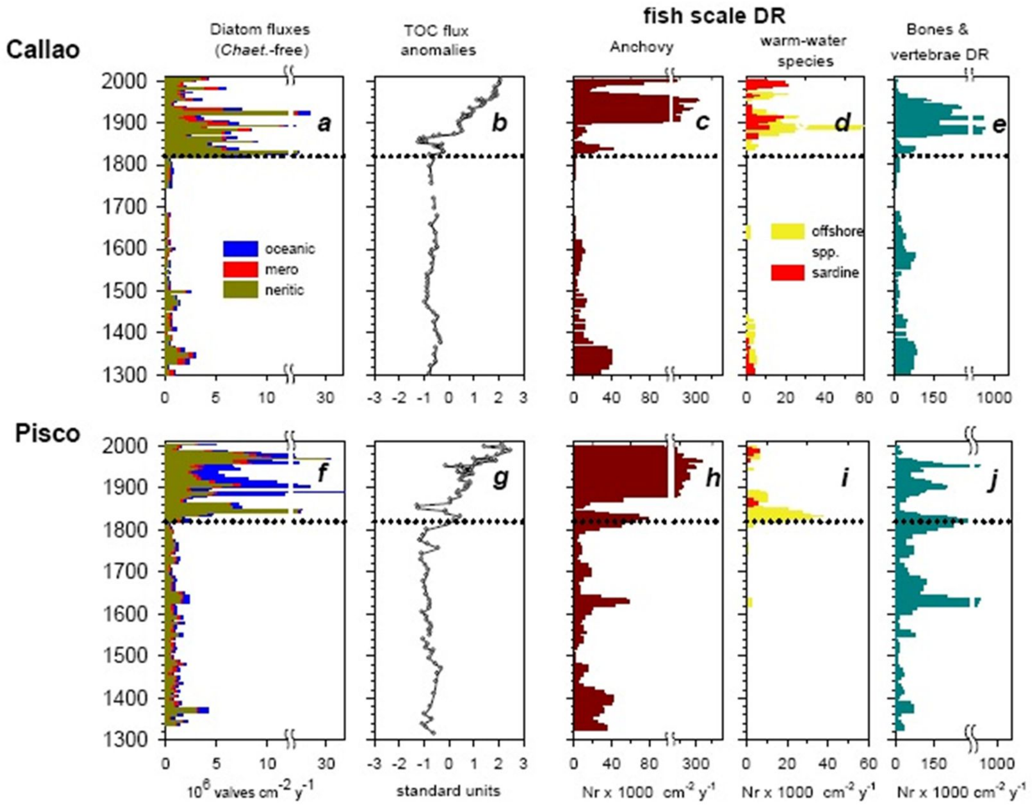

Figure 2.7. Pelagic ecosystem proxies off Peru (Callao, a–e; Pisco, f–j). (a, f) Chaetoceros free diatom accumulation rates (DAR) shown as neritic, meroplanktic and oceanic groupings (106 valves cm^{-2} y^{-1}); (b,

g) total organic carbon (TOC) flux anomalies, to permit comparisons of the variability between sites (standardized units); (c, h) 3-term running averages of anchovy scale deposition rates (Nr×1000 cm^{-2} y^{-1}); (d, i) 3-term running averages of sardine scale deposition rates and offshore pelagic (jack mackerel+ chub mackerel) scale deposition rates (Nr×1000 cm^{-2} y^{-1}); (e, j) 3-term running averages of deposition rates of bones and vertebrae (Nr×1000 cm^{-2} y^{-1}) (Source: Gutiérrez et al., 2009).

2.5.2. Decadal variability

The decadal scale variability is largely attributed to physical and biological mechanisms (Checkley *et al.*, 2009). These fluctuations have basin-wide effects on sea surface temperature (SST) and thermocline slope. During the cool eastern boundary regime, the basin-scale sea level slope is accentuated (lower in the eastern Pacific, higher in the western Pacific). A lower sea level is associated with a shallower thermocline and increased nutrient supply and productivity in the eastern Pacific; the inverse occurs in the western Pacific. In addition changes affect the transport of boundary currents, equatorial currents, and the major atmospheric pressure systems (Chavez *et al.*, 2003).

The interdecadal variability is characterized by periods of high and low abundance of small pelagics, termed "pseudo-cycles", because of their irregular periodicity (Fréon *et al.*, 2008). Historical data on catches and conventional stock abundance estimates showed that several fish populations, and especially small pelagic fishes inhabiting upwelling ecosystems, undergo large interdecadal variations in abundance with amplitudes equal, if not larger than, the interannual variability (Bakun, 1996; Spencer and Collie, 1997). According to Chavez *et al.* (2003) the sardine and anchovy fluctuations are associated with large-scale changes in ocean temperatures: for 25 years, the Pacific is warmer than average (the warm, sardine regime) and then switches to cooler than average for the next 25 years (the cool, anchovy regime). During warm period, the thermocline is deeper, the upwelling is weaker and productivity is lower. So the range of habitat favorable to anchovy is dramatically reduced while habitat favorable to sardine increases and spreads towards the continental shelf (Bertrand *et al.*, 2004b). However, this alternation in the abundance of anchovy and sardine has only been observed in the fishing records, covering less than a complete cycle. When looking at longer records, such as paleo-fish scales from sediments, this alternation seems to occur only occasionally (Gutiérrez *et al.*, 2009; Valdés *et al.*, 2008).

2.5.3. Interannual variability

The principal cause of interannual variability in the NHCS is related to the El Niño and La Niña events (ENSO) that produce positive sea-surface temperature anomalies (SSTA) in the equatorial and eastern Pacific (Chavez *et al*., 2011). The ENSO is due to a periodic instability of the ocean-atmosphere dynamics in the Pacific Ocean. During El Niño the equatorial Walker circulation is weakened, and the coast of Peru is characterized by an increase in SSTA, the sub-surface oxygenation increased and reduced productivity due to a deepening of the thermocline (Barber and Chavez, 2008). During El Niño events, the thermocline/nutricline is located deeper than during normal conditions, and there is much less fertilization of the upper section of the water column. In opposite, the La Niña events are characterized by lower SSTA in the eastern central equatorial Pacific (Figure 2.8).

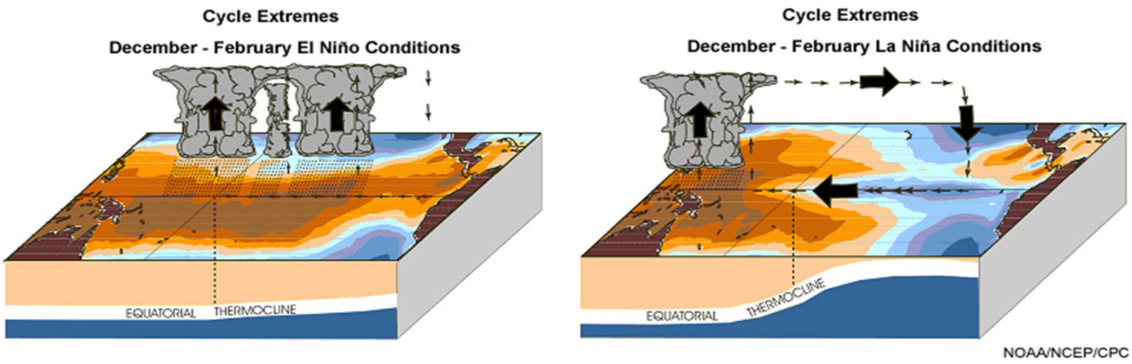

Figure 2.8. Schematic of upper ocean and atmospheric circulation during El Niño (left) and La Niña extremes (right). Source: NOAA/NCEP/CPC

It is well known that "no two El Niño events are quite alike" (Takahashi *et al*., 2011), yet the typical evolution of such an event was thought to consist in an initial warming off South America and later in the central equatorial Pacific during austral summer (Rasmusson and Carpenter, 1982). This belief changed with the extraordinary 1982–83 and 1997–98 El Niño events, which had large amplitudes and different evolutions (Takahashi *et al*., 2011; Dewitte *et al*., 2012), particularly as the maximum anomalies occurred simultaneously in the eastern and central equatorial Pacific during austral summer.

The ENSO has been categorized into two types of El Niño (Kug *et al*., 2009; Yeh *et al*., 2009; Dewitte et al., 2012): the traditional Cold Tongue El Niño or Eastern Pacific El Niño that consists of the SST anomaly developing and peaking in the eastern equatorial Pacific and the so-called Modoki El Niño (Ashok *et al*., 2007) or Central Pacific El Niño (Kao and Yu, 2009; Dewitte *et al*., 2012). However, Takahashi *et al.* (2011) propose three types of El Niño: the central Pacific El Niño, the "canonical" El Niño and the extraordinary events. In particular, present evidence that suggests that these are all part of the same non-linear phenomenon rather than independent modes of variability.

La Niña and El Niño events shape the spatial organization of living organisms by modifying the volume of their favorable habitat. Under El Niño, the extent of cold and nutrient rich waters (CCW) is reduced and sea surface temperature increases to the coast. In these conditions, anchovies concentrate closer to the coast if remaining CCW refuge area exist as for instance during the El Niño 1997-98 (Bertrand *et al.*, 2004b). However, Bakun and Weeks (2008) suggested that El Niño events could contribute to maintain the high fish production of the system by favoring fast growing fish species like anchovy, which take advantage of the low predation and rapidly increase their population and dominate the system.

2.5.4. Fine scale variability

A characteristic of pelagic ecosystems is that their 'substrate' consists of constantly moving water masses, where ocean surface turbulence creates ephemeral oases. Physical forcing results from a myriad of turbulent processes that span a wide range of scales and influence organism distribution and behaviour in a variety of ways. At the fine scale (~1–10m vertically), the importance of thin layers has recently been emphasized owing to their ubiquitous nature and their potential to induce ecological hotspots and increase trophic transfer rates from phytoplankton to higher trophic levels. At broader (horizontal) scales, strong evidence suggests that internal wave (IW; ~100m to 10–15 km), submesoscale (~1–20 km; for example, fronts and filaments) and mesoscale (~20–100 km; for example, eddies) activity modulates the concentration and distribution of marine organisms, thereby influencing ecosystem dynamics (Bertrand *et al.*, 2014). A recent study demostrated that the upper ocean dynamics at scales less than 10 km play the foremost role in shaping the seascape from zooplankton to seabirds in the NHCS. Both physical forcing and organism behaviour are implicit in the maintenance to the aggregate of living organism in patches, with the latter increasing in importance with each step up the trophic chain. Since predators are required to locate their prey, their foraging behaviour tends to reflect the patchy distribution of their prey (Bertrand *et al.*, 2014).

2.6. Description of the studied species

In this study we focused our investigations on three species, being major in human consumption in Peru: the Jumbo squid, the Jack mackerel and the Chub mackerel. The first species is a nektonic cephalopod; the following species are pelagic teleosts.

2.6.1. Jumbo squid *Dosidicus gigas*

The jumbo squid belongs to the family Ommastrephidae and the subfamily Ommastrephinae (Nesis, 1985), which is the most phylogenetically advanced subfamily of Ommastrephidae (Zuev *et al.*, 1975; Nigmatullin, 1979; Nesis, 1979, 1985). *D. gigas* is the largest ommastrephid squid, its dorsal mantle length (ML) is up to 1000-1200 mm and it weight up to 30-50 kg. The jumbo squid has a body (mantle) torpedo-shaped, cone-shaped on the back, with end flaps, cartilage siphon inverted T-shaped, with eight arms and two tentacles around the mouth, two rows of suckers on the arms and tentacles in four rows; the fourth pair of arms of males are modified for coupling (Figure 2.9).

Taxonomy

Phylum: Mollusca

Class: Cephalopoda

Order: Teuthida

Family: Ommastrephidae

Genus and species: *Dosidicus gigas*

Common names: Humboldt squid, jumbo flying squid, **jumbo squid**, jibia, pota.

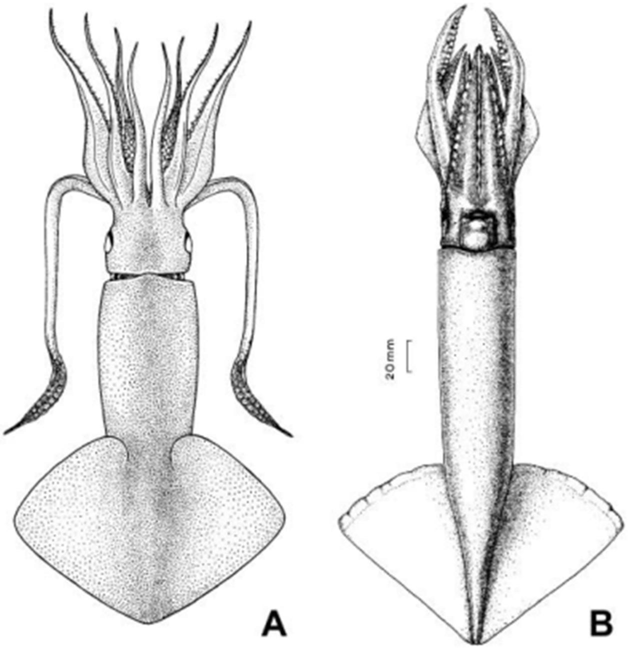

Figure 2.9. Jumbo squid Dosidicus gigas. A, dorsal view of a large specimen (50-80 cm ML) (Roper et al., 1984) B, ventral view of a specimen of 25.4 cm ML (Source: Wormuth, 1976).

Distribution

The jumbo squid is endemic to the Eastern Pacific Ocean (Nesis, 1983; Nigmatullin *et al.*, 2001) and is well known for occasional excursions into new areas that can be brief or quite long lasting (Gilly, 2005). *D. gigas* invaded Monterey Bay, CA for much of the 1930's (Croker, 1937) and then seemed to disappear until the 1997-98 El Niño. Since that time, it has become a commonly resident in that area (Zeidberg and Robison, 2007). Similarly, over the last eight years *D. gigas* has displayed a major range expansion in the waters from central California throughout the Pacific Northwest as far as north Alaska (Cosgrove, 2005; Wing, 2006; Bazzino *et al.*, 2010). In the equatorial area the range of westward distribution reaches 140°W. The horizontal distribution of *D. gigas* are found from 400 to 600 nm offshore (Figure 2.10).

General habitat

The jumbo squid is one of the most abundant nektonic squids in the epipelagic zone of the world ocean. The boundaries of its range pass along the Eastern peripheries of the large-scale oceanic gyres of the central water masses and are approximately coincident with the isoline of the average phosphate concentration 0.8 mg-at $P\text{-}PO_4^{3-}/m^2$ in the 0-100 m layer. This isoline indicates the boundary of highly productive water. Its upper temperature limits range from 15° to 28°C in surface waters, and even 30-32°C in equatorial areas, while its lower temperature limits are not less than 4.0-4.5ºC in the deeper water. During the day, squid stay within or just below the layer of the deep OMZ (Nigmatullin *et al.*, 2001). Adult squids undergo diel vertical migrations with a night lift to the 0-200 m water layer, plunging in the daytime to 800-1000 m and deeper (Yatsu *et al.*, 1999). The feeding occurs both at night and during the day in the OMZ below 300 m (Jereb and Roper, 2010).

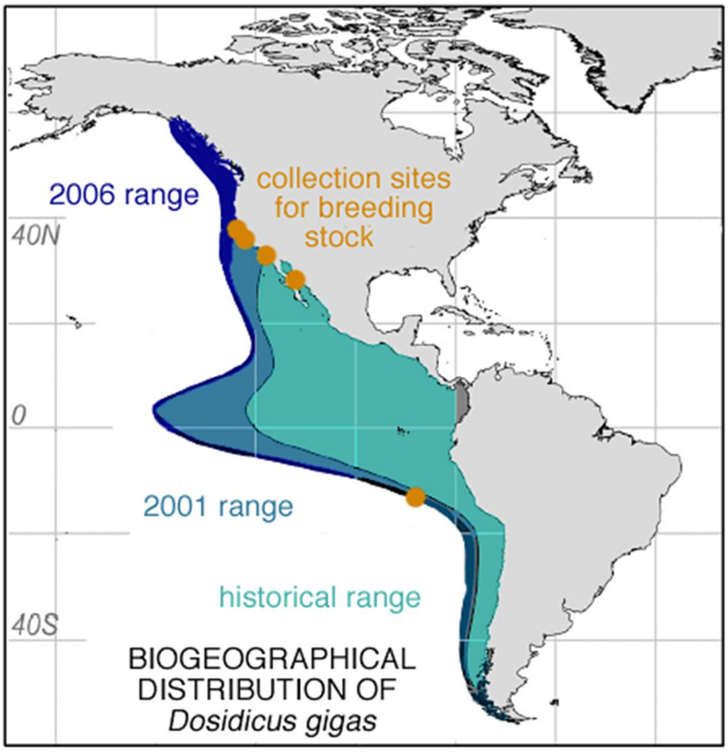

Figure 2.10. Distribution map of D. gigas. Green - Common historical distribution. Sky blue - 2001 expansion. Blue – 2006 expansion. Green, Sky blue and Blue is the total present distribution. (Source: http://www.asnailsodyssey.com/LEARNABOUT/OCTOPUS/octoEgg.php)

Reproductive characteristics

D. gigas is dioecious (separate sexes, Mangold, 1987) and exhibits external sexual dimorphism: the mantle of the males is harder and thicker compared with the one of females (Nesis, 1970). However, this dimorphism is inconspicuous (Ochoa-Báez, 1982; Michel *et al.*, 1986). Reproduction is mainly located between 25°N and 20-25°S, mostly not further than 50-150 nm from the shore. *D. gigas* is semelparous, i.e. females spawn once then die (Markaida, 2001; Tafur *et al.*, 2001, 2010; Keyl *et al.*, 2010; Liu *et al.*, 2010;). There is a distinct peak in spawning during spring and summer in the southern hemisphere (Nigmatullin *et al.*, 2001; Taipe *et al.*, 2001), and a secondary peak from July to August (Tafur and Rabí, 1997; Tafur *et al.*, 2001).

Feeding characteristic

D. gigas plays an important role in oceanic food webs, as prey and predator. Juveniles are preyed upon by large carnivorous fish, small tuna, squid and gulls. Sub-adults are preyed upon by dolphin fish, snake mackerel, yellowfin tuna, other large tunas and fur seals. Adults are preyed by sharks, swordfish, striped marlin, sperm whales and pilot whales (Nigmatullin *et al.*, 2001). Sperm whale stomach contents from the southeast Pacific showed that *D. gigas* was the main prey (Clarke *et al.*, 1988). Studies in the Gulf of California reported that jumbo squids fed predominantly on mesopelagic fishes such as myctophids. Pteropods, micronektonic squid, megalopae and euphausiids were also recovered in stomachs of jumbo squid (Markaida, 2006). The diet of *D. gigas* in the Southeast Pacific appears similar to the one found in the Gulf of California. Myctophids dominated and the Phosichthyidae *Vinciguerria lucetia* contributed significantly too (Shchetinnikov, 1989). The trophic role of cephalopods has been investigated mainly using stomach content analyses. However, cephalopod trophodynamic studies based on such methods are hampered because the ingested prey are often rapidly digested, rejected and more usually eaten in parts, making species identification difficult (Rodhouse and Nigmatullin, 1996; Cherel and Hobson, 2005). Stable isotope analysis (SIA) has emerged as a complementary tool in trophic ecology and has proven useful in squid feeding ecology (Cherel and Hobson, 2005). Results for the jumbo squid in Peru suggest very high variability in stable isotope values by latitude and by size (Argüelles *et al.*, 2012; Lorrain *et al.*, 2011). The latitudinal trend suggests that *D. gigas* is a relatively resident species at the scale of its isotopic turnover rate (i.e. a few weeks). The increasing trend of δ^{13}C values with mantle length and the strong relation between δ^{13}C values and distance to shelf break suggest that *D. gigas* migrate from oceanic to coastal waters, changing its foraging areas between juvenile and adults,although no significant diet shift was reported. There is no systematic increase in trophic position with size and latitude off Peru. Caution must then be taken when comparing individuals of different sizes in different environments (Argüelles *et al.*, 2012).

2.6.2. Jack mackerel *Trachurus murphyi*

Jack mackerels can grow up to 70 cm of fork length (FL). They have elongated and slightly compressed bodies. The head is large with well-developed transparent protective membranes covering the eyes. The mouth is large, with the rear edge of the lower jaw aligning with the front edge of the eyes. It possesses small teeth. The second dorsal fin is much longer than the first. The pectoral fin is long and pointed. The origin of the pelvic fin is below the bottom point of attachment of the pectorals. The anal fin is long, but shorter than the second dorsal fin. At its front are two strong spines. The upper parts of the body are metallic blue in color, while the bottom surfaces are a silvery white, on curved part lateral line with scales enlarged and scute-like (Kawahara *et al.*, 1988) (Figure 2.11).

Figure 2.11. Jack mackerel Trachurus murphyi (36 to 65 cm LT; Chirichigno and Cornejo, 2001).

Taxonomy

Phylum: Chordata

Class: Osteichthyes/Actinopterygii

Order: Perciformes

Family: Carangidae

Genus and species: *Trachurus murphyi* (Nichols, 1920)

Scientific synonyms: Historically *Trachurus symmetricus murphyi*

Common names: Chilean Jack mackerel (FAO, Chile, Russia), Murphy's mackerel (New Zealand), Pacific Jack mackerel (Russia), Peruvian Jack mackerel (Australia, Russia), Jack mackerel, horse mackerel, jurel (Chile, Peru, Ecuador).

Distribution

The Jack mackerel is distributed throughout the south eastern Pacific, both inside EEZs and on the high sea, ranging from the Galapagos Islands and south of Ecuador in the north to southern Chile, and ranging from the South America in the east to Australia and New Zealand in the west (Evseenko, 1987; Serra, 1991; Elizarov *et al.*, 1993; Kotenev *et al.*, 2006) (Figure 2.12). Serra (1991) summarized depths for aggregations of *T. murphyi* and Guzman *et al.* (1983) used hydroacoustic equipment to record the species down to 250 m off the coast of northern Chile. In central and southern Chilean waters, Bahamonde (1978) recorded Jack mackerels down to 300 m, and Japanese trawlers have caught it at depths of 300 m beyond the Chilean EEZ (Anon, 1985, 1984). Córdova (1998) described a diurnal migratory behaviour, with fish being found deeper during the day than at night.

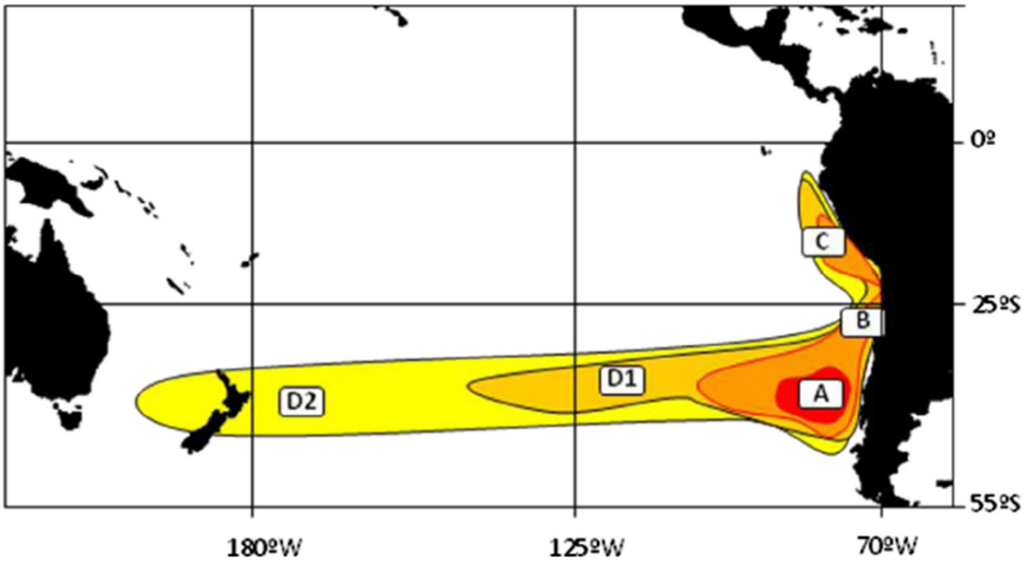

Figure 2.12. Extension and abundance of the jack mackerel, during periods of low (red area) to high abundance (yellow area). The letters in rectangles show the major patches of density. A: Central Pacific-Centre South Chilean stock; B: Northern Chilean stock; C: Peruvian stock; D1 and D2: Central South and Southwest Pacific Ocean stocks respectively (Source: Gerlotto et al., 2012).

General habitat

T. murphyi is a schooling pelagic species adapted to both neritic and oceanic environments. Jack mackerels are observed in temperate waters of high productivity, nutrient-rich waters and are associated with oceanic fronts formed by the Subtropical Surface Water (SSW) and the Cold Coastal Waters (ACF) in Peru (Dioses, 2013; Ñiquen and Peña, 2008). Also, Jack mackerel occupying waters with a broader range of SST (17–28 ºC) and salinity (32–35.6). Jack mackerel mainly distributed in warm and oxygenated water without a marked preference for one water mass, but with a ubiquitous distribution inside oceanic water masses (Bertrand *et al.*, 2004b). However, after El Niño 1997-98 the cold coastal waters extended far from the coast and had been associated with a reduction in *T. murphyi* abundance (Gutiérrez *et al.*, 2008a).

In Chile the coast is in the eastern boundary current system with several upwelling centers that are subject to a complex variety of physical influences (Sobarzo *et al.*, 2001). The main source of upwelling waters in the Humboldt Current System is Subsurface Equatorial Waters (AESS, Agua Ecuatorial Subsuperficial) associated with the Peru–Chile Undercurrent. Others studies (Daneri *et al.*, 2000) have reported high levels of primary and secondary production in the inshore environment along the coast of central–southern Chile. Offshore (outside the Chilean EEZ) a higher biological production zone has also been reported as a result of small and meso-scale oceanic eddies, meanders and oceanic upwelling (Grechina, 1998). All life history stages of *T. murphyi* were reported from within these zones, which were considered to be areas of high biological productivity (Chernyshkov *et al.*, 2008).

Reproductive characteristics

T. murphyi spawns in austral spring and summer throughout its whole distribution range, with the main spawning season from October to December (Perea *et al.*, 2013). Santander and Flores (1983) and Dioses *et al.* (1989) described Jack mackerel spawning in Peru as mainly occurring between 14º00'S and 18º30'S. However, more recent analyses by Ayón and Correa (2013) show that between 1966 and 2010, Jack mackerel larvae were present every year along the whole Peruvian coast, with clear year to year north-south shifts in the centers of higher larvae abundance associated with shifts in environmental conditions. The annual mean larvae densities for the positive stations in the period 1966-2010 estimated by Ayón and Correa (2013) ranged from 3 to 1131 larvae.m^{-2}, with a median of 21 larvae.m^{-2}. While the frequency and abundance of larvae was variable, no particular trend was highlighted during the 56 years of observations. The length at first maturity of *T. murphyi* in Peru was first estimated to be 25 cm fork length (FL) by Abramov and Kotlyar (1980) and 23 cm total length (21 cm FL) by Dioses *et al.* (1989). Recently, Perea *et al.* (2013) analyzed data from 1967 to 2012 and estimated a total length at first maturity of 26.5 cm, with no significant changes over the observed period.

Feeding characteristic

In the Eastern Pacific *T. murphyi* is considered as an opportunistic predator feeding on large forms of meso and macrozzoplanckton, including some fish species characterized by short life histories (Konchina *et al.*, 1996). In Chile, main prey in terms of relative importance were euphausiids (Antezana 2010). Other important prey were mesopelagic fish *Vinciguerria* sp. (Medina and Arancibia, 1989, 1992, 2002). In Peru Jack mackerel prey upon zooplankton, mesopelagic fish (Konchina, 1990; Konchina *et al.*, 1996) and pelagic fish such as anchovy (Sánchez de Benites *et al*., 1985; Sánchez de Benites and Muck, 1987). Among zooplankton, euphausiids was the main prey again (Alamo *et al*., 1996; Alamo and Espinoza, 1998). Larvae in their first stages of development feed on zooplankton, as cladocerans, nauplii, copepodites, barnacle larvae, euphausiids larvae, decapods larvae and isopods larvae (Ermolovich and Gardina, 1994). In Chile Jack mackerels of 26 to 40 cm fork length (FL) fed mostly on salps and jack mackerel from 41 to 50 cm FL fed mainly on euphausiids (Miranda *et al.* 1998).

2.6.3. Chub mackerel *Scomber japonicus*

Chub mackerel is a pelagic species with a hydrodynamic and fusiform elongate body (Figure 2.13). Growth of the species is characterised as very fast in the first two years, manifested in a high growth rate (*k*). Fishes can reach 50% of the asymptotic length in this period, considering that L_∞ are reported in the literature to be approximately 45 cm and longevity between 9 to 10 years. Entire body is covered with rather small scales. The distance between the two dorsal fins equals the length of the base of the first. Its coloration on the back is green-bottle and is decorated with many thick, wavy lines and vertical forming whimsical drawings. Each lobe of the tail at its base is a dark round spot (Castro Hernández and Santana Ortega, 2000; Collette and Nauen, 1983).

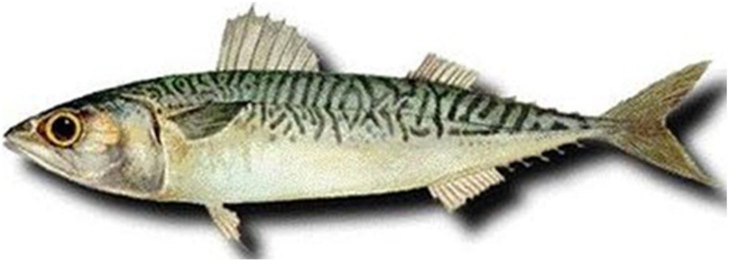

Figure 2.13. Chub mackerel Scomber japonicas (18 to 32 cm LH; Chirichigno and Cornejo, 2001)

Taxonomy

Phylum: Chordata

Class: Actinopterygii

Order: Perciformes

Family: Scombridae

Genus and species: *Scomber japonicus*, Houttuyn, 1782

Scientific synonyms: *Scomber colias*, *Scomber australasicus* (Note that *Scomber australasicus* Cuvier 1832 is a valid species in its own right, but appears to have an Australasian only distribution. *S. australasicus* has been used erroneously in the past as a synonym for *S. japonicus* in the eastern Pacific).

Common names: Chub mackerel, caballa, cavalinha, estornino, mackerel, blue mackerel.

Distribution

The distribution of *S. japonicus* is reported as cosmopolitan (Figure 2.14). In the Atlantic Ocean it occurs off the east coast of North America from New Scotia, Canada to Venezuela. On the South American east coast, it occurs from southeast Brazil to south Argentina. Matsui (1967) describes the distribution of *S. japonicus* in South Pacific to be from Panama to Chile, including Galapagos Islands, with austral limits at Guamblin Island at 45°4'S. The longitudinal distribution includes areas outside EEZ limits in the south (off Chile), but it occurs mainly within 100 nm of the coast in the north. On the European coast *S. japonicus* is reported from the United Kingdom to France. *S. japonicus* is reported from almost the whole coast of Africa. It occurs in the Mediterranean and Red Seas. It is apparently absent in the Indian Ocean, from Indonesia and Australia (Collette and Nauen, 1983).

General habitat

S. japonicus is a pelagic fish with gregarious behavior. In Chilean waters it can form mixed schools with Jack mackerel and sardine at the adult stages, but also with anchovy when smaller than 15 cm (Collette and Nauen, 1983). It is uncommon for *S. japonicus* to inhabit waters deeper than 50 m and according to Maridueña and Menz (1986), the species undertakes vertical migration to surface for feeding. However, Hernández (1991) observed the presence of *S. japonicus* over the continental slope around the Canaries Islands, from the surface to 300 m depth.

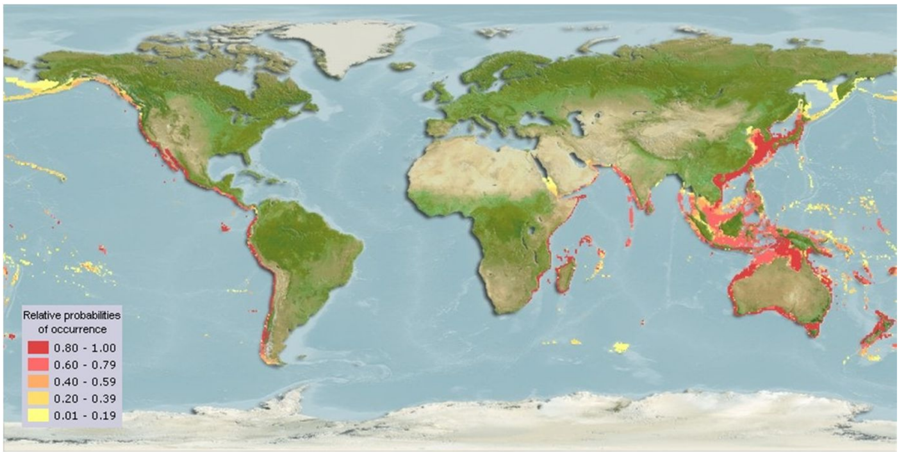

Figure 2.14. Distribution of Chub mackerel in the world (Source: FAO)

Reproductive characteristics

S. japonicus is a heterosexual fish with no external sexual dimorphism. Histological studies demonstrate *S. japonicus* as a partial spawner, with an extended period of reproductive activity. Off Peru the spawning season is described to be from August to March, mainly in high summer (January). Near Ecuador a secondary period occurs in September (Serra *et al.*, 1982; Maridueña and Menz, 1986). In Chilean waters the spawning season is identified from November to March in northern and southern areas. This has been confirmed with results from projects monitoring pelagic fisheries in these regions, which report an increase of mature fishes at the end of the year, and high values of gonadosomatic index (GIS) within January and March (Martinez *et al.*, 2006). The length of 50% maturity was estimated in the north region at 26 cm (Pardo and Oliva, 1992).

Feeding characteristic

Juveniles of Chub mackerel are zooplankton feeders and consume mainly euphausiids, copepods and mysids (Angelescu, 1980; Castro Hernández, 1991; Castro Hernández and Santana Ortega, 2000). Chub mackerel adults feed on a very wide range of organisms including invertebrates and fishes, thus demonstrating considerable feeding plasticity (Konchina, 1990).. The invertebrates found in the mackerel stomachs were siphonophore mollusks (bivalves and cephalopods), polychaetes, crustaceans (ostracods, copepods, mysids, amphipods, euphausiids, decapods), chaetognaths and tunicates (salps). Fishes were mainly juveniles and adults of the families Myctophidae and Engraulidae and eggs of teleost (Mendo, 1984; Konchina, 1982, 1990, 1993; Medina and Arancibia, 1992; Castro, 1993; Castro and Hernández-García, 1993; Alamo *et al.*, 1996).

Chapter III

Comprehensive model of jumbo squid Dosidicus gigas trophic ecology in the Northern Humboldt Current System.

3.1. Introduction

The ommastrephid jumbo squid *Dosidicus gigas* is the most abundant nektonic squid in the surface waters of the world ocean (Nesis, 1970; Nigmatullin *et al.*, 2001) and supports the largest cephalopod fishery. This squid, endemic to the Eastern Tropical Pacific, is mainly distributed in the oceanic domain (Roper *et al.*, 1984) over a wide bathymetric range (Zeidberg and Robison, 2007). *D. gigas* is a large squid with high fecundity (Nigmatullin *et al.*, 2001), a rapid growth rate and a short life span (up to ~32 months Arguelles *et al.*, 2001; Keyl *et al.*, 2010). The tolerance of this species to a wide range of environmental factors (temperature and oxygen) facilitates its geographic expansion (Jereb and Roper, 2010; Gilly *et al.*, 2012), such as the recent invasion into California waters (Rodhouse and Nigmatullin, 1996; Zeidberg and Robison, 2007).

D. gigas plays an important role in marine food webs both as predator and prey (Budelmann, 1994). This abundant and voracious squid forages on a large variety of prey using prehensile arms and tentacles coupled with an efficient sensory system (Boyle and Rodhouse, 2005; Yatsu *et al.*, 1999). The impact on exploited marine resources can be strong (Zeidberg and Robison, 2007) and the broad trophic niche of jumbo squid is enhanced further by physiological abilities. This squid can undertake extensive vertical migrations, up to 1200 m, foraging on deep, mid-water and surface organisms (Gilly *et al.*, 2006; Jereb and Roper, 2010; Markaida *et al.*, 2005; Nigmatullin *et al.*, 2001). In addition, its presence within anoxic or hypoxic waters was validated by tagging experiments in the Californian Current System (Gilly *et al.*, 2006, 2012). Indeed, the eastern tropical Pacific is characterised by the presence of an oxygen minimum zone (OMZ) (Helly and Levin, 2004) and *D. gigas* is a part-time resident of the OMZ thanks to adapted behavior and specific metabolic characteristics (Trübenbach *et al.*, 2013, 2012). Jumbo squid vertical migrations impact the vertical energy flow, providing an efficient energy transport from the surface to deeper waters (Gilly *et al.*, 2006; Jereb and Roper, 2010).

Previous studies showed that the feeding ecology of jumbo squid is highly variable in time and space (Markaida and Sosa-Nishizaki, 2003; Ibáñez *et al.*, 2008) The feeding ecology of jumbo squid was investigated in the eastern Pacific from stomach content (Chong *et al.*, 2005; Rosas-Luis, 2007; Field *et al.*, 2007, 2013) and stable isotopes (Ruiz-Cooley *et al.*, 2006, 2010; Lorrain *et al.*, 2011; Argüelles et al., 2012). By investigating stable isotope signatures along gladius, (Lorrain *et al.*, 2011) showed that jumbo squids living in the same environment at a given time can have different historical backgrounds. These differences in life history strategies, illustrating a high plasticity. Here, we used an extensive dataset of more than 4000 stomachs sampled between 2004 and 2011 in the northern Humboldt Current to provide new insight on the size-related and spatiotemporal variability of feeding habits of *D. gigas*. We also decipher one paradox in the jumbo squid diet: why do they hardly forage on the tremendous anchovy (*Engraulis ringens*) biomass distributed of coastal Peru? We show that the shallow OMZ present off coastal Peru could hamper the co-occurrence of jumbo squids and anchovies, impacting jumbo squid foraging behaviour. We finally propose a conceptual model on jumbo squid trophic ecology including the ontogenetic cycle, oxygen and prey availability.

3.2. Material and methods

3.2.1. Sample collection

A total of 5320 stomachs were collected from jumbo squids caught between 2004 and 2011 by the authorized industrial jigging fishery off Peru (3ºS - 17ºS - from the coastal area to 605 km from the coast) (Figure 3.1). No animals (squids i.e. invertebrates) were killed specifically for this research. Samples were collected by technicians of the Peruvian Sea Institute (IMARPE) aboard fishing vessels according to standard protocols. In each fishing set, 20 individuals were randomly sampled, covering the captured size range. On board or in the laboratory, the length (mantle length ML, in cm) and the total weight (in g) were measured and the sex and maturity stages (I: immature; II: in maturing; III: mature; and IV: spawning) were determined according to (Nesis, 1970, 1983) and validated by Sánchez (2011). Each fishing set was characterized according to the distance to the shelf break (negative to the continental shelf and positive towards offshore, in km), the season (austral summer, fall, winter and spring) and the diel periods. Sea surface temperature anomalies (SSTA, in ºC) were used as a proxy of environmental conditions.

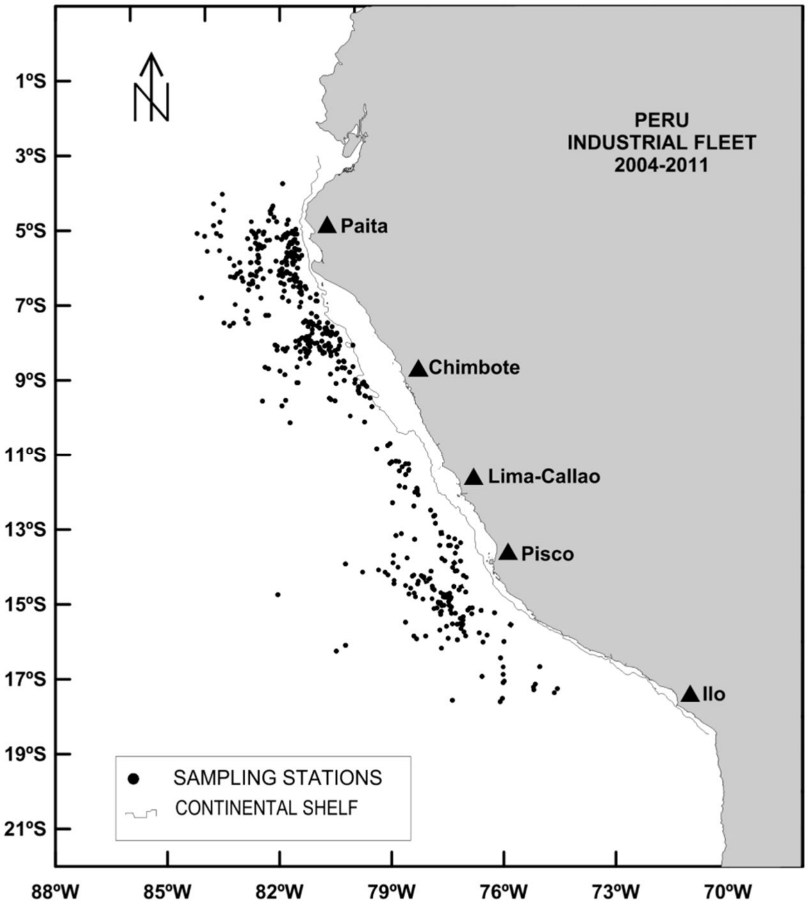

Figure 3.1. Location (black dots) of the sampling points of jumbo squids collected from the industrial jig fleet between 2004 and 2011

3.2.2. Stomach content analysis

All stomach contents were washed through a sieve mesh of 500 µm in order to retain prey remains and diagnostic hard parts (fish otoliths, cephalopod beaks, crustacean exoskeleton). Stomach contents were weighed and the different items constituting a single taxon were sorted, counted and weighed. Jigging vessels use 2 kW lights (no use of bait) to attract jumbo squids. Biases can be associated with fishing gear and tactic but jigging is recommended for diet studies (Ibáñez *et al.*, 2008) Jigging avoids overestimating the occurrence of target commercial species in the stomach contents of jumbo squids that can feed after capture. Light is a powerful stimulus that attracts individuals independently of their satiety. In addition jumbo squids are known to be extremely voracious and thus can continue to feed once their stomachs are full. However, this fishing tactic and the squid voracity artificially increase the proportion of cannibalized jumbo squids in the stomach contents (Cubillos *et al.*, 2004; Markaida, 2006). To remove this unnatural feeding, the easily identifiable fresh jumbo squid portions were systematically eliminated from the stomach contents. Even after this procedure, jumbo squid was still by far the dominant prey by wet weight and reached 75%, indicating that fishery-induced cannibalism was not fully eliminated. This high rate was mainly due to 859 stomachs containing *D. gigas* only. We were therefore not able to precisely estimate the importance of natural cannibalism with our dataset that was still blurred by artificially induced cannibalized JS. We thus removed these 859 stomachs and worked with the remaining 4461 (83.9%), from which 3618 were not empty (68% of the total number of stomachs) (Table 3.1). We probably eliminated some samples that were not affected by the fishing tactic but this protocol clearly allowed us to improve the relevance of the results.

Identifiable fresh remains and diagnostic hard parts were used to determine the number of each prey item. For fish otoliths and cephalopod beaks, the maximum number of left or right otoliths and the greatest number of either upper or lower beaks were used to estimate the number of fish and cephalopods, respectively. Prey items were identified to the most precise possible taxonomic level using keys and descriptions for fish (Fitch and Brownell, 1968; García-Godos Naveda, 2001), crustaceans (Newel, 1963; Méndez, 1981) cephalopods (Wolff, 1984), and other molluscs (Alamo and Valdivieso, 1997). The degree of digestion of the stomach contents can preclude the identification of all prey remains. However, fresh remains made up the largest percentage of our stomach content samples. The meticulous analyses of the stomach contents performed in our laboratory allowed us to divide into broad prey classes (Cephalopods n/i, Teleosteii n/i, Crustacea n/i) the unidentified remains (see Appendix Table A3.1). A total of 55 prey taxa were identified at different taxonomic levels (see Tables A3.1 and A3.2). Prey were quantified by frequency of occurrence, numbers and wet weight. Mean percentages by number (%N) and by weight (%W) were computed by averaging the percentages of each prey taxon found in the individual stomachs. We thus treated individual squid as the sampling unit, allowing us to compute standard deviations (Chipps and Garvey, 2007). As the identification level was not homogeneous during the 2004-2011 period, we aggregated prey in 11 groups based on their consistency and their ecological importance in the Humboldt Current system (Table A3.1).

A stomach fullness weight index (FWI, in %) was calculated (Rasero *et al.*, 1996):

$$FWI = \frac{W_{st} \times 100}{W - W_{st}}$$

where W_{st} is the wet weight of the stomach content (g) and W the body wet weight of the individual (g).

3.2.3. Data analyses

A clear relationship exists between squid size and maturity stages (Figure A3.1) indicating that size is, to a certain extent, a proxy for ontogenetic processes. To avoid using correlated covariates we only used the size to study life cycle effect on jumbo squid diet. Jumbo squid diet did not significantly vary with sex (results not shown). This factor was thus not taken into account in further analyses. Jumbo squid were generally captured by jigging after dusk and therefore night samples (62%) dominated the dataset. Preliminary analyses were performed on night data and on the whole data set. Results were similar and we therefore only report results with the complete set of data.

In order to analyse the potential effects of explanatory variables on the number of taxa per stomach, a proportional-odds model for ordinal response (McCullagh and Nelder, 1989) was fitted to the vector of prey richness, i.e. the number of different taxa recovered in each stomach $(y_i)_{i\geq 1}$ that was assumed to be a realization of a random variable Y. Y takes its values in the set $E = \{1, 2, \ldots, S\}$ with S equals the maximum observed richness in the 3618 non empty stomachs. The model was written in terms of the cumulative probability function of Y, conditional on three continuous exogenous covariates (size, stomach fullness index and distance to the shelf break). The logistic form was chosen to predict the probabilities of observing different prey richness as a function of the covariates of interest.

The potential effects of explanatory variables (mantle length, season, distance to the shelf break, SSTA) on stomach fullness index and diet of jumbo squid were first investigated using Kruskal-Wallis (KW) non-parametric tests. This preliminary approach allowed us to process an initial inspection of the dataset. Length, distance to the shelf break and SSTA were then each divided in four ordered categories, according to their ecological interpretation (the number of stomachs is given for each category); for mantle length: less than 40 cm (559), 41-60 cm (1553), 61-80 cm (934), over 80 cm (572); for distance to the shelf: less than 50 km (840), 51-75 km (682), 76-130 km (829), over 130 km (1267); for SSTA: less than -1.5°C (616), -1.49 to -0.5°C (899), -0.49 to 0.5°C (1299), over 0.5°C (804). The numbers for the 4 seasons were: summer (690 stomachs), fall (1068), winter (997) and spring (863). However these approaches did not account for dependence and interactions between explanatory variables, and then did not elucidate the complex relationships between the type of prey and the environmental niches. In addition the sampling scheme is very unbalanced in space and time. To cope with these issues, we applied the classification and regression tree (CART) approach proposed by (Breiman *et al.*, 1984) and adapted to diet data by

(Kuhnert *et al.*, 2011). Classification tree was used here as a tool to identify the relationships between explanatory variables and the distribution of prey groupings. This non-parametric method gives a clear picture of the structure of the data, and allows an intuitive interpretation of the interactions between variables. The classification tree uses a partitioning algorithm to estimate a series of binary decision rules that divide the data into smaller homogeneous subgroups in an optimal way. The whole dataset is represented by a single node at the top of the tree. Then the tree is built by repeatedly splitting the data. Each split is defined by a simple rule based on a single explanatory variable. Splits are chosen to maximize the homogeneity of the resulting two nodes. We followed the approach of (Kuhnert *et al.*, 2011) and transformed the diet data as follows: each row represents a unique predator-prey combination, where the proportion by wet weight of one of the eleven prey taxa potentially present in the stomach of a predator is used as a case weight for the classification tree. As the splitting procedure grows an overlarge tree, we applied a prune back procedure to keep the tree reasonably small to focus on the first most informative splits. Each terminal node (or leaf) of the final tree is characterized by a predicted prey distribution (percentage by weight of 11 groups), given three explanatory continuous variables (stomach fullness index, distance to the shelf break and SSTA) and two categorical variables (season: summer, fall, winter and spring; and individual size (cm) divided into four ordered categories). Year effect was also tested but this factor had no significant effect on the pruned tree and was removed from the final model (Table A3.2 for detailed data per year).

Analyses were conducted using the statistical open source R software (R Core Team 2013), with the *MASS* package for the proportional odds-model (Venables and Ripley, 2002) and the *rpart* package for the classification tree.

3.3. Results

3.3.1. Overall diet description

The size of the 4461 selected squids after excluding fishery-induced cannibalism ranged from 14.3 to 114.2 cm ML (Table 3.1). Overall, 19% of the stomachs were empty. For the 3618 non-empty ones, stomach fullness weight index (see Figure A3.2 for details on FWI distribution) decreased significantly with size (Figure 3.2A; KW, H = 499.6, df = 3, P <0.01) and increased significantly with distance to the shelf (Figure 3.2C; KW, H = 177.8, df = 3, P < 0.01). On the opposite, effect of SSTA was not significant (Figure 3.2D; KW, H = 8.5, df = 3, P >0.05), but slightly higher values of stomach fullness weight index occurred in spring (Figure 3.2B; KW, H = 93.8, df = 3, P <0.01).

Table 3.1. Overall description of sampled jumbo squid stomachs during 2004-2011

	2004	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**Total**
N° Dietary groups	27	23	24	18	24	30	33	29	55
N° Stomachs	650	283	589	320	657	922	603	437	4461
N° Non-empty stomachs	520	224	479	239	542	740	523	351	3618
% Non-empty stomachs	80	79.2	81.3	74.7	82.5	80.3	86.7	80.3	81.1
Size range (cm)	21.0–104.5	28.7–91.0	27.4–98.0	28.3–109.5	14.3–112.5	23.6–111.5	16.8–108.6	24.5–114.2	14.3–114.2
Latitude range (°S)	5.0–15.5	4.7–15.2	5.7–15.2	4.3–10.7	5.1–17.6	3.7–16.0	4.8–17.6	4.0–16.2	3.7–17.6
Longitude range (°W)	75.8–82.3	76.6–82.6	76.3–81.9	79.2–83.8	74.6–83.0	76.0–84.0	75.0–82.8	77.0–84.2	74.6–84.2
Distance to the shelf break range (km)	−10.4–210	−15.4–245.8	5.7–218.6	15.5–260.2	23.5–254.5	16.1–342.4	20.6–553.9	62.1–330.8	−15.4–553.9
Distance to the coast range (km)	39.8–300.2	73.8–357.1	70.4–347.8	37.3–271.3	48.9–261.4	40.3–390.6	40.9–604.7	77.3–363.8	37.3–604.7

Cephalopoda (*Dosidicus gigas* and Other Cephalopoda) were the dominant food source in %O, %N and %W (Table 3.2). Both taxa were observed in 13.2 and 44% of the stomachs, respectively, and contributed together 40% by weight and 30% by number. The Phosichthyidae *Vinciguerria lucetia* occurred frequently in the stomach contents (36%), representing an average percentage of nearly 20% by weight and 25% by numbers. The three Myctophidae taxa (*Myctophum* spp., *Lampanyctus* sp. and other Myctophidae) occurred in 1577 samples (8.4, 13.6 and 21.7% respectively), and contributed 15% by weight and 18.3% by number. Teleosteii were frequent in the stomachs (21.7%) and represented 12.7% by weight and 11.7% by number.

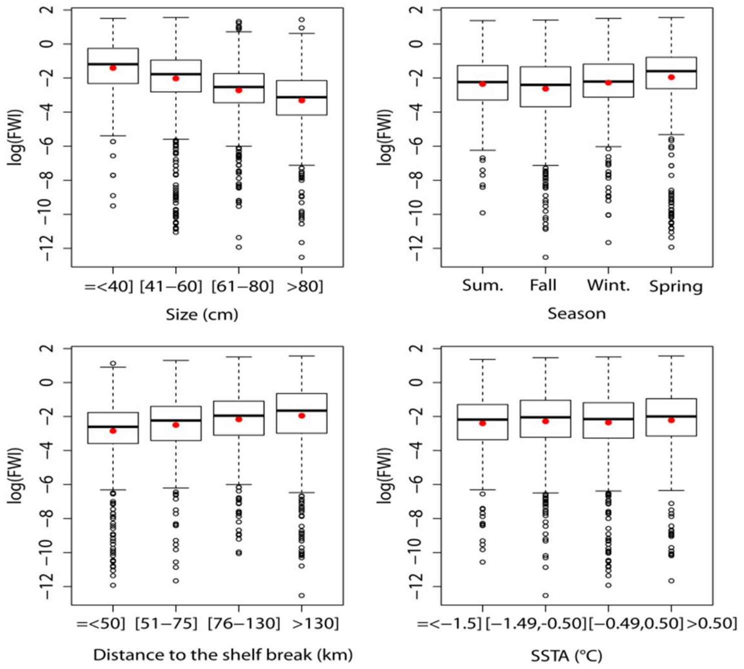

Figure 3.2. Distribution of the logarithm of the Fullness Weight Index (log(FWI) according to the individual size (A), the season (B), the distance to the shelf-break (C), and the Sea Surface Temperature Anomaly (SSTA) (D).

The diet composition of jumbo squid in weight varied according to size (Figure 3.3A). The main pattern was the steady increase of the percentage of cephalopods with size: *D. gigas* and other Cephalopoda accounted for 24.3% of the diet of small squids (ML<40 cm) and reached 43.2% for large squids with ML>80 cm. The percentage of Euphausiidae also increased significantly (Table A3) with size, except for the smallest squids: 6% for the size class under 40 cm, 3.5% in individuals between 40 and 60 cm, 8.4% in individuals between 60 and 80 cm, and 12.4% in individuals larger than 80 cm. On the opposite, the importance of *V. lucetia* (21.0% to 5.6%) and *Myctophum* sp. (7.2% to 1.3%) decreased significantly while jumbo squid increased in size (Table A3.3).

No clear tendency appeared with the season (Figure 3.3B), except a significantly higher percentage of *V. lucetia* (32%) in spring and less Cephalopoda (26%), Euphausiidae (2.8%) and Teleosteii (9.3%) (Table A3.3). In summer, Euphausiidae were at their maximum (10%) while the percentage of *V. lucetia* was low (13.7%) and Engraulidae were very rare (0.4%).

Table 3.2. Distribution of the eleven dietary groups recovered from jumbo squid stomach contents off Peru between 2004 and 2011.

Dietary groups	**Prey code**	**N° Stomachs**	**%FO**	**%W**	**%N**
Dosidicus gigas	Dgig	478	13.2	8.6 (±25.5)	3.4 (±11.7)
Other Cephalopoda	Ceph	1591	44.0	31.2 (±44.2)	26.4 (±39.7)
Euphausiidae	Euph	299	8.3	6.4 (±23.7)	7.8 (±26.3)
Pleuroncodes monodon	Pleu	83	2.3	1.7 (±12.4)	1.7 (±12.5)
Engraulidae	Engr	142	3.9	2.7 (±15.3)	2.1 (±12.4)
Lampanyctus sp.	Lamp	491	13.6	4.6 (±19.6)	5.1 (±17.8)
Myctophum spp.	Mycg	302	8.4	3.6 (±17.5)	3.5 (±15.4)
Other Myctophidae	Mycf	784	21.7	6.7 (±23.7)	9.7 (±24.4)
Vinciguerria lucetia	Vluc	1299	35.9	19.7 (±37.6)	24.4 (±37.8)
Teleosteii	Tele	786	21.7	12.7 (±31.7)	11.7 (±28.2)
Other	Othe	333	9.2	2.0 (±12.8)	8.8 (±17.1)

For each prey group are indicated, the corresponding number of stomachs (N° Stomachs), the frequency of occurrence (%FO), and the percentage of prey group per stomach by weight (%W) and by number (%N) (mean value ± standard deviation).

The diet composition of *D. gigas* varied significantly with the distance to the shelf break (Figure 3.3C; Table A3.3): Euphausiidae slightly decreased, Cephalopoda decreased from 36.3% inside the 50 km to 26.8% out of the 130 km, while percentages of *V. lucetia* increased from 13.8% inside the 50 km to 24.2% out of the 130 km. The percentage of Engraulidae also increased with the distance to the shelf break except for distances greater than 130 km.

Diet changed according to SSTA (Figure 3.3D). Trend from negative towards positive anomaly was associated to a significant increase in *V. lucetia* (from ~15 to 28.6%) and a significant decrease in cannibalism (from ~11 to 6.6%) (Table A3.3).

3.3.2. Prey taxa richness

Based on the detailed 55 prey taxa, the prey richness in the stomachs was very low. A maximum of seven prey taxa was observed in one stomach only, while a single prey taxon was recovered in 48.0% of the stomachs and 30.7% had two prey taxa (mean=1.87, sd=1.10). Results were similar with the eleven aggregated taxa: a maximum of seven prey taxa, 48.6% with one prey taxon and 31.1% with two prey taxa (mean=1.82, sd=1.02). Consequently, analyses were performed with the 11 taxa aggregated database (Table 3.2.).

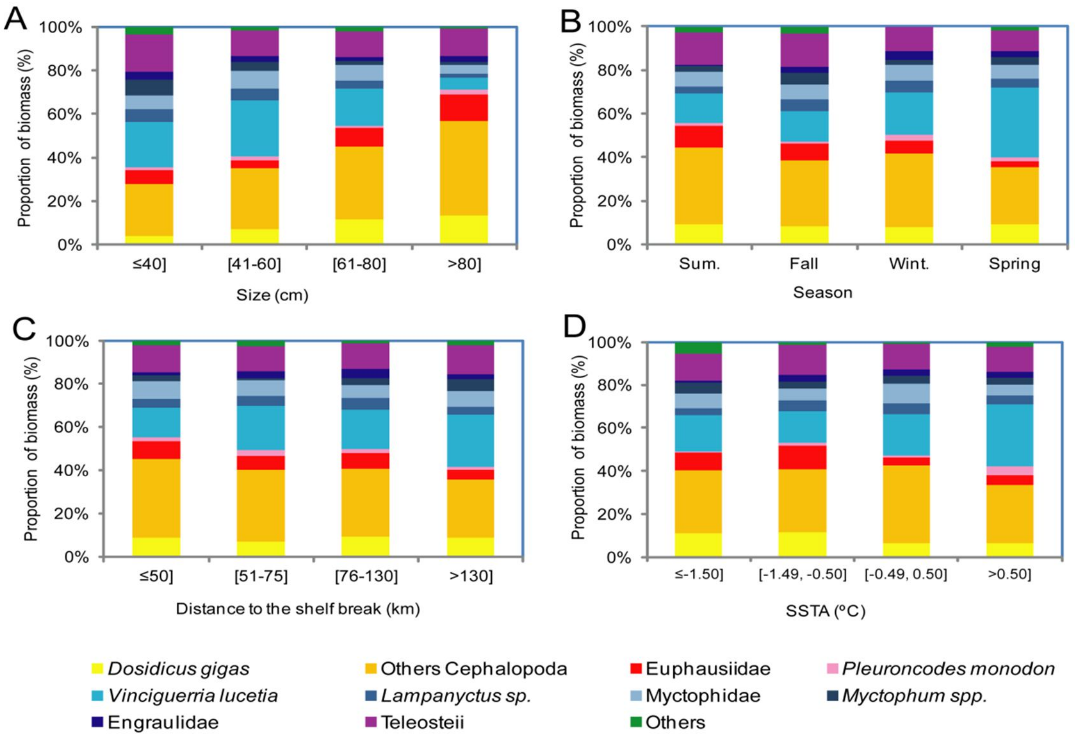

Figure 3.3. Jumbo squid diet composition in weight (%) according to the individual size (A), the season (B), the distance to the shelfbreak (C), and the Sea Surface Temperature Anomaly (SSTA) (D).

According to AIC, the proportional-odds model with two covariates (fullness and distance to the shelf, AIC=8691) was the most parsimonious (adding squid size did not improve the fit, AIC=8692). The estimated values of the parameters were used to compute the probabilities of observing 1, 2, or 3+ (i.e., at least 3) prey taxa in a stomach as a function of stomach fullness or distance to the shelf. Increasing the stomach fullness led to a sharp increase in the probability of recovering 3+ prey taxa in a stomach and to a marked decrease of the probability to observe only one taxon (Figure 3.4A). After a short plateau, the probability for two taxa roughly decreased with stomach fullness too. On the other hand, the probability to find one taxon only decreased with the distance to the shelf, while the probabilities to recover more than two prey taxa increased with this covariate (Figure 3.4B).

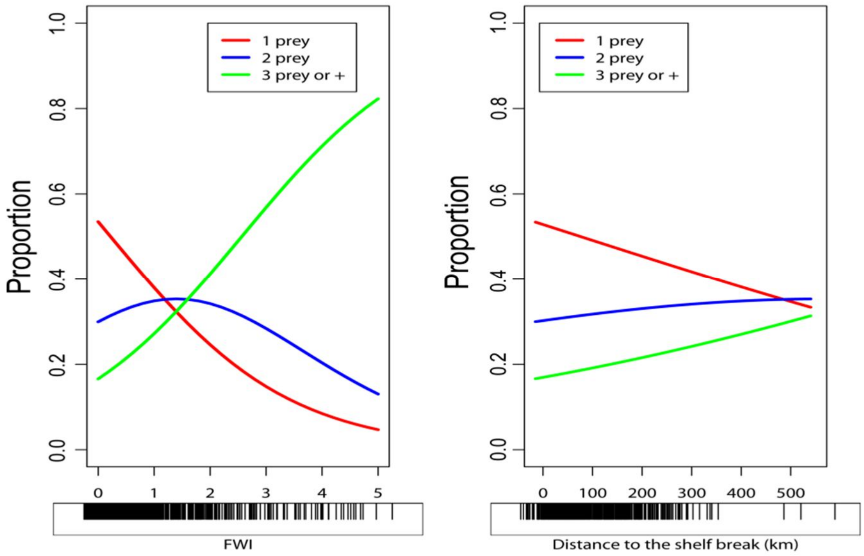

Figure 3.4. Proportional odds model. Prediction of the number of prey groups (1, 2, 3 or more) in a given stomach according to the fullness weight index (FWI) (A) and the distance to the shelf-break (B). Black tick marks under the x-axes show the location of the data points.

3.3.3. Multivariate approach

The pruned classification tree showed 13 nodes (Figure 3.5). The first split separated four nodes corresponding to a very low fullness (<0.2) from the others. Among this group, the nodes 1 to 3 predicted diet compositions dominated by cephalopods (predicted cephalopod probability = 0.48, 0.35 and 0.34, respectively), which occurred more likely in individuals larger than 80 cm ML (node 1), in individuals smaller than 80 cm ML caught in summer and fall (node 2), and in individuals located within the 191 km from the shelf break caught during winter and spring (node 3). The node 4 however showed a high incidence of *V. lucetia* (predicted probability = 0.44) at a distance to the shelf break higher than 191 km, in winter and spring. The node 5 showed a high probability of cannibalism (predicted probability = 0.32) for medium size (between 60 and 80 cm ML) individuals with stomach fullness higher than 0.2. From the node 6 on, squids had a smaller ML (less than 60 cm). The node 6 also showed a high probability of cannibalism (predicted probability = 0.46) for SSTA <0.425ºC, in individuals with fullness greater than 2.08, located at less than 209 km to the shelf break. The node 7, characterised by the Teleostei (predicted probability = 0.60), had the same characteristics than the node 6, except a more offshore location. Nodes 8 to 10 showed a relatively balanced diet and were separated from nodes 6 and 7 by a lower fullness (<2.08). Nodes 11 to 13 corresponded to fullness ≥0.2, size <60 cm and SSTA ≥0.425ºC. Node 11 was associated to high SSTA (≥1.09ºC), short distance to the shelf break (<197 km), and predicted a dominance of cephalopods (predicted probability = 0.37). In nodes 12 (distance to the shelf break greater than 197 km) and 13 (SSTA < 1.09ºC), *V. lucetia* was largely dominant (predicted probability = 0.38 and 0.55, respectively).

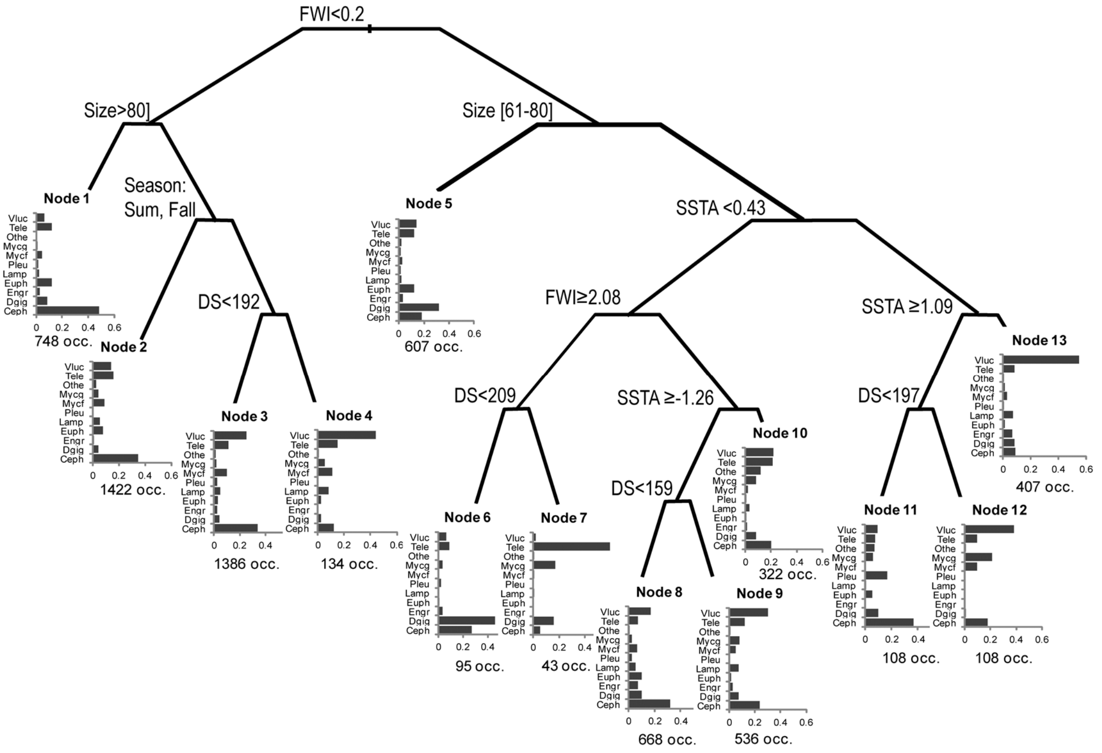

Figure 3.5. Classification tree of jumbo squid diet (prey groups) according to the Fullness Weight Index (FWI), the Distance to the Shelf (in km) (DS), the Sea Surface Temperature Anomaly (SSTA, in 6C), the mantle length (Size in cm) and the Season. For each final node, the predicted probabilities of occurrence of the 11 prey groups is detailed (histograms) and the number of prey occurrences (occ) is given. See Table for prey codes.

3.4. Discussion

This work is based on an extensive dataset on jumbo squid diet encompassing a large range of spatiotemporal location and sizes. Beyond the usual description of organism diet, our results allowed us to provide new knowledge on jumbo squid trophic ecology, in particular on prey distribution under different environmental conditions and on the role that could be played by the dissolved oxygen.

3.4.1. Prey richness

Using the detailed (55 taxa) or aggregated (11 taxa) databases, prey richness in stomachs was similar with an average of 1.8 taxa per stomach. This unexpected result has several consequences. It first empirically validates the eleven aggregated taxonomic groups (Table A3.1). Second, it shows that when jumbo squid foraged on one prey among the 55 taxa, it did not feed on extra prey belonging to the same group of 11 aggregated taxa. A spatial segregation of prey of jumbo squids may explain this observation. If a taxon from one group of the 11 aggregated taxa occurred in a location where jumbo squids seek their prey, the probability of the presence of an extra taxon belonging to the same group was low. On the contrary, jumbo squid could select the most abundant or energetic taxon of a group, neglecting the other available prey belonging to the same group. Our data did not allow us to support either one of these hypotheses. However, predictions of the multinomial model showed that stomach fullness increased with the number of prey taxa, while most of the stomachs contained one or two prey taxa only. We could have expected an opposite pattern. Indeed, other top predators such as tuna exhibit high foraging efficiency (high fullness) in presence of large and dense monospecific prey aggregations in surface layers (Bard *et al.*, 2002; Bertrand *et al.*, 2002a; Potier *et al.*, 2008). Once a prey concentration of one target species is detected, tunas can feed on this concentration until satiation (Menard and Marchal, 2003). On the contrary, when prey are scarce and dispersed in the environment (Auster *et al.*, 1992), tunas forage on a higher diversity of prey but with a lesser efficiency (Potier *et al.*, 2007). On the case of the jumbo squid our results therefore question the usual hypothesis according to which marine top predators may seek locally dense aggregations of monospecific prey.

3.4.2. Dietary composition, environmental conditions and size-related patterns

Identifying cephalopods food is tricky (Budelmann, 1994): the beak can bite off small pieces of tissue of large prey; diagnostic hard parts of prey, such as fish otoliths, skeletons, crustacean integuments or cephalopod beaks are often rejected. Selective rejection can also occur and blur diet composition. In addition, digestion is known to be rapid among cephalopods. However, we carefully dealt with the intrinsic biases linked to the data sampling and with the identification of prey items that was carried out by the same scientific team following a constant protocol.

Consequently, the extensive set of data over a large time period allowed us to elucidate the foraging behaviour of jumbo squids in the northern Humboldt Current system. We assume that changes in prey composition according to squid size and spatiotemporal features were more related to prey accessibility rather than to specific/size-related preferences. Jumbo squid perform ontogenetic migration with small individuals distributed further offshore than larger individuals (Arguelles *et al.*, 2001). Spawning in less productive offshore waters is used by other species to avoid predation on first stages (e.g. the South Pacific jack mackerel, *Trachurus murphyi*; (Barbieri *et al.*, 2004). This spatial dynamics is evidenced once more here, with small individuals distributed further offshore than the large ones. However, the biggest ones (> 80 cm ML) seem to move back offshore, probably to spawn (Tafur *et al.*, 2001) but not as far as the smallest individuals that are advected further offshore at early stages. Note that warmer waters (offshore in our case) are suitable for spawning (Field *et al.*, 2013). Prey composition in the stomach contents matches this pattern. Euphausiids contributed at a higher level as prey of large rather than of small squids, according to the known spatial distribution of euphausiids. Ballón *et al.* (2011) showed indeed that the biomass of euphausiids was maximal off the shelf-break until a distance of ca. 150 km. This range corresponds to that where the larger individuals spawn (Tafur *et al.*, 2001). Therefore, contrary to most past studies (Rahm, 1937; Nesis, 1983, 1970; Markaida and Sosa-Nishizaki, 2003; Markaida, 2006) zooplankton contribution does not systematically decrease with the size. In addition, isotope signatures along jumbo squid gladius in the northern Humboldt Current system showed that large individuals can significantly forage on low trophic levels (Lorrain *et al.*, 2011).

Mesopelagic fish (*V. lucetia* and myctophiids) recovered in the jumbo squids stomachs confirmed the structuring role of spatial matching in the jumbo squid-prey interactions. This prey group contributed more during spring and far from the coast, when jumbo squid was more offshore. In addition, small jumbo squids distributed far from the coast consumed more mesopelagic fish than larger individuals located closer to the coast. This pattern was unexpected again, but is in accordance with the distribution pattern of mesopelagic fish that are distributed more offshore than euphausiids (Cornejo and Koppelmann, 2006).

Cannibalism accounted for more than 8% in weight. High levels of cannibalism are frequently observed in jumbo squid (Markaida and Sosa-Nishizaki, 2003; Ibáñez *et al.*, 2008). Yet, cannibalism can be overestimated depending of the fishing gear used for capture (Ibáñez *et al.*, 2008; Ibáñez and Keyl, 2009). In this study we followed various steps to remove as far as possible artificially induced cannibalism. On the other hand, cannibalism may also be underestimated. Indeed, squid muscles sections with a high degree of digestion are difficult to determine. When it was not possible to identify the squid prey species, the corresponding items were incorporated in the group of other cephalopods. It is thus likely that some digested *D. gigas* were considered as 'other cephalopoda'.

Several hypotheses are proposed to explain cannibalism in squid. This behavior may be part of an energy storage strategy of the population, allowing cephalopod to react to favorable and adverse environmental conditions by increasing or reducing their number (Ibáñez and Keyl, 2009). Cannibalism can also provide a competitive advantage among young and adults and can be beneficial for survival during periods of food shortage (Caddy, 1983). We observed the classic pattern of steady increase of cannibalism with size related to the increase in predator's ability to capture and handle the prey (Christensen, 1996; Lundvall *et al.*, 1999). Large specimens can access to highly energetic food when feeding on conspecifics (Amaratunga, 1983). However, the relative spatial segregation of this species by size (Arguelles *et al.*, 2001) may be a response to limit cannibalism on juveniles.

3.4.3. The anchovy paradox: does oxygen matter?

In the California Current system *D. gigas* forages substantially on coastal fish, particularly anchovy (*Engraulis mordax*) (Markaida *et al.*, 2008; Field *et al.*, 2013). Surprisingly *D. gigas* consumes very few anchovy in Peru, whereas a tremendous biomass of anchovy is potentially available. Furthermore, off Peru, anchovy is concentrated in schools or dense aggregations within the thin surface oxygenated layer (Bertrand *et al.*, 2008; Bertrand *et al.*, 2010), which makes anchovy an easy prey for mobile predators (Gerlotto *et al.*, 2006). Unlike in California (Field *et al.*, 2013), the jumbo squid distribution hardly overlaps with that of anchovy, which is very coastal (Figure 3.6). Why does jumbo squid not distribute closer to the coast and benefits from the huge anchovy stock? Oxygen may be the answer. Anchovy is not adapted to anoxia and cannot enter the oxygen minimum zone. However this small fish (oxygen supply per body size decreases as fish size/weight increases) can forage at low cost (so low oxygen demand) on macrozooplankton and is thus adapted to inhabit the unsaturated surface coastal waters (Bertrand *et al.*, 2011). On the contrary, jumbo squid is adapted to anoxia since it undertakes diel vertical migration and occupies the oxygen minimum zone (OMZ) during the day (Gilly *et al.*, 2006, 2012; Rosa and Seibel, 2008, 2010; Bazzino *et al.*, 2010; Trübenbach *et al.*, 2012; Seibel, 2013). *D. gigas* succeeds in the OMZ by managing hypoxia *via* metabolic suppression (Rosa and Seibel, 2008, 2010; Trübenbach *et al.*, 2012, 2013), coupled with a high-affinity respiratory protein, the hemocyanin (Seibel, 2013). However normoxic conditions are needed in surface during the night to supply the oxygen demand that was not achieved in hypoxic waters at greater depths (Seibel, 2011, 2013). In coastal Peru the OMZ is much more intense than in California, the upper OMZ is shallower and, above the oxycline, oxygen concentration and saturation are low (Rosa and Seibel, 2008). In such conditions jumbo squid may be prevented to enter the coastal waters where the anchovy is situated, as was previously evidenced for sardine (Bertrand *et al.*, 2011). Indeed, off Peru, the abundance of jumbo squid biomass increases with oxygen saturation (Figure 3.6). When upwelling is strong, anchovy partly distributes off the shelf break and should be more accessible to jumbo squid. However, such conditions correspond also to an extension of the surface oxygen unsaturated waters (Bertrand *et al.*, 2011).

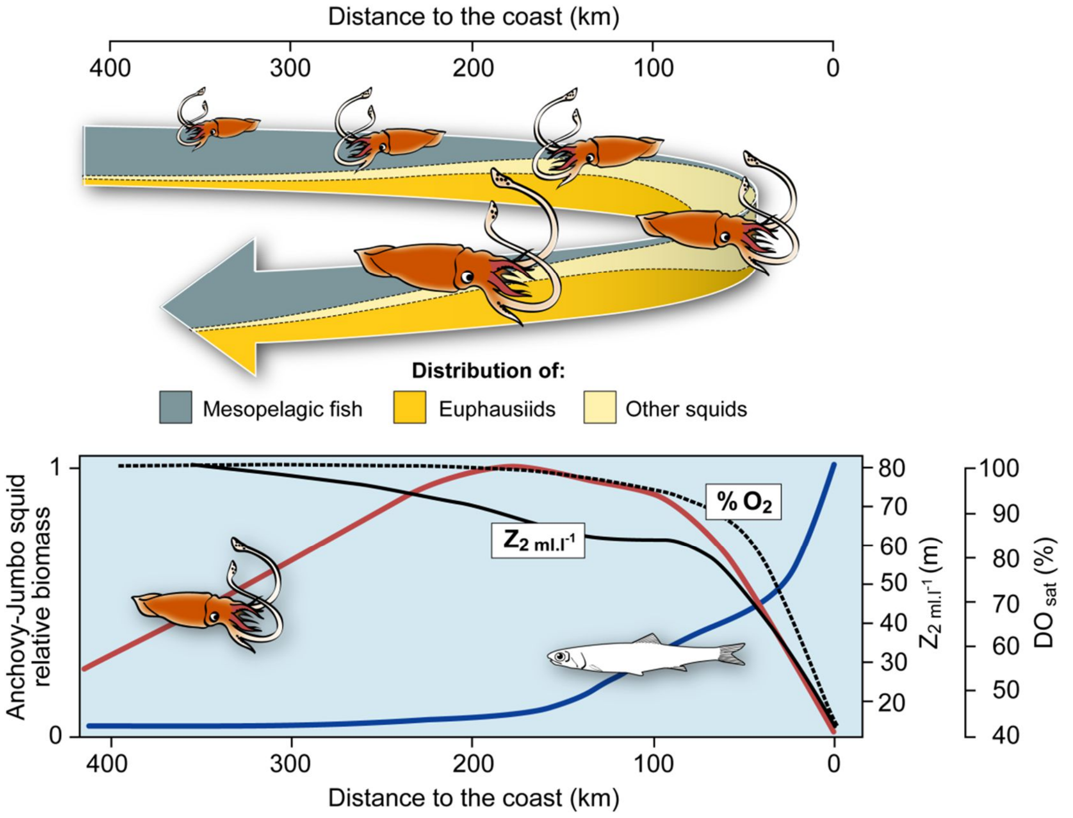

Figure 3.6. Conceptual model and cross-shore profiles of oxygen and organisms distribution. The lower panel shows the mean (spline smooth) cross-shore profiles of dissolved oxygen saturation in % (grey dashed line), depth of the 2 $ml.l^{-1}$ isoline in m (black solid line) and the acoustic-estimated biomass of anchovy (blue solid line) and the jumbo squid acoustic-estimated biomass (red solid line). Oxygen and anchovy data come from Bertrand et al. (2011); jumbo squid data come from IMARPE, unpublished data. Note that the oxygen data cover the range 7°S to 18°S. The upper part shows the cross-shore distribution of jumbo squid along its ontogenetic cycle. The colours in the arrow represent the schematic range of distribution and proportional abundance of the three main prey groups i.e., the other cephalopoda, euphausiids and mesopelagic fish.

3.5. Synthesis

As a synthesis we propose a comprehensive model of jumbo squid *Dosidicus gigas* trophic ecology in the northern Humboldt Current system (Figure 3.6). Small jumbo squid (<400 mm) are mostly distributed far offshore where they largely forage on mesopelagic fish. As they grow, they move closer to the coast and increase their consumption of other cephalopoda. However, off Peru, contrarily to other systems (Field *et al.*, 2013), *D. gigas* does not occupy very coastal waters where a dramatic biomass of anchovy is present. We hypothesize that jumbo squid cannot enter the coastal waters that present low surface oxygen saturation. Although jumbo squid can forage in hypoxic deep waters it needs surface normoxic waters afterwards (Seibel, 2013). Oxygen concentration may thus limit the co-occurrence of both species and then preclude predator-prey interactions. Large squids move further offshore (without reaching the oceanic distribution of smaller jumbo squids), and increase their consumption of squids (including jumbo squid) and euphausiids. Note that euphausiids consumption is rather low considering its availability, indicating that, when possible *D. gigas*, appears to seek for more energetic prey. The global pattern we described illustrates the opportunistic foraging behaviour of jumbo squid, which is impacted by ontogenetic migration and most likely by oxygen conditions. Also, even if the global scheme described in Figure 6 seems consistent, as was already described (Argüelles *et al.*, 2012a; Lorrain *et al.*, 2011), high variability exists between individuals and the differences in jumbo squid life history strategies highlight the high degree of plasticity of the jumbo squid and its high potential to adapt to environmental changes.

Chapter IV

Diet diversity of jack and chub mackerels and ecosystem changes in the Northern Humboldt Current System: a long-term study

4.1. Introduction

The diet of predatory fishes integrates many ecological components including feeding behaviour, habitat use over time and space, diversity and availability of forage fauna, energy intake and fish condition, inter- and intraspecific interactions, and environmental forcing. Food habits are therefore critical for understanding trophic functioning of marine ecosystems and then sustainability of exploited fish populations. In the Humboldt Current system, *Trachurus murphyi* (Jack mackerel, JM hereafter) and *Scomber japonicus* (Chub mackerel, CM hereafter) are important pelagic resources with high content of essential fatty acids (Celik, 2008). They are heavily exploited by artisanal and industrial fisheries (Arcos *et al*., 2001; Gerlotto *et al*., 2012).

JM occurs from the equator to the austral region of Chile and from the coast of South America to New Zealand and Tasmania (Grechina 1998; Gerlotto *et al*., 2012). The JM fishery has been one of the largest worldwide, with a maximum yearly yield of almost 5 million tonnes in 1995. Since the late 1990s, JM landings dropped off to reach ca. 0.5 million tonnes (Figure 4.1). This trend is attributed to both overfishing and climate variability (Gerlotto *et al*. 2012). Depicting the relative importance of natural and anthropogenic forcing is complex, making difficult the management of this highly migratory and transzonal resource, which is distributed in several EEZ and in international waters. JM has therefore become a concern for the South Pacific Region Fisheries Management Organization (SPRFMO: www.southpacificrfmo.org).

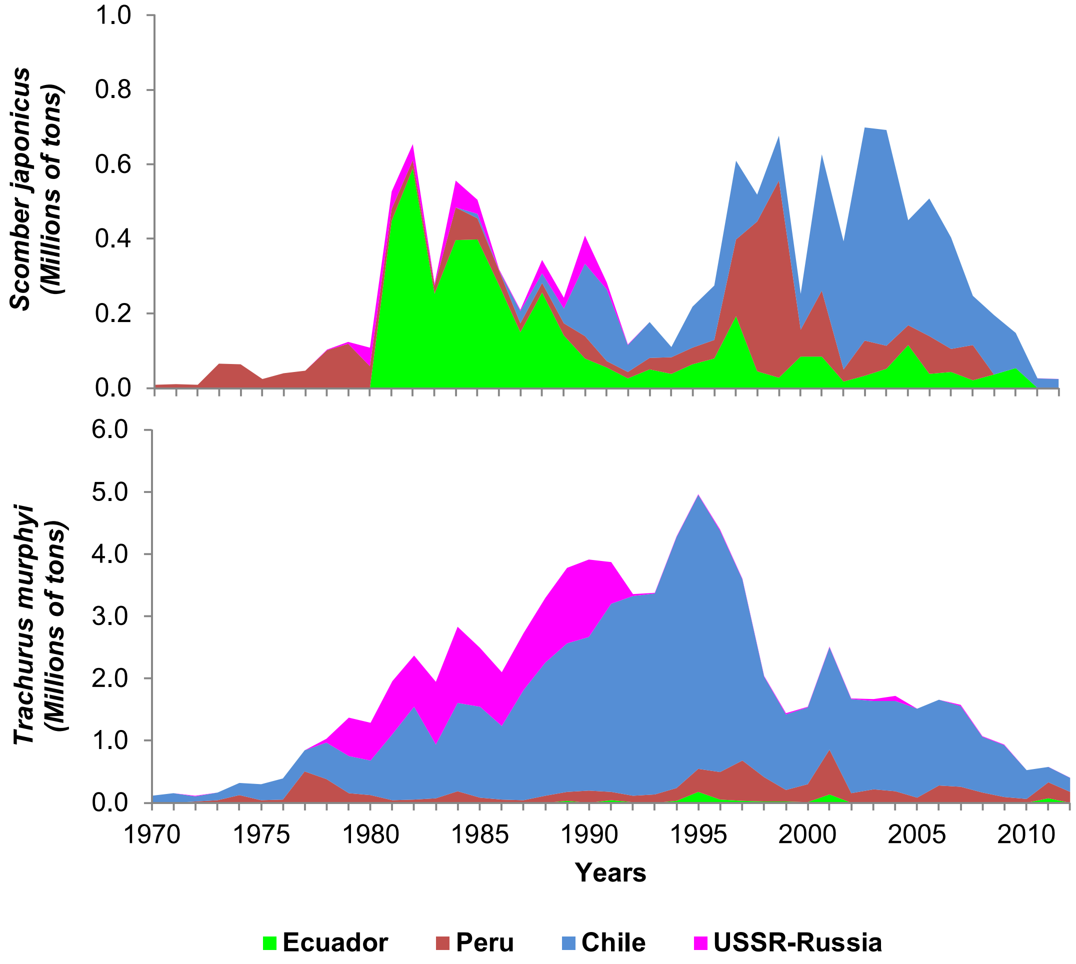

Figure 4.1. Evolution of catches for the same 4 fleets (in million tonnes) for T. murphyi and S. japonicus during the period 1970-2012. The 4 main fleets are Ecuador, Peru, Chile and USSR-Russia. Below: (Source: FAO, 2014a).

CM is an important commercial coastal-pelagic species with a worldwide distribution (Collette and Nauen, 1983; Castro Hernández and Santana Ortega, 2000). In the Southeastern Pacific CM distribution extends from the Ecuador to Darwin Bay in Chile (45°S) (Castro Hernández and Santana Ortega, 2000; Konchina, 1982). In this region CM catches showed rises and falls during the last 40 years but a clear declining trend occurred after a maximum of ca. 0.7 million tonnes in 2003.

Variation in distribution and abundance of both species is related to a variety of abiotic (e.g. Ganoza, 1998; Arcos *et al.*, 2001; Bertrand *et al.*, 2006) and biotic factors (e.g. Quiñones *et al.*, 1997; Grechina, 1998; Bertrand *et al.*, 2006, 2004a). Both species exploit a large range of oceanographic conditions (Bertrand *et al.*, 2004b) and are considered opportunistic predators (Konchina, 1981; Konchina, 1982). Their distribution and abundance depends on a large extend on food availability (Konchina, 1981, Quiñones et al., 1997; Bertrand *et al.*, 2006, 2004a). Investigating the dietary changes of JM and CM should allow us to better understand on the one hand their respective trophic niches, and on the other hand their resilience to climatic changes including El Niño Southern Oscillation (ENSO) events and decadal changes that strongly impact marine resources and affect the structure of the Humboldt Current system.

In this paper, we analyzed an extensive dataset of more than 47,000 stomachs sampled over 40 years (1973-2013) and provided new insight in the variability in space and time of feeding habits and prey diversity of JM and CM in the northern Humboldt Current system (NHCS). We show that (i) both species are opportunistic and present a trophic overlap but surprisingly, JM does not seem more voracious than CM; (ii) fish diet presented high spatiotemporal variability, the shelf break being a main biogeographical frontier; (iii) fish diet composition is not necessarily a good indicator of changes in prey biomass since prey accessibility and energy content does matter; (iv) unexpectedly, El Niño events have a weak effect on stomach fullness and the diet of CM and JM; and (v) our results challenge the paradigm of positive correlation between diversity and temperature in the NHCS.

4.2. Material and methods

4.2.1. Sample collection

JM and CM were collected between 1973 and 2013 along the Peruvian coast up to 470 km from the coast (Figure 4.2), from scientific cruises carried out by the Peruvian Sea Institute (IMARPE), the industrial fishing fleet, and the Eureka program (quick synoptic surveys to collect biological and qualitative acoustic information aboard fishing vessels, see Gutiérrez *et al.*, 2012). As far as possible, three individuals of both species were randomly sampled by fishing set and by size classes of one centimetre covering the captured size range. In the laboratory, fork length (in cm; hereafter, fish size refers to fork length), total weight (in g) were measured and the sex and maturity stages (using the five-stage scale of Sánchez *et al.*, 2013) were determined. Stomachs were fixed in 96% alcohol or in 10% formaldehyde. Samples were characterized according to year, season, latitude, zone (north 3°-6°S, centre-north 6°S-10°S, centre-south 10°-15°S, south 15°-18°S), distance to the shelf break (in km, negative to the continental shelf and positive towards offshore), sea surface temperature anomalies (SSTA, in °C) and depth of isotherm 15°C ($Z_{15^{\circ}C}$, in m; see Flores *et al.*, 2013). In addition, fish length and distance to the shelf break were classified in ordered categories: less than 20 cm, then by 10 cm bins above, for length; -100 to -10 km (i.e. continental shelf), -10 to 10 km (around shelf break), 10 to 40 km, 40 to 80 km and >80 km, for distance to the shelf break.

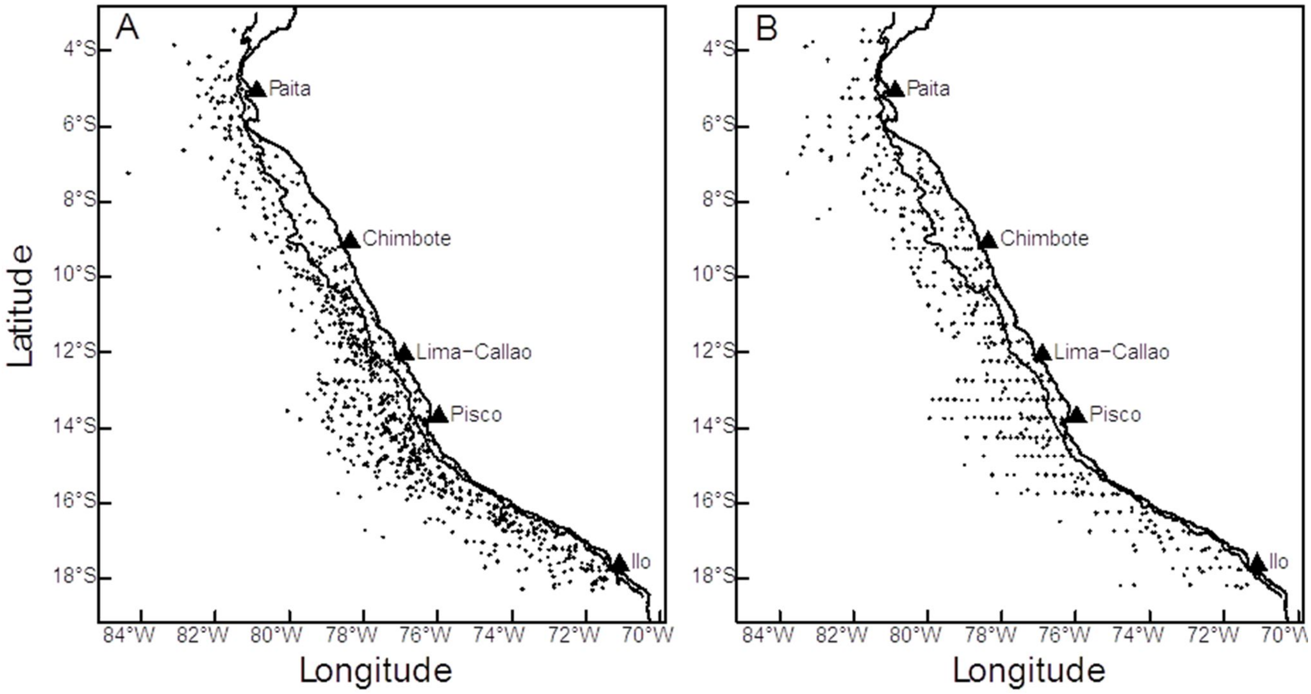

Figure 4.2. Distribution of stomach samples (black dots) of (A) Trachurus murphyi and (B) Scomber japonicus. The black solid line indicates the 200 m isobath used as a proxy for shelf break position.

4.2.2. Stomach content analysis

Stomachs contents were washed through a sieve mesh of 300 µm in order to retain prey remains and diagnostic hard parts (fish otoliths, cephalopod beaks, crustacean exoskeleton). The different items constituting a single taxon were sorted, counted and weighed to the nearest 0.01 g. Prey were determined using a binocular microscope to the lowest possible taxon using keys and descriptions for Teleosteii (Fitch and Brownell, 1968; Chirichigno and Cornejo, 2001; García-Godos Naveda, 2001), crustaceans (Newel, 1963; Méndez, 1981), zooplankton (Trégouboff and Rosse, 1957), cephalopods (Wolff, 1984) and molluscs (Alamo and Valdivieso, 1997). A total of 90 and 102 prey taxa were identified for JM and CM, respectively. However the identification level varied over the 1973-2013 period. In particular crustanceans and especially Zoea larvae were identified very precisely in 2009 because a specific investigation was performed on that taxonomic group during this year. We therefore homogenized the prey taxa during the sampling period, and obtained a total of 60 and 62 prey taxa mixing different taxonomic levels for JM and CM, respectively (Table 4.1). In addition and for the sake of clarity of our quantitative assessments, we aggregated the prey taxa in 13 groups based on their consistency and their ecological importance in the NHCS (Table 4.2): tunicata, cephalopoda, copepoda, Zoea larvae, Euphausiidae, the squat lobster *Pleuroncodes monodon*, other crustacea, Engraulidae, mesopelagic fishes, coastal fishes, other teleostei, eggs and larvae of teleostei, and other prey. Prey taxa were quantified by frequency of occurrence and by wet weight. Mean percentages by wet weight (%W) were computed by averaging the proportions of each prey taxa found in the individual stomachs (Chipps and Garvey, 2007). We thus treated individual as the sampling unit, allowing us to compute standard deviations.

A stomach fullness weight index (FWI, in %) was calculated as:

$$FWI = \frac{W_{st} \times 100}{W - W_{st}}$$

where W_{st} is the wet weight of the stomach content (in g) and W the body wet weight of the individual (in g).

4.2.3. Index of condition

Variation in the condition of the two fish species was investigated using the relative condition factor K_n (Le Cren, 1951) computed for each weighed (We, observed eviscerated weight) and measured (FL, length in cm) individual:

$$K_n = We \,/\, We',$$

where We' is the predicted weight of an individual of a given length FL ($We' = 10^{\alpha}.FL^{\beta}$).

The following parameters were estimated for CM: a = -2.233 ± 0.0098, β= 3.243 ± 0.0067 and for JM: a = -1.786 ± 0.0046, β = 2.906 ± 0.0031.

Table 4.1. Overall description of the prey taxa observed in jack mackerel (T. murphyi) and chub (S. japonicus) mackerel stomach sampled off Peru during 1973–2013. Are indicated, the taxonomic information, the dietary group, the mean value (±standard deviation) of the proportion by weight (%W), and the frequency of occurrence (%O).

						T. murphyi		***S. japonicus***	
Phylum	***Class***	***Order***	***Family***	***Species***	***Dietary group***	***%W***	***%O***	***%W***	***%O***
Algae				Algae n/i	Other	0.08 (2.8)	0.08	0.0001 (0.01)	0.01
Rhizaria	Radiolaria			Radiolaria n/i	Other	0.00	0.00	0.00003 (0.002)	0.003
Cnidaria				Cnidaria n/i	Other	0.02 (1.4)	0.03	0.04 (2.00)	0.04
Chaetognatha				Chaetognatha n/i	Other	0.00	0.00	0.0001 (0.01)	0.002
Annelida	Polychaeta			Polychaeta n/i	Other	0.05 (1.8)	0.05	0.21 (3.58)	0.29
		Phyllodocida	Alciopidae	Alciopidae n/i	Other	0.03 (1.6)	0.03	0.01 (0.36)	0.12
Mollusca				Mollusca n/i	Other	0.00	0.00	0.00003 (0.003)	0.01
	Gastropoda			Gastropoda n/i	Other	0.11 (3.1)	0.21	0.10 (2.60)	0.25
		Thecosomata		Thecosomata n/i	Other	0.17 (4.2)	0.18	0.08 (2.82)	0.09
			Cavoliniidae	*Diacria* spp.	Other	0.30 (5.4)	0.28	0.06 (2.41)	0.06
		Littorinimorpha	Atlantidae	*Atlanta* spp.	Other	0.00	0.00	0.02 (1.27)	0.02
			Naticidae	*Natica* spp.	Other	0.09 (2.7)	0.15	0.23 (4.21)	0.62
	Bivalvia			Bivalvia n/i	Other	0.01 (0.6)	0.02	0.03 (1.44)	0.07
		Veneroida	Semelidae	*Semele* spp.	Other	0.10 (3.1)	0.06	0.00	0.00
	Cephalopoda			Cephalopoda n/i	Cephalopoda	0.29 (5.2)	0.27	1.76 (12.83)	1.77
				Cephalopoda paralarvae	Cephalopoda	0.00	0.00	0.03 (1.55)	0.03
		Myopsida	Loliginidae	Loliginidae n/i	Cephalopoda	0.15 (3.6)	0.14	0.16 (3.83)	0.15
		Octopoda	Argonautidae	*Argonauta* spp.	Cephalopoda	0.00	0.00	0.08 (2.84)	0.08
		Oegopsida		Oegopsida n/i	Cephalopoda	0.00	0.00	0.04 (1.71)	0.02
			Enoploteuthidae	*Abraliopsis affinis*	Cephalopoda	0.09 (3.0)	0.09	0.13 (3.37)	0.14
			Ommastrephidae	*Dosidicus gigas*	Cephalopoda	0.03 (1.5)	0.03	0.15 (3.35)	0.13
			Pyroteuthidae	*Pterygioteuthis giardi*	Cephalopoda	0.02 (1.3)	0.02	0.00	0.00
Arthropoda				Crustacea n/i	Other Crustacea	0.32 (5.4)	0.29	0.16 (3.57)	0.14
				Crustacea eggs	Other Crustacea	0.06 (2.5)	0.06	0.02 (0.83)	0.04
				Crustacea larvae	Other Crustacea	0.00	0.00	0.11 (2.40)	0.1
	Maxillopoda			Cirripedia n/i	Other Crustacea	0.02 (1.4)	0.03	0.00	0.00
				Copepoda n/i	Copepoda	7.10 (25.1)	7.26	14.29 (31.98)	15.44
	Ostracoda			Ostracoda n/i	Other Crustacea	0.07 (2.1)	0.09	0.20 (4.12)	0.12
		Podocopida	Cyprididae	Cypris larvae	Other Crustacea	0.0002 (0.02)	0.01	0.02 (0.94)	0.07
	Malacostraca	Amphipoda		Amphipoda n/i	Other Crustacea	0.29 (5.2)	0.33	0.57 (6.39)	0.86
			Gammaridae	Gammaridae n/i	Other Crustacea	0.05 (2.1)	0.07	0.05 (1.80)	0.1
			Hyperiidae	Hyperiidae n/i	Other Crustacea	0.02 (1.4)	0.04	0.25 (3.42)	0.77
			Caprellidae	Caprellidae n/i	Other Crustacea	0.05 (2.2)	0.05	0.001 (0.09)	0.03
		Decapoda		Decapoda n/i	Other Crustacea	0.78 (8.6)	0.78	0.50 (6.40)	0.54
				Decapoda eggs	Other Crustacea	0.00	0.00	0.01 (0.88)	0.004
				Zoea larvae	Zoea larvae	12.29 (32.4)	12.49	13.35 (31.87)	13.05
				Megalopa larvae	Other Crustacea	1.09 (9.9)	1.12	1.58 (11.32)	1.54
			Hippidae	*Emerita analoga*	Other Crustacea	0.14 (3.4)	0.17	0.23 (4.65)	0.13
			Munididae	*Pleuroncodes monodon*	*P. monodon*	7.66 (26.3)	7.6	5.39 (1.99)	5.24
		Euphausiacea	Euphausiidae	Euphausiidae n/i	Euphausiidae	49.31 (49.3)	49.08	27.45 (42.68)	26.51
		Stomatopoda		Stomatopoda n/i	Other Crustacea	0.21 (4.4)	0.26	0.28 (4.86)	0.31
			Squillidae	*Squilla* spp.	Other Crustacea	0.04 (1.9)	0.04	0.04 (1.59)	0.06
Echinodermata				Echinodermata n/i	Other	0.00	0.00	0.003 (0.24)	0.01
Chordata				Tunicata n/i	Tunicata	0.09 (3.0)	0.09	0.30 (5.16)	0.34
	Thaliacea			Thaliacea n/i	Tunicata	0.00	0.00	3.46 (17.52)	2.99
	Actinopterygii			Teleostei n/i	Other Teleostei	6.88 (24.9)	6.87	12.55 (32.25)	11.99
				Teleostei eggs	Eggs larvae Teleostei	1.06 (9.9)	0.94	0.96 (8.98)	1.2
				Teleostei larvae	Eggs larvae Teleostei	0.60 (7.3)	0.63	2.69 (15.32)	2.66
			Atherinopsidae	*Odontesthes regia*	Coastal fishes	0.40 (6.2)	0.4	0.39 (6.18)	0.36
		Aulopiformes	Paralepididae	Paralepididae n/i	Mesopelagics	0.00	0.00	0.02 (1.12)	0.02
		Clupeiformes	Clupeidae	*Sardinops sagax*	Other Teleostei	0.03 (1.5)	0.03	0.03 (1.63)	0.03
			Engraulidae	Engraulidae n/i	Engraulidae	0.39 (6.1)	0.36	2.39 (15.05)	2.3
				Anchoa spp.	Engraulidae	0.14 (3.7)	0.14	0.25 (4.92)	0.25
				Engraulis ringens	Engraulidae	4.44 (20.4)	4.33	5.99 (23.50)	5.76
		Gadiformes	Bregmacerotidae	*Bregmaceros* spp.	Other Teleostei	0.02 (1.3)	0.02	0.00	0.00
			Merlucciidae	*Merluccius gayi peruanus*	Other Teleostei	0.83 (9.0)	0.84	0.00	0.00
		Myctophiformes	Myctophidae	Myctophidae n/i	Mesopelagics	1.48 (11.7)	1.42	0.43 (6.23)	0.42
		Osmeriformes	Bathylagidae	Bathylagidae n/i	Mesopelagics	0.01 (1.0)	0.01	0.05 (2.26)	0.05
			Osmeridae	Osmeridae n/i	Mesopelagics	0.00	0.00	0.002 (0.27)	0.002
		Perciformes	Blenniidae	Blennidae n/i	Coastal fishes	0.01 (0.7)	0.003	0.00	0.00
			Carangidae	Carangidae n/i	Other Teleostei	0.09 (2.8)	0.08	0.30 (5.44)	0.3
			Centrolophidae	Centrolophidae n/i	Other Teleostei	0.01 (1.0)	0.01	0.05 (2.13)	0.05
			Labrisomidae	Labrisomidae n/i	Coastal fishes	0.01 (0.6)	0.01	0.00	0.00
			Sciaenidae	*Sciaena deliciosa*	Coastal fishes	0.01 (1.0)	0.01	0.00	0.00
			Sphyraenidae	*Sphyraena* spp.	Coastal fishes	0.00	0.00	0.02 (1.27)	0.02
			Trichiuridae	*Lepidopus* spp.	Coastal fishes	0.01 (1.0)	0.01	0.00	0.00
				Trichiurus lepturus	Coastal fishes	0.01 (1.0)	0.01	0.00	0.00
		Pleuronectiformes	Cynoglossidae	Cynoglossidae n/i	Coastal fishes	0.01 (0.4)	0.01	0.00	0.00
		Scorpaeniformes	Normanichthyidae	*Normanichthys crockeri*	Coastal fishes	0.70 (8.2)	0.65	0.93 (9.46)	0.91
		Stomiiformes		Stomiiformes n/i	Mesopelagics	0.00	0.00	0.01 (0.91)	0.01
			Phosichthyidae	Phosichthyidae n/i	Mesopelagics	0.00	0.00	0.0004 (0.04)	0.003

		Vinciguerria lucetia	Mesopelagics	1.56 (12.0)	1.48	1.22 (10.59)	1.11
	Sternoptychidae	Maurolicinae n/i	Mesopelagics	0.15 (3.4)	0.13	0.18 (3.69)	0.15
Syngnathiformes	Syngnathidae	Syngnathidae n/i	Coastal fishes	0.00	0.00	0.06 (2.44)	0.06
		Leptonotus blainvilleanus	Coastal fishes	0.07 (2.5)	0.07	0.13 (3.27)	0.08

Table 4.2. Distribution of the thirteen dietary groups recovered from jack and chub mackerels stomach contents off Peru during 1973-2013. Are indicated, the dietary group, the prey code, the number of stomachs with presence, the mean value (±standard deviation) of the proportion by weight (%W), and the frequency of occurrence (%O).

		Trachurus murphyi			***Scomber japonicus***		
	Prey code	***N° Stomachs***	***%W***	***%O***	***N° Stomachs***	***%W***	***%O***
Tunicata	Tunic	11	0.09 (3.01)	0.1	568	3.76 (18.21)	3.33
Cephalopoda	Cepha	79	0.57 (7.27)	0.56	366	2.34 (14.6)	2.33
Copepoda	Copep	936	7.10 (25.09)	7.26	2993	14.29 (31.98)	15.49
Zoea larvae	Zoea	1539	12.29 (32.38)	12.51	2412	13.35 (31.87)	13.08
Euphausiidae	Eupha	5732	49.31 (49.27)	49.09	4120	27.45 (42.68)	26.54
Pleuroncodes monodon	Pleur	907	7.66 (26.27)	7.61	778	5.39 (21.99)	5.24
Other Crustacea	Crust	496	3.15 (16.84)	3.35	1127	4.01 (17.48)	4.71
Engraulidae	Engra	575	4.96 (21.47)	4.83	1126	8.64 (27.77)	8.3
Mesopelagics	Mesop	413	3.20 (17.02)	3.03	297	1.90 (13.13)	1.75
Coastal fishes	Coast	148	1.21 (10.68)	1.16	208	1.52 (12.03)	1.43
Other Teleostei	Teleo	941	7.85 (26.49)	7.85	1847	12.93 (32.67)	12.37
Eggs and larvae Teleostei	EgLar	231	1.66 (12.29)	1.58	733	3.65 (17.61)	3.86
Other	Other	171	0.95 (9.37)	1.09	433	0.78 (7.67)	1.58

4.2.4. Data analyses

The proportions of empty stomachs per fishing set were computed for both species, using sets with at least 8 individuals of the same species. The effect of several covariates (fish length, sex, maturity, latitude and distance to the shelf break) was tested on the diet composition of CM and JM, using log-likelihood G tests for independence and the Williams' correction (Sokal and Rohlf, 1995). In addition, covariates were assessed on stomach fullness index *FWI* and on condition factor K_n using Kruskal-Wallis and Wilcoxon rank sum tests. To investigate potential impact of ENSO events, we selected the periods encompassing the strongest El Niño (Oct. 1982 to May 1983 and Oct. 1997 to May 1998) and La Niña (Jan. 1975 to March 1976; July 1988-April 1989; all 1999 and 2000; August 2010-May 2011) events. Other periods are considered as 'Neutral'. As very few CM were captured during El Niño events (only 39 stomachs), ENSO impact was investigated for JM data only. But large JM (size>40cm) were then removed because they were mainly captured during the very first years of the survey period. The diel effect on JM and CM trophic ecology could not be fully assessed in this study due to a lack of information on time in most (>90%) of the dat base. We however tested for diel effect on FWI on a subsample for which time was available and did not observed any robust pattern.

To explore cross-shore patterns, the density of stomachs according to distance to the shelf break (km) was estimated for the whole data set of non empty stomachs with known distance to shelf break and for the subsets containing Euphausiidae, *P. monodon* or Engraulidae. A Gaussian kernel was used for modelling density with a bandwidth selected according to Venables and Ripley (2002).

To take into account potential dependence and interactions between explanatory variables, we performed classification and regression tree (CART) analyses proposed by Breiman *et al.* (1984) and adapted to diet data by Kuhnert *et al.* (2011). Classification tree allows identifying the relationships between explanatory variables and the distribution of prey groupings. This non-parametric method uses a partitioning algorithm to estimate a series of binary decision rules that divide the data into smaller homogeneous subgroups in an optimal way. The whole dataset is represented by a single node at the top of the tree. Then the tree is built by repeatedly splitting the data. Each split is defined by a simple rule based on a single explanatory variable. Diet data were transformed following Kuhnert *et al.* (2011). Each row represents a unique predator-prey combination, where the proportion by wet weight of one of the thirteen prey taxa potentially present in the stomach is used as a case weight for the classification tree. As the splitting procedure grows an overlarge tree, we applied a prune back procedure. Each terminal node (or leaf) of the final tree is characterized by a predicted probability distribution of prey composition (proportion by weight of groups), given explanatory continuous and categorical variables. We first performed a CART analysis on the stomachs of JM (1973-2013) using four explanatory continuous variables (fish length, year, SSTA, $Z_{15^{\circ}C}$) and two categorical variables (zones: north, centre-north, centre-south, south; distance to the shelf break: -100 to -10 km, -10 to 10 km, 10 to 40 km , 40 to 80 km and >80 km). This analysis allowed us to account for the temporal variation (year effect) that could not be considered with CM data due to the absence of data for eight years (see Figure 4.5D). We then implemented a new CART analysis with diet data of both species using the same exploratory variables and species (CM and JM) as well, but without year.

JM and CM were also used as biological samplers for documenting the diversity of the forage fauna. Diet composition can indeed provide valuable information on diversity changes over time and space. Datasets based on occurrences of a total of 60 and 62 prey taxa identified in the stomachs of JM and CM respectively were used to compute average tables of occurrences of prey taxa per year, per zone and per category of distance to the shelf break. A correspondence analysis performed on the average table per year for JM (analysis not performed on CM due to the absence of data for eight years) showed that the first axis was a good proxy of the temporal evolution of the composition of prey taxa. The first axis was thus used to order year and taxa in the graphical representation of this average table. A hierarchical clustering of the years according to their coordinates in the correspondence analysis was used to perform a typology of the main groups of years based on their prey taxa composition. In addition we estimated the richness of forage fauna of CM and JM by computing the species richness indexes S_{obs} on the 60 and 62 prey taxa and for all the modalities of the factors of interest (year, zone and categories of distance to the shelf break). But sample size (i.e., number of stomachs) strongly influences species richness. To deal with this bias, we applied a bootstrap procedure and randomly took with replacement m stomachs from the n recovered in a modality of a given factor. This procedure was repeated 500 times and a $(S_{boot})_i$ was calculated for all the samples i = 1,… 500. We choose m = 100 for year and m = 500 for zone and distance to the shelf break, according to the corresponding sampling effort by modality. Years with less than 100 stomachs were discarded. Finally, for both species, we computed the mean and standard deviation of the bootstrap samples $(S_{boot})_i$ for each modality and for all the factors of interest.

The Sørensen index was used to compare the similarity of El Niño vs. La Niña periods and before/after 1996 periods in terms of presence/absence of taxa.

Analyses were conducted using the R software (R Core Team 2013), with the *rpart* package for the classification tree (Venables and Ripley, 2002).

4.3. Results

4.3.1. Overall diet description

In total 47,535 stomachs (18,377 CM and 29,158 JM) were analysed, of which 23,570 (12,476 CM and 11,094 JM) were non-empty. The proportion of empty stomachs was much higher for JM (62%) than for CM (32%). This proportion was lower for samples collected by research vessels (36% and 22% for JM and CM, respectively) than by commercial vessels (64% and 33% for JM and CM, respectively). In addition, considering all samples the distribution of the proportion of empty stomachs per fishing set was different for CM and JM (Figure 4.3). For CM, 39% of the fishing sets had less than 10% of empty stomachs and only 6% had more than 90% of empty stomachs. In contrast, empty stomachs of JM were concentrated in some fishing sets: 21% of the fishing sets had more than 90% of empty stomachs.

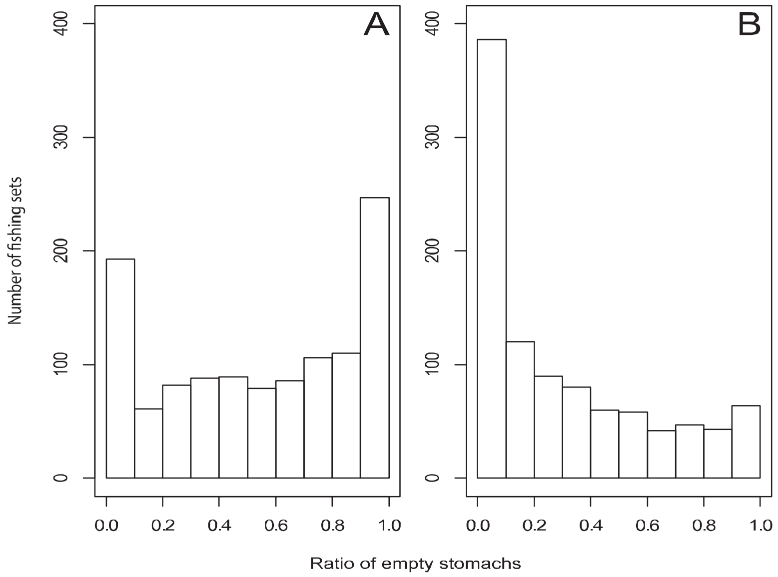

Figure 4.3. Distribution of the ratio of empty stomachs per fishing set for (A) Trachurus murphyi and (B) Scomber japonicus.

Despite some disparity, the overall diet composition in wet weight (Figure 4.4) was not significantly different between JM and CM (G = 14.6, p = 0.265). Euphausiidae was the dominant prey for both species and contributed to 49.3 and 27.4% for JM and CM, respectively. Zoea larvae (12.3%), *P. monodon* (7.7%), copepods (7.1%) and other teleostei (7.0%) were the additional main prey groups for JM, while copepods (14.3%), Zoea larvae (13.3%), other teleostei (12.9%) and Engraulidae (8.6%) were the extra main prey groups for CM (Figure 4.4). Overall diets of both species were dominated by zooplankton (74% and 82% and for CM and JM, respectively), and contribution of fish was higher in CM diet (25% and 17% for CM and JM, respectively).

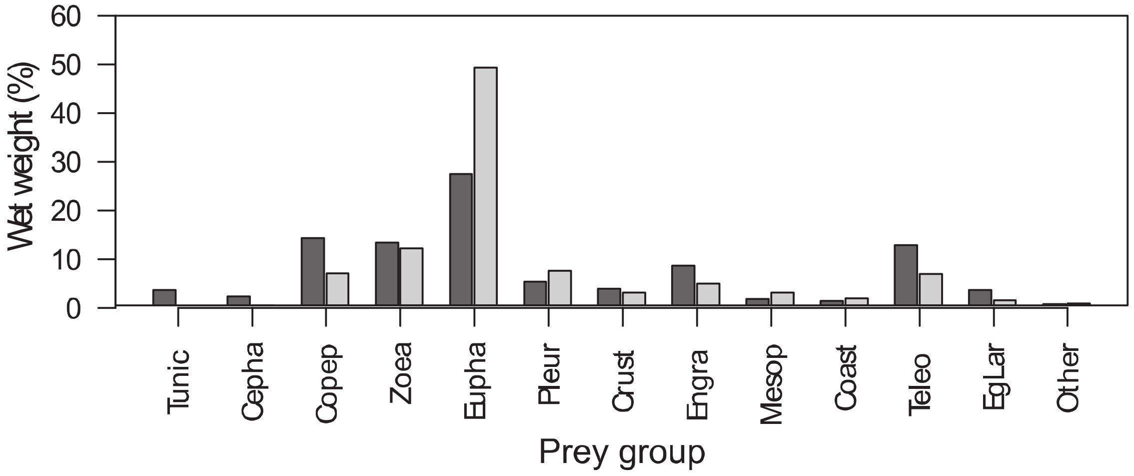

Figure 4.4. Trachurus murphyi (light grey bars - 11094 stomachs) and Scomber japonicus (dark grey bars - 12476 stomachs) diet composition in wet weight (%) by prey group.

The diet composition of JM varied significantly (G = 277.7; $p < 0.0001$) according to size (Figure 4A). Euphausiidae contribution by wet weight increased with size until 40 cm (41.8% for JM less than 21 cm and 56.5% for fish size ranging 31-41 cm), but decreased to 6% for individuals larger than 51 cm. Fish contribution was low for JM < 41 cm (maximum contribution 16.2%) but this pattern reversed for larger sizes. Engraulidae dominated indeed the fish diet composition of JM larger than 41 cm, and the largest JM (> 51 cm) foraged mainly on Engraulidae (55.5%) and other teleostei (25.3%). CM did not exceed 40 cm and its diet composition (Figure 4.5A) did not very significantly with size (G = 29.8; p = 0.19). Euphausiidae contribution however increased from 12.7% for CM < 21 cm to 28.3% for CM larger than 31 cm. Diet composition according to maturity stages had similar trends to those observed for fish size, and neither diet composition of JM and CM varies with sex (G = 2.51, p = 0.99 and G = 0.72, p = 1, respectively). Sex and maturity stages were therefore not taken into account in further analyses.

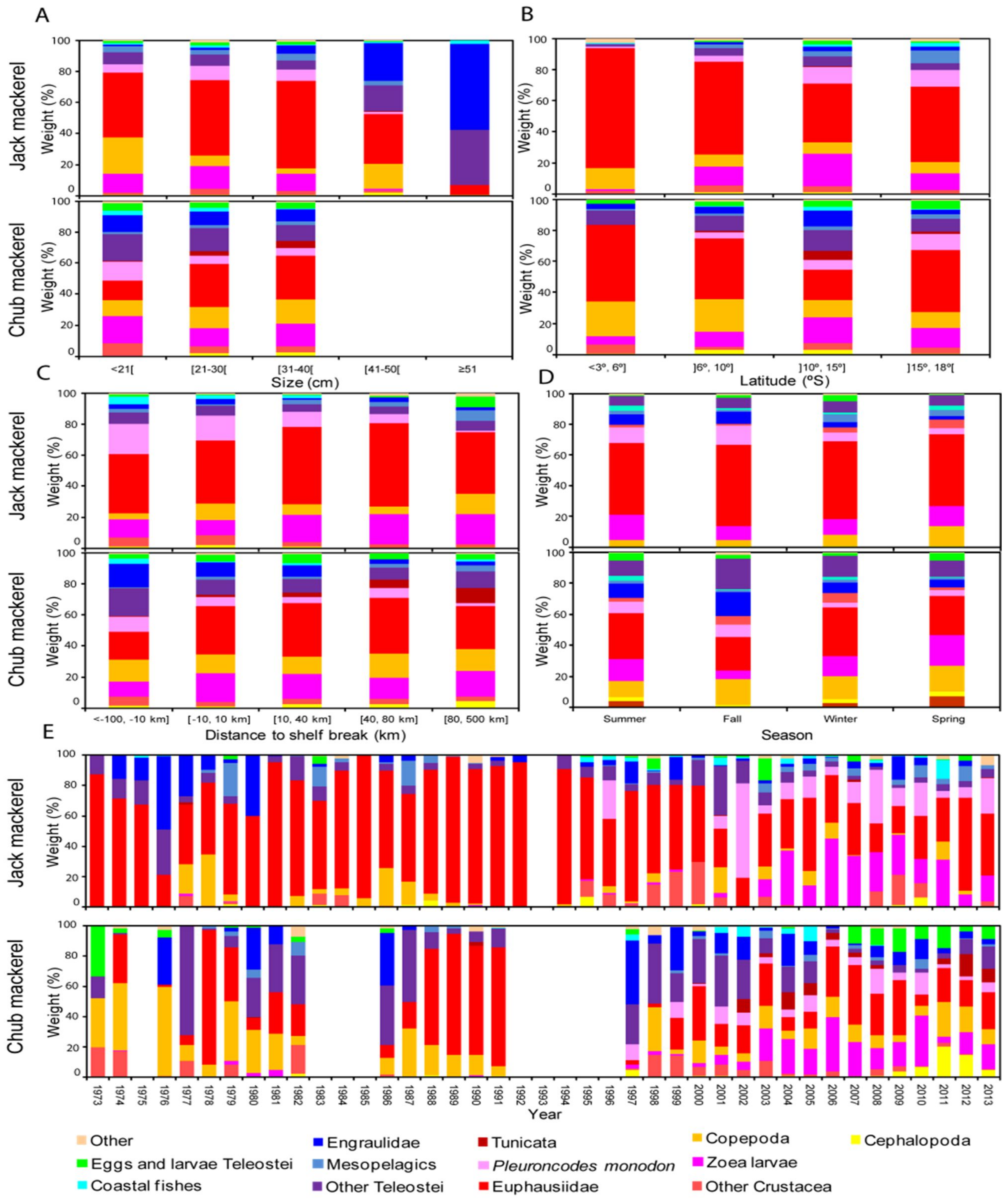

Figure 4.5. (A) Diet composition of Trachurus murphyi (JM) and Scomber japonicus (CM) in mean weight percentage (%W) according to the individual fork length (in cm). (B) Diet composition of JM and CM in %W according to the latitudinal zone. (C) Diet composition of JM and CM in %W according to the distance to the shelf break (in km, negative inshore and positive offshore). (D) Diet composition of JM and CM in %W per season. (E) Diet composition of JM and CM in %W per year from 1973 to 2013.

4.3.2. Spatial patterns

JM and CM diet composition had similar trends according to latitudinal zones (Figure 4.5B). The contribution of species associated to the coastal upwelling (e.g. Engraulidae, costal fishes, *P. monodon*, Zoea larvae) increased in the centre-south zone (10-15°S) while other species (e.g. Euphausiidae and copepod) showed an opposite trend.

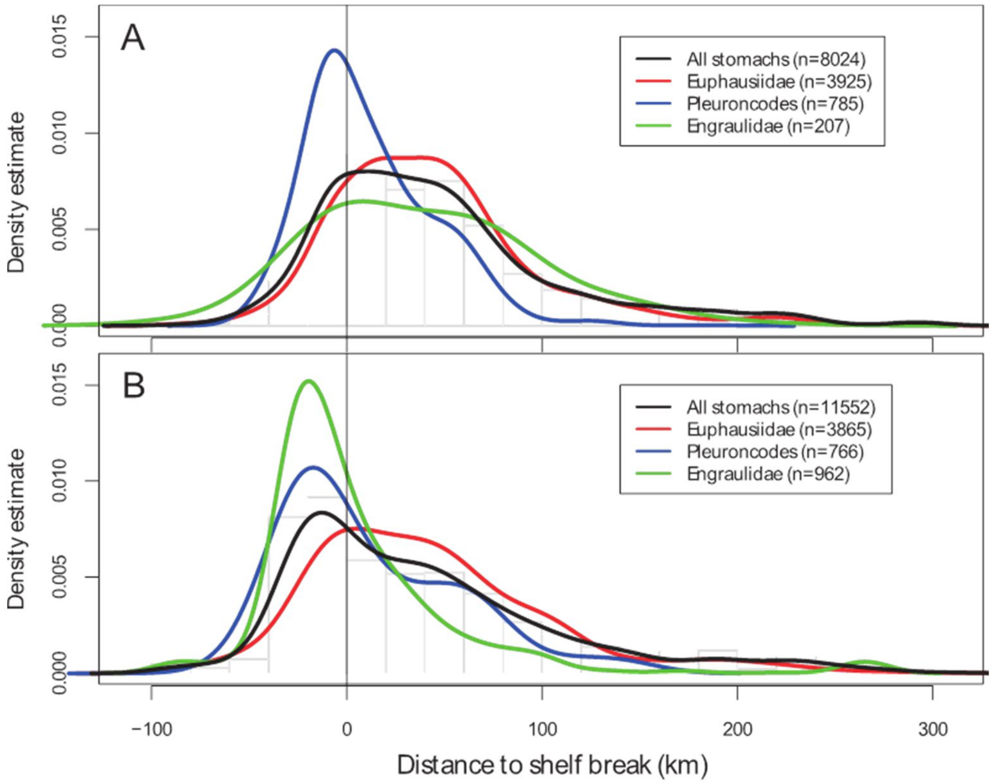

Figure 4.6. Kernel density estimates of stomachs numbers for the whole datasets and for the subsets containing Euphausiidae, P. monodon and Engraulidae according to distance to the shelf break (in km, negative inshore and positive offshore) for (A) Trachurus murphyi and (B) Scomber japonicus; the numbers in parenthesis indicate the number of stomachs.

Diet composition according to the distance to the shelf break (Figure 4.5C) illustrates the higher contribution of coastal species over the shelf (distance ≤ 10 km). The density distribution of the occurrence in the stomachs of two 'coastal' prey taxa (Engraulidae and *P. monodon*) and of one ‘oceanic’ one (Euphausiidae), showed that the highest density for *P. monodon* was located before the shelf break for both JM and CM (Figure 4.6). The distribution of Engraulidae was similar to the one of *P. monodon* for CM, but more widely extended for JM. Finally, Euphausiidae were clearly distributed after the shelf break, with a wide distribution for both CM and JM. Note that these cross-shore patterns were not related to changes in fish size except for CM that presented slightly smaller sizes inshore.

4.3.3. Temporal patterns

Seasonal variations in JM and CM diet composition were slight and rather inconsistent between species (Fig. 4.5D). We can note, however, a lesser importance of Zoea larvae in fall and an opposite pattern for Engraulidae. Yearly changes between 1973 and 2013 highlight the fact that Euphausiidae clearly dominated by wet weight the diet of JM before year 2000 (67.7% ± 46.2) whereas contribution was reduced by half after 2000 (31.9% ± 45.6) (Figure 4.5E). Proportion of Zoea larvae showed an opposite trend (0.3% ± 4.7 before year 2000 and then 23.8% ± 42.0), such as *P. monodon* (1.3% ± 11.0 before year 2000 and then 13.8% ± 34.1). Fish consumption by JM (especially Engraulidae) was rather modest except in 1975-1977. Temporal patterns were blurred for CM because of a lack of data for several years. However, as for JM but to a lesser extent, Euphausiidae contribution by wet weight was higher until year 2000 (41.0% ± 47.1 *vs.* 22.0% ± 39.5 after 2000). Once more, proportions of Zoea larvae and *P. monodon* exhibited an opposite trend (1.4% ± 10.7 before 2000 *vs.* 18.2% ± 36.0 after for Zoea larvae; 1.0% ± 9.7 before 2000 *vs.* 7.2% ± 25.1 after for *P. monodon*). In addition, the mean condition factor of JM computed for the period 1973-1999 was significantly lower than the mean computed after 1999: $K_n = 0.96 \pm 0.11$ before year 2000 and $K_n = 1.05 \pm 0.10$ for the period 2000-2013 ($p<0.0001$; Figure 4.7A). The condition factor of CM exhibited the same significant pattern despite the missing years: $K_n = 0.94 \pm 0.15$ *vs.* 1.04±0.10 ($p<0.0001$; Figure 4.7B). On the contrary, the fullness of non-empty stomachs for both species was significantly higher for the period 1973-1999 than for the period 2000-2013 (JM: FWI=0.94 ± 1.51 *vs.* 0.77 ± 1.22, $p<0.000$; CM: FWI=1.62 ± 2.01 *vs.* 1.22 ± 1.51, $p<0.0001$; Fig. 4.7).

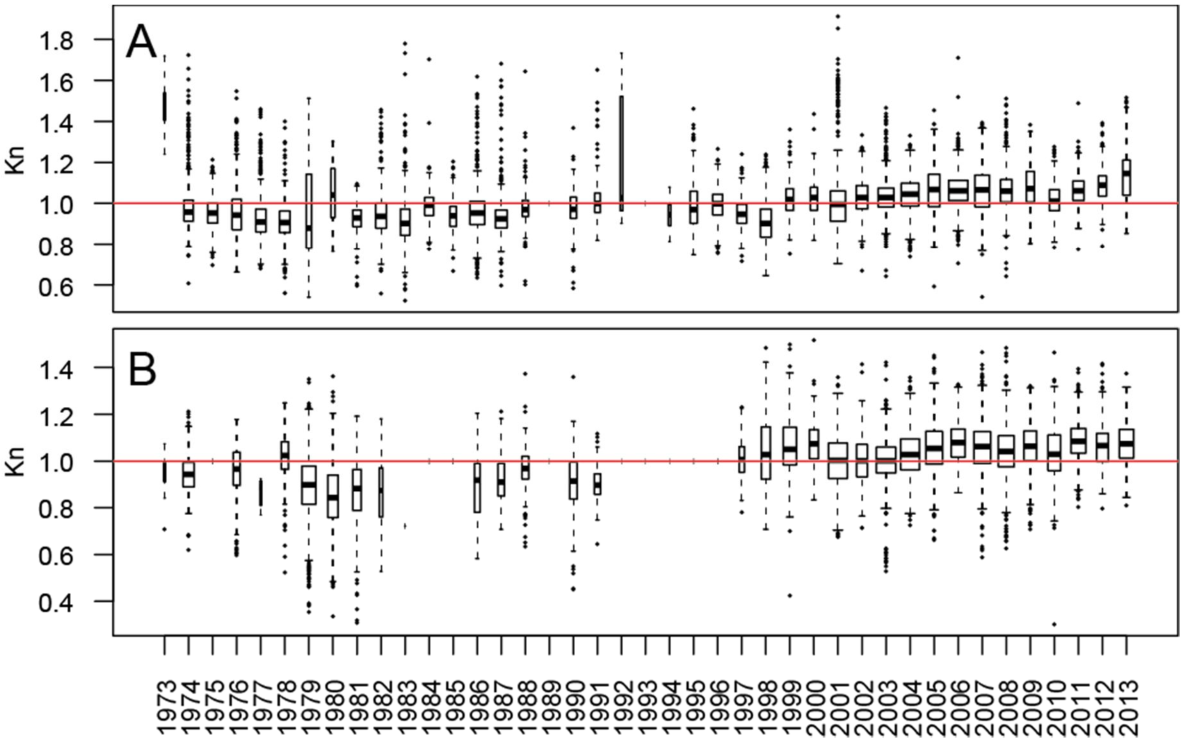

Figure 4.7. Year evolution of the relative condition factor (Kn) of (A) Trachurus murphyi and (B) Scomber japonicus. Box width is proportional to square root of the number of stomachs sampled for a given year. The red line corresponds to a theoretical value of Kn=1.

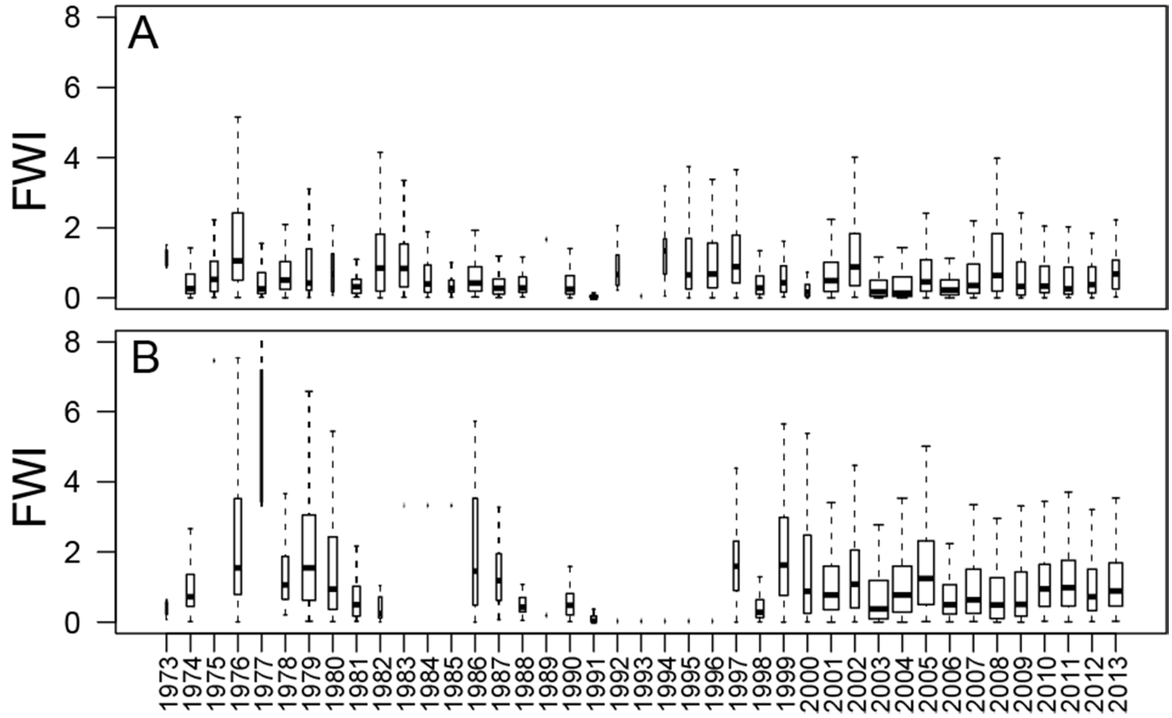

Figure 4.8. Year evolution of the Fullness Weight Index (FWI) for non empty stomachs of (A) Trachurus murphyi and (B) Scomber japonicus. Box width is proportional to square root of the number of stomachs sampled for a given year. Outliers are not printed.

4.3.4. El Niño and La Niña

For JM less than 40 cm, the percentage of non-empty stomachs was identical during El Niño and La Niña periods (24.3%). However the fullness of non-empty stomachs was significantly higher during El Niño than during La Niña periods (1.55 ± 1.56 *vs.* 0.71 ± 1.00, p<0.0001), whereas the condition factor K_n was significantly lower during El Niño than during La Niña periods (0.92 ± 0.12 *vs.* 1.02 ± 0.10, p<0.0001). Diet composition did not differ between El Niño, La Niña (and 'Neutral') periods (Figure 4.9) despite higher contributions by wet weight of teleostei (17.8% *vs.* 3.9%) and of eggs and larvae of teleostei (8.6% *vs.* 0.2%), a lower proportion of Zoea larvae (<1% *vs.* 7.3%) and an absence of *P. monodon* during El Niño period (10.4% during La Niña). The contribution of Euphausiidae did not vary between El Niño and La Niña periods (52.0% *vs.* 53.9%).

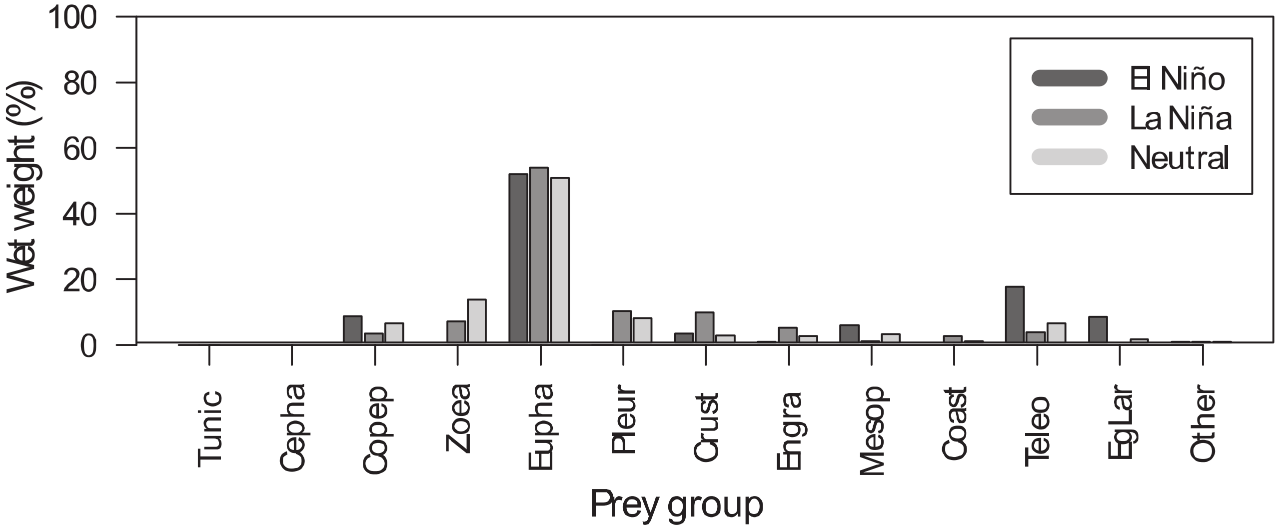

Figure 4.9. Trachurus murphyi diet composition in wet weight (%) by prey group during El Niño (dark grey bars), La Niña (grey bars) and Neutral (light grey bars) periods.

4.3.5. Multivariate approach

Figure 4.10 shows the pruned classification tree performed on JM diet data. The first split separated stomachs according to time. Before 2000, JM diet was dominated by Euphausiidae. Among this group, the main node (Node #4; n=5031) encompassed individuals smaller than 40 cm with a predicted diet dominated by Euphausiidae (predicted probability = 0.74). The predicted diet of JM larger than 40 cm showed the dominance of copepoda (Node #1; n=125) and Euphausiidae (Node #2; n=198) for individuals collected from 1978 to 1999 (predicted probability = 0.77 and 0.60, respectively) and of Engraulidae for fish collected before 1978 (Node #3; n=459; predicted probability = 0.51). From 2000, a second temporal split occurred in 2002. In 2000 and 2001 the predicted diet was dominated by *P. monodon* when $Z_{15^{\circ}C}$ was deeper than 85 m (Node #6; n=143; predicted probability = 0.85) and by other teleostei and Euphausiidae when $Z_{15^{\circ}C}$ was shallower than 85 m (Node #5; n=804; predicted probability = 0.30 and 0.27, respectively). From 2002 the predicted diet composition was more diverse. Zoea larvae (Node #9; n=1662; predicted probability = 0.45) and Euphausiidae (main predicted prey in Nodes 7 and 8 with probability of 0.37 and 0.36, respectively) were the dominant prey but other prey taxa such as *P. monodon* contributed a lot (e.g. predicted probability = 0.24 in Node #8 and 0.10 in Nodes #7 and #9).

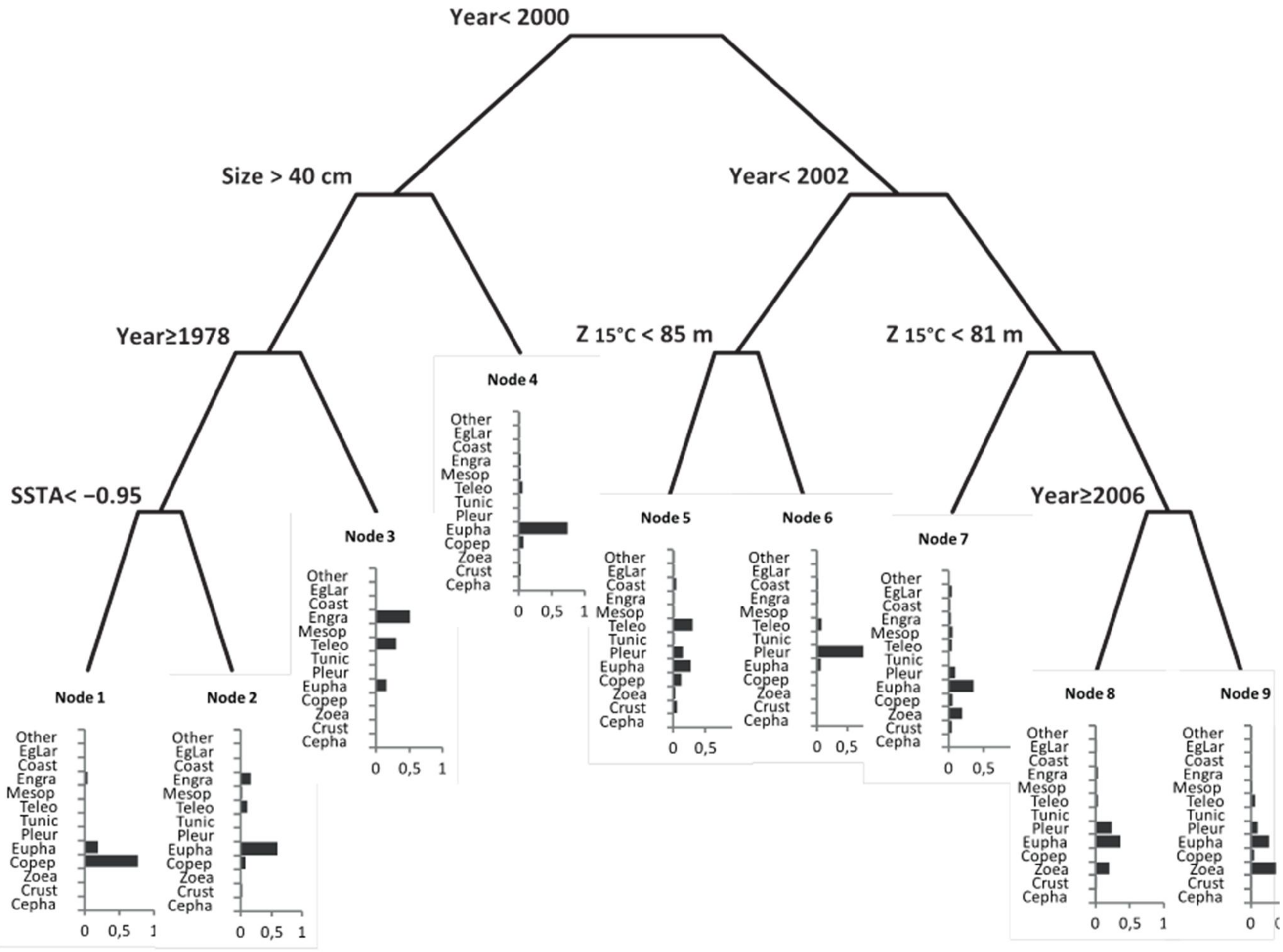

Figure 4.10. Classification tree of Trachurus murphyi diet (prey groups) according to the year, $Z_{15^{\circ}C}$ (in m), the size (in cm), the SSTA (in °C), the distance to the shelf break (in km, negative inshore and positive offshore) and the zone (North, Centre, South). For each final node, the predicted probabilities of occurrence of the 13 prey groups is detailed (histograms). See Table 2 for prey codes.

The second classification tree was performed on both JM and CM diet, without taking into account the year effect (Figure 4.11). The pruned classification tree showed seven nodes and the first split discriminated the two species. The predicted diet of JM smaller than 43 cm was dominated by Euphausiidae (Node #7; n=11,447; predicted probability = 0.51). The diet of larger JM distributed in waters with $Z_{15^{\circ}C} < 89$ m was dominated by copepods (Node #4; n=79; predicted probability = 0.97) and by Euphausiidae (Node #5; n=395; predicted probability = 0.36), while those distributed in waters with $Z_{15^{\circ}C} \geq 89$ m fed mainly on Engraulidae (Node #6; n=258; predicted probability = 0.65). The predicted diet of CM in the north, centre-north and south zones was dominated by Euphausiidae (Node #1; n=5937; predicted probability = 0.43). In the centre-south zone, the predicted diet composition of CM distributed around and off the shelf was mainly distributed between Euphausiidae, Zoea larvae, copepoda and other teleostei (Node #3; n=8143; predicted probability = 0.24, 0.17, 0.14, and 0.12, respectively). The predicted diet of CM distributed over the shelf was dominated by teleostei, Engraulidae, *P. monodon* and Zoea larvae (Node #2; n=2928; predicted probability = 0.24, 0.18, 0.12, and 0.12, respectively).

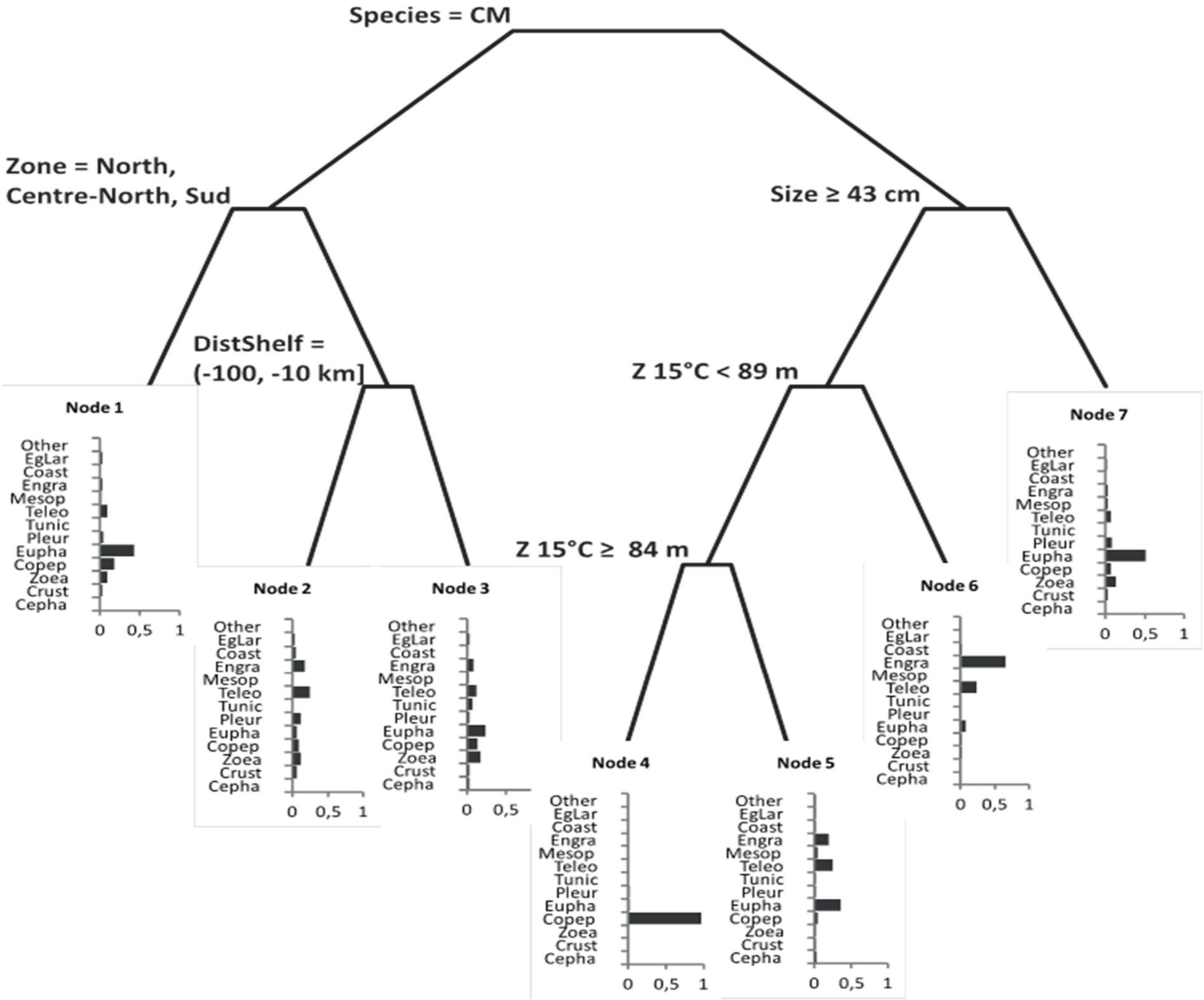

Figure 4.11. Classification tree of Trachurus murphyi and Scomber japonicus diet (prey groups) according to the species, $Z_{15^{\circ}C}$ (in m), the size (in cm), the SSTA (in °C), the distance to the shelf break (in km, negative inshore and positive offshore) and the zone. For each final node, the predicted probabilities of occurrence of the 13 prey groups is detailed (histograms). See Table 2 for prey codes.

4.3.6. Diversity of the prey taxa

The average occurrence of the 60 prey taxa of JM per year showed a clear temporal pattern (Figure 4.12), summarized by the first axis of the Correspondence Analysis. Years were classified into two groups, before and after 1996. The classification satisfied temporal contiguity except year 1997 grouped in the first period (note that in 1997 most of samples were collected before the rise of El Niño).

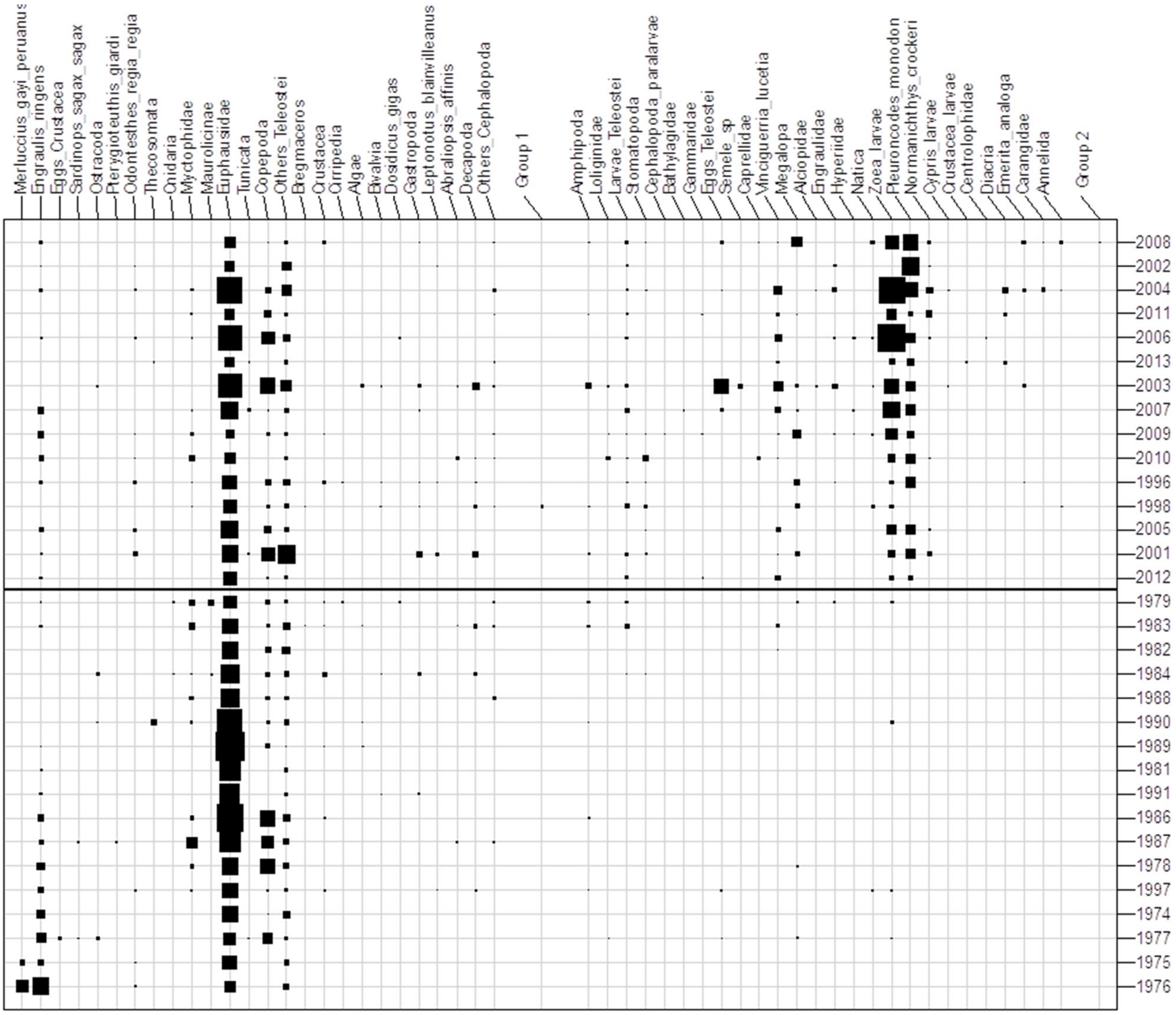

Figure 4.12. Mean occurrence of Trachurus murphyi prey taxa per year. Group 1: Anchoa sp., Lepidopus sp., Squilla sp. and Trichiurus lepturus ; Group 2: Blenniidae, Cynoglossidae, Labrisomidae. Prey taxa and years are ordered after their position on the first axis of the correspondence analysis of the table which expresses a temporal gradient in the prey distribution. The solid horizontal line discriminates between the two clusters obtained by the hierarchical clustering.

The first period is characterised by low diversity (mainly 15 prey taxa); the main prey were Euphausiidae, other teleostei, copepoda and Engraulidae. Some other taxa such as the hake *Merluccius gayi peruanus*, were also reported (in 1975 and 1976). On the opposite, a larger number of taxa were observed from 1996. Among them, Zoea larvae and *Pleuroncodes monodon* were largely dominant, but other taxa such as *Vinciguerria lucetia*, teleostei larvae and stomatopoda were also frequently observed in the JM stomach content. Finally, Euphausiidae, copepoda, other teleostei, occurred throughout the whole study and composed the stable part of the prey taxa community.

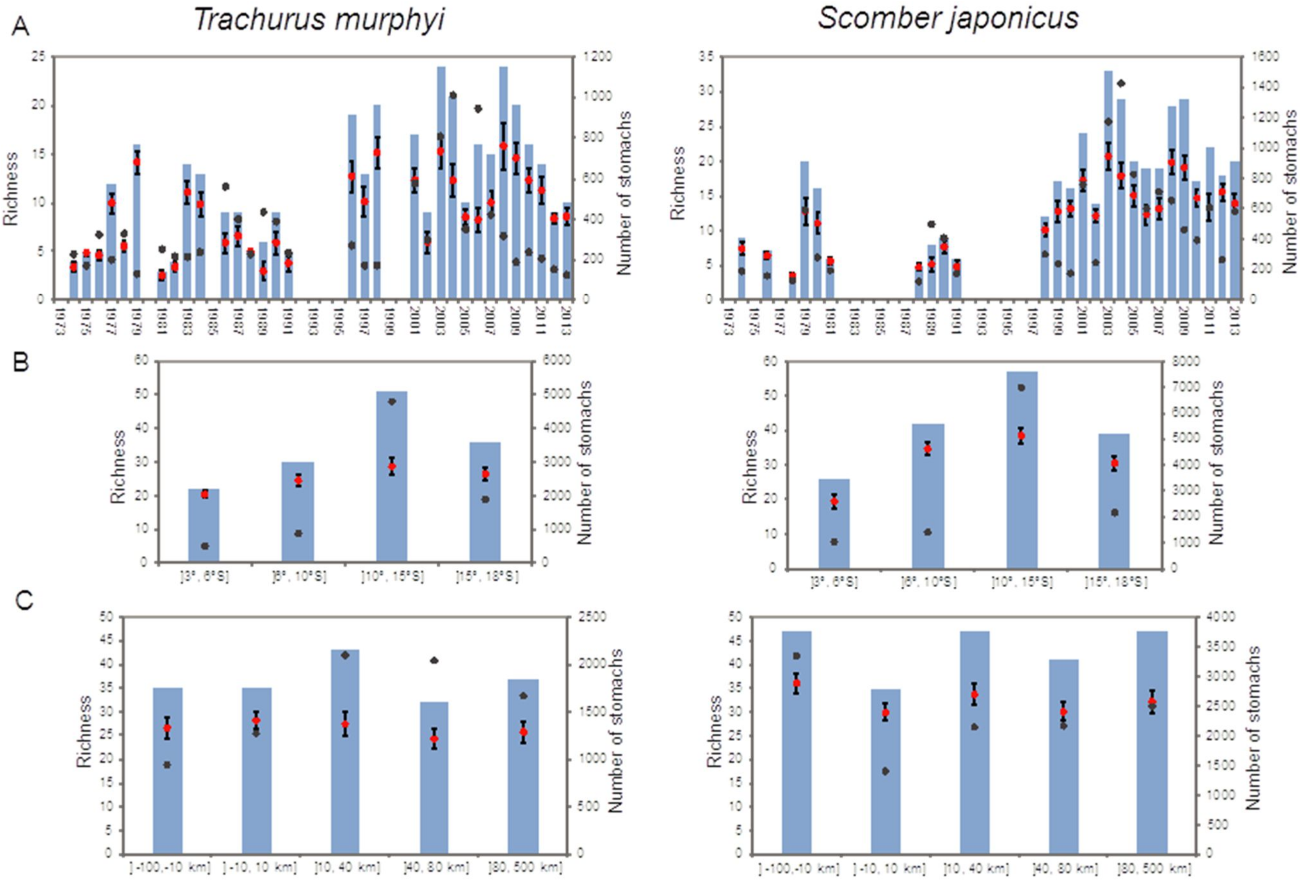

Figure 4.13. Observed and estimated (see text) index of prey taxa richness for Trachurus murphyi (left panels) and Scomber japonicus (right panels) computed according to (A) the year; (B) the latitudinal zone; and (C) the distance to shelf break (in km, negative inshore and positive offshore). The number of observed stomachs (grey circles) is indicated on the right axis. The estimated index is given for 100 stomachs for years and for 500 stomachs for latitudinal zones and categories of distance to the shelf break.

For both species, the estimated richness index S_{boot} per year for 100 stomachs (Figure 4.13A) was significantly ($p < 0.0001$) higher since 1996 (11.3±2.9 for JM; 15.1±3.1 for CM) than before (6.2±3.4 for JM; 6.9±3 for CM). This is confirmed by the the Sørensen (1948) index of similarity calculated between both periods (before and after 1996). The index value was 0.68, with 31 prey taxa common to both periods but 6 versus 23 unique prey taxa before and after 1996 respectively.

Regarding the estimated richness index for 500 stomachs per latitudinal zone (Figure 4.13B), the highest values were observed in the Centre-South zone (10°-15° S) for both species (28.7±2.4 for JM and 38.5±2.4 for CM). The Centre-North (6°-10°S) and the Southern (15º-18ºS) zones presented similar estimated richness with 24.5±1.8 and 24.5±2.0 for JM, and 34.7±1.8 and 30.5±2.1 for CM; while the Northern zone (<3º-6ºS) presented the lowest richness (20.4±1 for JM and 19.5±2 for CM). Finally, the estimated richness for 500 stomachs per categories of distance to the shelf break (Figure 4.13C) varied between 24 and 28 taxa for JM and between 30 and 36 taxa for CM. All differences between categories of distance to the shelf break were significant, except for CM between (-10 to 10 km) and (40 to 80 km), but no trend was clearly identified.

We also tested the impact of El Niño and La Niña periods on JM prey diversity. The diversity was significantly ($p<0.001$ in all cases) lower during El Niño (11.5±1.6) than neutral (15.7±2.3) and La Niña (16.2±2.0) periods. The Sørensen index of similarity (1948) strengthens these findings. The index value was 0.57 between El Niño and La Niña periods, with 12 common prey taxa but 5 versus 13 unique prey taxa for El Niño and La Niña periods, respectively.

4.4. Discussion

This work is based on a wide dataset on JM and CM diet encompassing a large range of spatiotemporal location and sizes. Beyond the usual diet description, our results provide new knowledge on the comparative trophic behaviour of these species, in particular the role of geographical features and how interannual and decadal climatic variability impact ecosystem structure and fish trophic ecology.

4.4.1. Overall diet, size effect and comparative trophic ecology

JM and CM distribute over an area larger than the Peruvian EEZ (Bertrand *et al.* 2004a) and are considered as opportunistic foragers adapting their trophic behaviour to prey accessibility (Konchina, 1981; Konchina, 1982; Muck and Sánchez, 1987). Our results confirm such opportunistic trophic behaviour since both species foraged over a large variety of taxa (60 and 62 for JM and CM, respectively) but the picture of the diet combining all data (Figure 4.4) hides high spatiotemporal variability. The global diet of both species was widely dominated by zooplankton (82% and 74% for JM and CM, respectively). Such results are in accordance with most published studies (e.g.

Konchina, 1982; Konchina *et al*., 1996; Castro Hernández and Santana Ortega, 2000; Antezana, 2010). The diet of JM varied with size (Figures 4.5A, 4.10). Individuals less than 40 cm consumed mainly zooplankton, in particular euphausiids, Zoea larvae, *P. monodon* and, for the smallest (<21 cm), copepods. Over ~40 cm the diet shifted toward a dominance of fish with an important contribution of Engraulidae that exceeded 50% for JM larger than 50 cm. Such shift has already been reported (Muck and Sánchez, 1987; Ermolovich and Gardina, 1994). This change in diet composition with fish size can be attributed to the predator's ability to capture and handle the prey (Christensen, 1996; Lundvall *et al*., 1999). Large JM have access to highly energetic prey such as the Peruvian anchovy *Engraulis ringens*. However overfishing removed these large JM from the system (Gerlotto *et al*., 2012). This could explain why high fish proportion in the diet was only observed in the first years of our time series before the JM commercial fishing development (Figure 4.5D). On the opposite, CM, which has a lower size-range than JM, did not present clear ontogenetic trend towards larger prey. Such pattern was already mentioned by Konchina (1982). Indeed in her and our study (but not in Muck and Sánchez, 1987) CM foraged on small zooplankton (Copepoda) at all size class and its contribution was even greater in CM >30 cm while small CM could paradoxically consume more fishes than large CM (Figures 4.5A, 4.11).

The proportion of non-empty stomach was low (38%) for JM, in accordance with other studies (Medina and Arancibia, 2002). This proportion reached 68% for CM; such high proportion was also reported by Konchina (1982, 1990) off Peru. This specific difference could be due to higher food regurgitation during capture for JM or to a difference in feeding behaviour (see Konchina, 1990). In our dataset, the distribution of proportion of empty or non empty JM stomach per fishing set (Figure 4.3) was not homogeneous, indicating that the behavioural hypothesis with JM foraging actively only at given periods/places is the most likely.

Even if there is a trophic overlap between JM and CM, as observed by other authors (Konchina, 1992; Medina and Arancibia, 1998), their diet exhibited various differences. Surprisingly despite their smaller maximal size, CM consumed more fish than JM (25% vs. 17%). This contradicts the idea of JM being more voracious than CM (Medina and Arancibia 1998). Actually CM diet was more diverse (Table 4.1) and it consumed a larger amount of large prey (fish) but also of small prey (copepoda and eggs and larvae of teleostei).

4.4.2. Spatial patterns

JM and CM diet varied according to the along-shore (latitude) and cross-shore (distance to the shelf break) ranges with related patterns. The contribution of Euphausiidae and other oceanic components (e.g. mesopelagic fishes) was greater off the shelf break but also in northern (north of ~10ºS) and southern (south of ~15ºS) Peru. On the opposite the contribution of coastal taxa (e.g. *P. monodon*, Engraulidae and coastal fishes) was higher in central Peru (from ~10º-15ºS). The latitudinal pattern can be related to genuine latitudinal effects on plankton distribution (Ayón et al., 2008a) and the geography of the Peruvian coast than. Indeed the shelf offshore extension is much larger in central Peru than in the north and south boundaires (see Figure 4.2 for the shelf break position as illustrated by the 200 m isobath). The shelf break is thus a strong biogeographical barrier affecting species distribution (e.g. Ballón *et al.*, 2011) and therefore the fish diet.

4.4.3. Long term trend and the Euphausiidae paradox

Euphausiids were strongly dominant in JM diet before 2000, while after 2000 *P. monodon* and Zoea larvae took much more importance. The increase of *P. monodon* in fish diet is consistent with the dramatic increase in *P. monodon* observed off Peru since the late 1990s (Gutiérrez *et al.*, 2008). Similarly, the population of coastal sand crab *Emerita analoga*, which makes the bulk of Zoea larvae (Blaskovic *et al.*, 2009), was likely favoured by the increase in productivity observed off Peru during the last decades (Sifeddine *et al.*, 2008; Gutiérrez *et al.*, 2009). The case for Euphausiidae is more paradoxical. Indeed Euphausiidae contribution to JM diet was very high from the late 1970 to the late 1990s and dropped then after. This trend is contradictory with the actual trend in euphausiids abundance off Peru (Ayón *et al.*, 2011) that presented lower biomasses in the late 1970-1990s when the NHCS was less productive and more oxygenated than before and since the late 1990s (Ayón *et al.*, 2011; Bertrand *et al.*, 2011).

Let us consider JM and CM be opportunistic foragers as indicated in Konchina (1981, 1982), Muck and Sánchez (1987) and in the present work; changes in their diet should then as indicated changes in the ecosystem. Indeed JM abundance and biology is know to be affected by climatic regime (Csirke, 2013). Here we showed that changes in prey contribution actually correspond to observed changes in the ecosystem in the case of *P. monodon* but not for Euphausiidae. This paradox can be explained by the fact that *P. monodon* and Zoea larvae are prey easy to handle and, as part of the epipelagic community, they are concentrated in dense patches within a thin surface layer above the oxycline (Bertrand *et al.*, 2011, 2014). Additionally, they are accessible during the complete diel cycle when most Euphausiidae perform diel vertical migration and are inaccessible during the day (Ballón *et al.*, 2011). Furthermore, *P. monodon* energy content is high. Aurioles-Gamboa *et al.* (2004) showed that the fatty acid composition of a close species, *P. planipes*, directly depended of the available food quality. In the highly productive NHCS, *P. monodon* has high protein and fatty acid content (Gutierrez, 2002) and is exploited to produce seafood oil, and protein concentrates. JM thus responded and adapted to the increased abundance increased availability and biomass of *P. monodon* and Zoea larvae. The temporal shift in diet composition was accompanied by a shift in fish condition: the condition factor of JM was significantly lower before than after 2000. Such difference can be due to a change towards better food quality but also to density dependence processes. Indeed JM has been over-exploited in the southeastern Pacific (www.southpacificrfmo.org) and was more abundant during the late 1970-mid 1990s when macrozooplankton (in particular Euphausiidae) abundance was lower (Ayón *et al.*, 2011). On the opposite, in recent year, when JM was less abundant, macrozooplankton biomass was high (Ayón *et al.*, 2011; Ballón *et al.*, 2011) and prey were concentrated over a thin surface layer (Bertrand *et al.*, 2011). The incomplete time series for CM diet blurs the conclusion that could be drawn on decadal patterns. However as for JM, CM foraged on a high proportion of *P. monodon* and Zoea larvae since the early 2000s when they were abundant in the system. Its condition factor was also higher after 2000 than before.

Our findings show that diet composition of CM and JM reveal ecosystem changes but is not always a good indicator of specific changes in prey biomass as illustrated in the euphausiids case. Indeed the decadal changes in JM diet point out that it target the most abundant prey, and within these prey would prefer those that are the most accessible(e.g. along the whole diel cycle and concentrated in dense layer), demand less energy to grab or catch and provide a higher energy intake per energy invested. Foraging behaviour does matter in our long-term feeding study.

4.4.4. El Niño and La Niña events: do they matter?

The NHCS is a region notably affected by El Niño southern oscillation (Chavez *et al.*, 2008). Exceptional El Niño events, such as those that occurred in 1982-83 and 1997-98, affect all marine ecosystems components (e.g. Barber and Chavez, 1983; Arntz and Tarazona, 1990; Fiedler, 2002) including JM and CM populations (Arcos *et al.*, 2001; Bertrand *et al.*, 2004b; Gerlotto *et al.*, 2012). Actually, the condition factor was lower during El Niño than La Niña periods. Surprisingly we observed an opposite pattern in terms of fullness since the percentage of non-empty stomach was identical during El Niño and La Niña periods (24.3%) but the fullness of non-empty stomachs was significantly higher during El Niño than La Niña periods. This counterintuitive result also observed by Dioses (1985) could be due to a higher metabolic requirement during warmer El Niño condition. However, specific bioenergetic 499 studies need to be conducted to propose a robust interpretation..

Prey diversity was significantly lower during El Niño (see also next section) but contrary to previous studies (Muck and Sánchez, 1987; Sánchez de Benites and Muck, 1987) we did not observed strong differences in diet composition between El Niño, La Niña and neutral periods (Figure 4.9). Comparable results were observed on anchovy diet with no clear changes in diet composition and stomach fullness related to El Niño or La Niña events (Espinoza and Bertrand, 2008). The difference between our studies and those reporting an ENSO effect (e.g. Sánchez de Benites and Muck, 1987) is most likely due to samples size. Comparing two years (e.g. an El Niño versus a La Niña year) can lead to misleading conclusion when number of samples is low. Indeed our findings demonstrated a high spatiotemporal variability in diet composition of CM and JM. Over-interpretation could have been resulting from data collected in narrower spatial and/or temporal ranges.

The reason for such a weak effect of ENSO events on pelagic fish trophic ecology is puzzling. euphausidae are the main prey group for pelagic fishes (this study, Espinoza and Bertrand, 2008; Espinoza *et al.*, 2009), and their occurrence and abundance seem highly resilient to El Niño events (Brinton, 1967; Ballón *et al.*, 2008; Aronés *et al.*, 2009). Other pelagic components with a wide range of distribution may also be little affected by El Niño events, in particular when local efficient upwelling occurs as during El Niño 1997-98 (Bertrand *et al.*, 2004b). However additional information is required to disentangle the different mechanisms and understand this paradoxical result.

4.4.5. When prey diversity decreases with temperature

Although the reasons of this gradient are still debated (Clarke and Gaston, 2006) temperature and species richness are strongly correlated (e.g. Frank *et al.*, 2007). This pattern leads to a global negative association between taxonomic richness and latitude (e.g. Willig *et al.*, 2003) Interestingly our results challenge such paradigm. Indeed, prey diversity was significantly lower in northern Peru, where the warm tropical and equatorial waters matter (Swartzman *et al.*, 2008), than further south where colder upwelling waters dominate. In addition our findings clearly evidenced such a counterintuitive pattern at a decadal time scale over a large latitudinal range (15°). The system was characterised by warmer conditions between the early 1970s to the mid-1990s than then after. On the basis of the temperature-diversity relationship we would expect more diversity, with an increase of tropical species, before than after the mid-1990 but the opposite was observed with a twofold increase in diversity during the cooler period. The increase was mainly due to 'cold species'. Factors other than temperature were thus the dominant drivers of diversity. It is thus important to point out that the period ranging between the early 1970s to the mid 1990s was warmer but also less productive and more oxygenated compared with the period from the mid 1990s (Chavez *et al.*, 2003; Bertrand *et al.*, 2011; Gutiérrez *et al.*, 2011). In the same sense prey diversity was lower during the 'warm' El Niño periods than during neutral or La Niña periods. These spatiotemporal patterns seem to indicate that diversity in the NHCS is probably more driven by productivity than temperature. Interestingly, the latitudinal variability of temperature is peculiar in eastern boundary upwelling systems, since most of it results from combined effects of solar seasonal heating and latitudinal variations in upwelling-favourable wind intensity (Fréon *et al.*, 2009) so to chemical energy. However, oxygen may also play a role. Actually even if some species, such as sardine, are 'expulsed' from the system in cold-productive-low oxygen periods (Bertrand *et al.*, 2011) others species associated to cooler conditions, such as the squat lobster, dramatically increase in biomass (Gutiérrez *et al.*, 2008b). Furthermore, under conditions of low oxygen and high production (such as in the late 2000s), the epipelagic community is concentrated within a thin surface layer (Bertrand *et al.*, 2011) where ephemeral fine scale oases boost up trophic interactions and thus energetic transfer (Bertrand *et al.*, 2014).

4.5. Conclusion

In summary, from this long term study of stomach content data, we provided a comprehensive description of the trophic ecology of two important pelagic fish, the jack and chub mackerels according to spatiotemporal patterns. Further, the vast amount of data used in this study allowed addressing questions beyond classic diet description. Indeed we demonstrated that fish diet composition reveal ecosystem changes but is not always a good indicator of changes in prey biomass since prey accessibility and energy content do matter. In addition we revisited the impact of El Niño events on fish diet and showed that these events have weak but unexpected effects. Finally, our results challenge the paradigm of positive correlation between diversity and temperature in the Humboldt Current System; energy content of forage species and the intensity of the oxygen minimum zone most likely play an important role.

Chapter V

General conclusions and perspectives

The Northern Humboldt Current System (NHCS) is a highly productive ecosystem, but it is also highly variable at a wide range of temporal and spatial scales (Chavez et al., 2003). On the one hand the temporal variability is expressed by short (seasonal), medium (interannual), long (secular) and very long term (climate change) temporal patterns (Chavez et al., 2003; Valdés et al., 2008; Gutiérrez et al., 2009; Espino and Yamashiro, 2012; Salvatteci, 2013; Espino, 2013). The NHCS is the region where El Niño Southern Oscillation (ENSO) and climatic variability in general are indeed outstanding (cf Introduction section). On the other hand environmental conditions that fluctuate in time also affect the spatial organization of living organisms by shaping habitat and determining resource availability. Predator-prey relationships are therefore directly impacted by environmental variability that lead to the match or mismatch between predator requirements and resource availability. Thanks to this variability in the NHCS, the species have had to evolve rapid adaptive strategies in space and time (Bertrand et al., 2004c).

The results of this thesis provide a better understanding of the trophic ecology of the jumbo squid *Dosidicus gigas* and two fish predators the jack mackerel *Trachurus murphyi* and the chub mackerel *Scomber japonicus* in the NHCS (Chapters III and IV).

5.1. Synthesis of the foraging ecology of jumbo squid, chub mackerel and jack mackerel

We investigated the trophic ecology of the three species of interest using the standard method of stomach content analyses. We used the gravimetric method as an indicator of diet composition by wet weight, because this method is relevant when large amounts of material are collected, as it is the case for this study. Processing diet data by dry weight is much more time consuming and is usually employed when accurate determination of calorific intake are required (Li & Brocksen, 1977 in Hyslop, 1980).

The availability of an extensive dataset of diet composition provided a novel knowledge on the trophic ecology of the three species. A total of 27,188 non-empty stomachs were analyzed allowing us characterizing the highly variable feeding patterns of these species at different temporal and spatial scales. Hence we provided new knowledge on the comparative trophic behaviour of these species, defined as opportunistic by previous investigations (Konchina, 1982; Konchina et al., 1996; Nigmatullin et al., 2001; Markaida and Sosa-Nishizaki, 2003). More interestingly we shed light on the spatial organization of the forage fauna of these predators that shape the resource partitioning.

Opportunistic foragers are considered as actual indicators of ecosystem changes. We showed here that diet composition is not always a good indicator of changes in prey biomass. We provided new insight on the changes in prey composition according to size and spatiotemporal features of local environment (Chapters III and IV) and on the major role played by dissolved oxygen (Chapter III). Our findings helps to better understand the resilience of jack mackerel and chub mackerel to climatic changes including El Niño Southern Oscillation (ENSO) events (Chapter IV).

The ontogenetic and spatiotemporal variability of jumbo squid diet, described in Chapter III, constitute the first work based on more than 4,000 non-empty stomachs. We described the opportunistic trophic behavior of jumbo squid and confirmed that this species forage on a large variability in prey composition; similar to what was observed in other latitudes (Nigmatullin et al., 2001; Markaida and Sosa-Nishizaki, 2003; Chong et al., 2005; Rosas-Luis, 2007; Ibáñez et al., 2008). The predictions of the multinomial model showed that, while most of the stomachs contained one or two prey taxa only, stomach fullness increases with the number of prey taxa. These results do not support the hypothesis that jumbo squids select the most abundant or energetic taxon in a prey assemblage, neglecting the other available prey. Indeed, other top predators such as tuna exhibit high foraging efficiency (high fullness) in presence of large and dense monospecific prey aggregations in surface layers (Bard et al., 2002; Bertrand et al., 2002a; Menard and Marchal, 2003; Potier et al., 2008). We showed that the shallow OMZ present off coastal Peru could hamper the co-occurrence of jumbo squids. In addition we proposed a conceptual model on jumbo squid trophic ecology including the ontogenetic cycle, oxygen and prey availability.

We investigated the foraging behavior of jack mackerel and chub mackerel (Chapter IV) based on a wide dataset of more than 23,000 non-empty stomachs. To the best of our knowledge, this is the first study that uses diet information of jack mackerel and chub mackerel, collected during a time series of more than 40 years. This work provided new insights into the spatiotemporal variability of feeding habits of jack mackerel and chub mackerel and on prey diversity in the NHCS. We showed for the trophic behaviour of both species are adapted to forage on more accessible species, such as for example *P. monodon* squat lobster and Zoea larvae that focus on dense patches within a surface layer above the oxycline (Bertrand et al., 2014, 2011). Besides, these species foraged over a large variety of taxa and the diet was dominated by zooplankton. Such results are in accordance with others studies focusing on the diet of these species (Antezana, 2010; Castro Hernández and Santana Ortega, 2000; Konchina et al., 1996). Both species present a trophic overlap. But surprisingly, jack mackerel was not as voracious as chub mackerel, contradictorily to what was observed by others authors (Medina and Arancibia 1998). Fish diet presented high spatiotemporal variability, and shelf break appeared as a strong biogeographical frontier. Diet composition of our fish predators was not necessarily a consistent indicator of changes in prey biomass, since prey accessibility and energy content do matter. Unexpectedly, El Niño events had a weak effect on stomach fullness and on the diet of chub mackerel and jack mackerel, challenging the paradigm of positive correlation between diversity and temperature in the NHCS.

5.2. The oxygen minimum zone (OMZ) plays a key role and shapes predator – prey interactions in the NHCS

The upwelling of the NHCS generates areas favorable for the development of primary and secondary producers (phytoplankton and zooplankton) that are the main source of food for other species in a bottom-up control system (Bertrand et al., 2008b). Living organisms tend to aggregate in patches. Physical forcing and organism behaviour are implicit of this patchiness The foraging behaviour of predators tends to reflect the patchy distribution of their prey (Bertrand et al., 2014). Then forage fish and other predators are concentrated where conditions of food and oxygen are favorable (Bertrand et al., 2014), However, for fish, oxygen might be more difficult to obtain than food in systems where anoxia occurs (Pauly, 2010). In response to global warming and direct anthropogenic influences, OMZs of the World Ocean are expanding (Diaz and Rosenberg, 2008; Stramma et al., 2008). The upper limit of OMZs is rising and consequently, the vertical extent of the well-oxygenated surface layer shrinks, constraining the vertical habitat of epipelagic organisms. Intensification of oxygen-poor and acidic conditions could severely impact marine communities. Upwelling regions are particularly vulnerable given that they encompass the largest OMZs (Helly and Levin, 2004; Bertrand et al., 2010). This is particularly critical in the NHCS, which encompasses one of the most intense and shallow OMZ in the world (Helly and Levin, 2004; Chavez et al., 2008; Fuenzalida et al., 2009; Paulmier and Ruiz-Pino, 2009).

We described in Chapter II the characteristics of the OMZ in the NHCS. The NHCS is characterized by the presence of one of the more intense and surface OMZ of the global ocean (Helly and Levin, 2004; Chavez and Messié, 2009; Paulmier and Ruiz-Pino, 2009). This OMZ is very shallow and has important effects on the distribution of marine organisms, the oxycline forms a barrier for marine species intolerant to hypoxia (Ayón et al., 2008a; Bertrand et al., 2010) .

Cephalopods play an important role in marine ecosystems, because they consume a wide variety of invertebrates and fish, and are therefore at a high trophic level in food webs (Rodhouse and Nigmatullin, 1996; Rosas-Luis et al., 2008). They also have high growth rates, associated with high daily rations and rapid digestion (Boyle and Rodhouse, 2005). In this context, it has been suggested that these organisms could impact drastically the populations of their main prey (Rodhouse and Nigmatullin, 1996). This idea becomes challenging when prey have an economic importance (Ibáñez, 2013). This could have been the case of jumbo squid in the NHCS, as this cephalopod is an active predator (Nigmatullin et al., 2001) and the Peruvian anchovy a potential abundant and vulnerable prey, which supports the largest fishery in the world (Pikitch et al., 2014). But the jumbo squid unexpectedly consumed a very low percentage of anchovy. Why? Chapter III attempted to explain this paradox.

We showed jumbo squid did not occupy coastal waters where a huge biomass of anchovy is present. Jumbo squid is adapted to anoxia since it undertakes diel vertical migration and occupies the oxygen minimum zone (OMZ) during the day (Gilly et al., 2006, 2012; Bazzino et al., 2010; Seibel, 2013). However, in the OMZ the jumbo squid adapts to hypoxia via metabolic suppression (Rosa and Seibel, 2008, 2010; Trübenbach et al., 2012, 2013). Although, jumbo squid can live in hypoxic deep waters, they need surface normoxic waters afterwards during the night. Oxygen concentration may thus limit the co-occurrence of jumbo squid (predator) and anchovy (prey).

In NHCS the OMZ is much more intense and shallower than in California (Rosa and Seibel, 2008). In this situation jumbo squid may be not permitted to come in the coastal waters where habit huge biomass of anchovy. Off Peru, the abundance of jumbo squid biomass increases with oxygen saturation (Figure 5.2).

With respect to jack mackerel and chub mackerel, generalized additive model (GAMs) showed the Z_2 ml.l^{-1} (the depth of the 2 ml.l^{-1} oxygen concentration isoline, in m). The acoustic-estimated biomass of both species was significantly correlated to the depth of the 2 ml.l^{-1} oxygen concentration (Figure 5.1). The effect of oxygen on chub mackerel biomass (Figure 5.2 B) was comparable than for jack mackerel (Figure 5.2 A). Both species were more abundant when Z_2 ml.l^{-1} is deeper than 20 m (Bertrand unpublished Figure 5.2). Contrary to anchovy, this species it's not affected by very shallow oxycline (<10 m) (Bertrand et al., 2011). This behaviour in both species may explain the low incidence of anchovy in the diet of jack mackerel and chub mackerel during cold years when oxycline was very shallow.

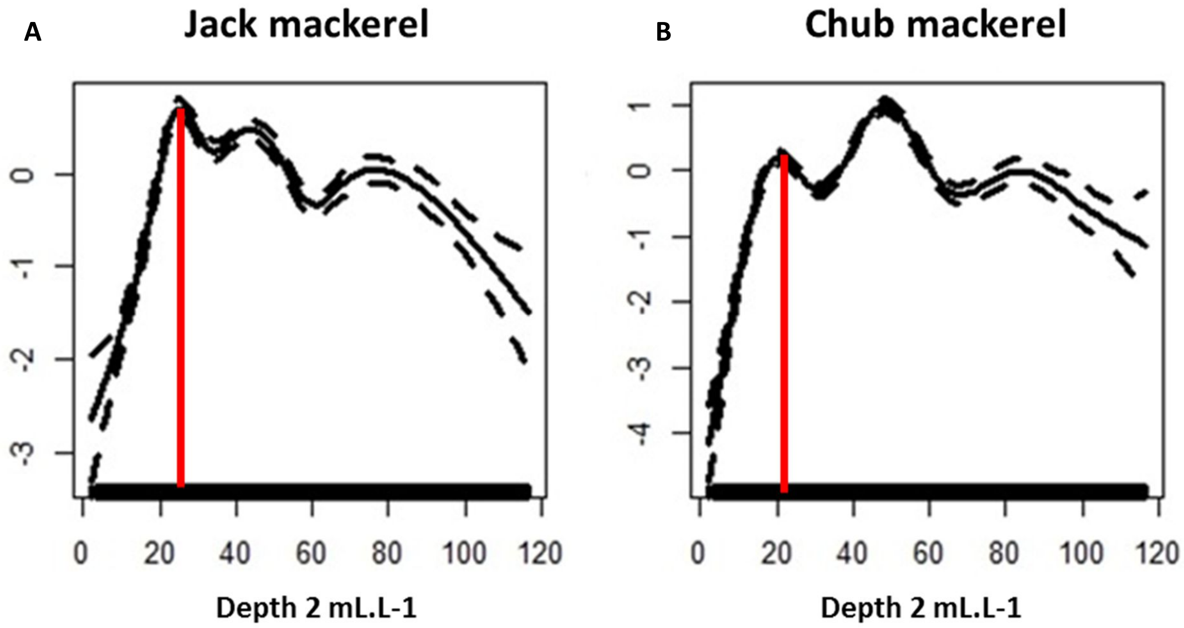

Figure 5.1. GAM modelling approach to depth of the oxygen concentration 2 ml.l^{-1} isoline in m of jack mackerel (A) and chub mackerel (B) in relationship of acoustic-estimated biomass. Cubic spline smoother fits (black solid lines) of confidence intervals (dotted lines show 95% confidence limits) (Source: Bertrand unpublished).

The period between the early 1970s to the mid 1990s was warmer, less productive and more oxygenated compared with the period from the mid 1990s (Chavez et al., 2003; Bertrand et al., 2011). Consequently, during this period, jack and chub mackerels could distribute closer to the coast and anchovy prey was more accessible. The Figure 5.2 shows that the jack mackerel, chub mackerel and jumbo squid distribution don't overlap with anchovy, which is very coastal. The OMZ play an important role in foraging behaviour and prey accessibility.

The spatial relationship between predators and prey has important implications for landscape processes. The distribution of prey influences the movement of predators and has important consequences for the dynamics of nutrient and energy fluxes in ecosystems. Most organisms live in environments where food resources are distributed heterogeneously; the distribution of resources influences the movement of consumers across landscapes; and the spatial configuration of prey utilization by predators has important consequences for the dynamics of nutrient and energy fluxes in ecosystems (Russell et al., 1992).The prey size and predator size also are important factors influencing trophic interactions and foraging success in marine predators (Scharf et al., 2000).

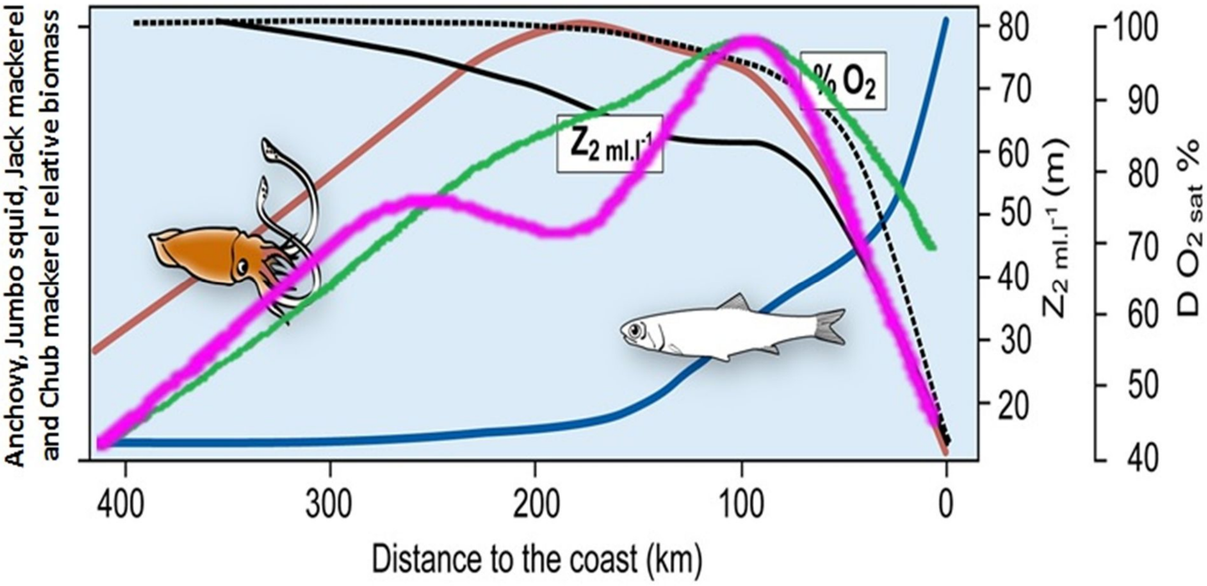

Figure 5.2. Conceptual model and cross-shore profiles of oxygen and organisms distribution. The panel shows the mean (spline smooth) cross-shore profiles of dissolved oxygen saturation in % (grey dashed line), depth of the 2 ml.l^{-1} isoline in m (black solid line) and the acoustic-estimated biomass of anchovy (blue solid line), jumbo squid acoustic-estimated biomass (red solid line), jack mackerel (purple solid line) and chub mackerel (green solid line). Oxygen and anchovy data come from Bertrand et al. (2011), jack and chub mackerel data come from Bertrand (unpublished), jumbo squid data come from Alegre et al. (2014).

5.3. Predator size, prey accessibility and shelf break matter in the NHCS

In the NHCS our findings showed that the diet composition of jumbo squid (Chapter III) differed according to predator size. The main pattern was the steady increase of the percentage of cephalopods (conspecifics or not) with size. The percentage of Euphausiidae also increased significantly. On the contrary, the contribution of *V. lucetia* and *Myctophum* sp. decreased significantly while jumbo squid increased in size (Figure 3.3A). We assumed that diet changes were more related to prey accessibility, than specifically to jumbo squid size (Argüelles et al. 2012), we showed jumbo squid perform ontogenetic migration with small individuals distributed further offshore than larger individuals. In the Figure 3.6 we presented a comprehensive model of jumbo squid distribution. The small individuals are distributed during spring further offshore mainly where they forage on mesopelagic fishes. This pattern matches with the known distribution of mesopelagic fish, especially the lightfish *Vinciguerria lucetia* (Rosas-Luis et al., 2011). The larger jumbo squid located close to the coast increases their consumption of other cephalopods including conspecifics. Cephalopods are generally restricted in their ability to store energy. It is thus assumed that cannibalism is part of a population energy storage strategy enabling cephalopod populations to react to adverse environmental conditions by reducing their number (Ibáñez and Keyl, 2009). Near the shelf break the euphausiids are present (Ballón et al., 2011) and contribute to the diet of the biggest jumbo squid. Lorrain et al. (2011) demonstrated with isotopes signatures that large individuals can significantly forage on low trophic levels. Argüelles *et al.* (2012) (Figure 5.3) observed decreasing δ^{13}C in mantle of *D. gigas* values with increasing distance to the shelf break, this results are consistent with higher δ^{13}C values corresponding to highest productivity in coastal waters than in oceanic waters (Miller et al., 2008; Pennington et al., 2006). Besides, δ13C values also increased with organism size, and this agrees with Ruiz-Cooley *et al.* (2006) who found an increasing trend of δ^{13}C with mantle length in *D. gigas* in the Gulf of California. Studies showed that carbon isotopic changes primarily reflect increases in body mass (Herzka, 2005). Related with food web, carbon differences in δ^{13}C occur primarily at primary production, with small increases with increasing trophic level (0.4 %; Post, 2002). The hypothesizing that δ^{13}C values only reflect changes in habitat, the increasing trend of δ^{13}C values with ML would suggest that *D. gigas* might change of habitat while growing. Nigmatullin *et al.* (2001) indeed reported that if *D. gigas* seasonally migrates to coastal waters to grow, mature and feed, they could return to oceanic waters to spawn.

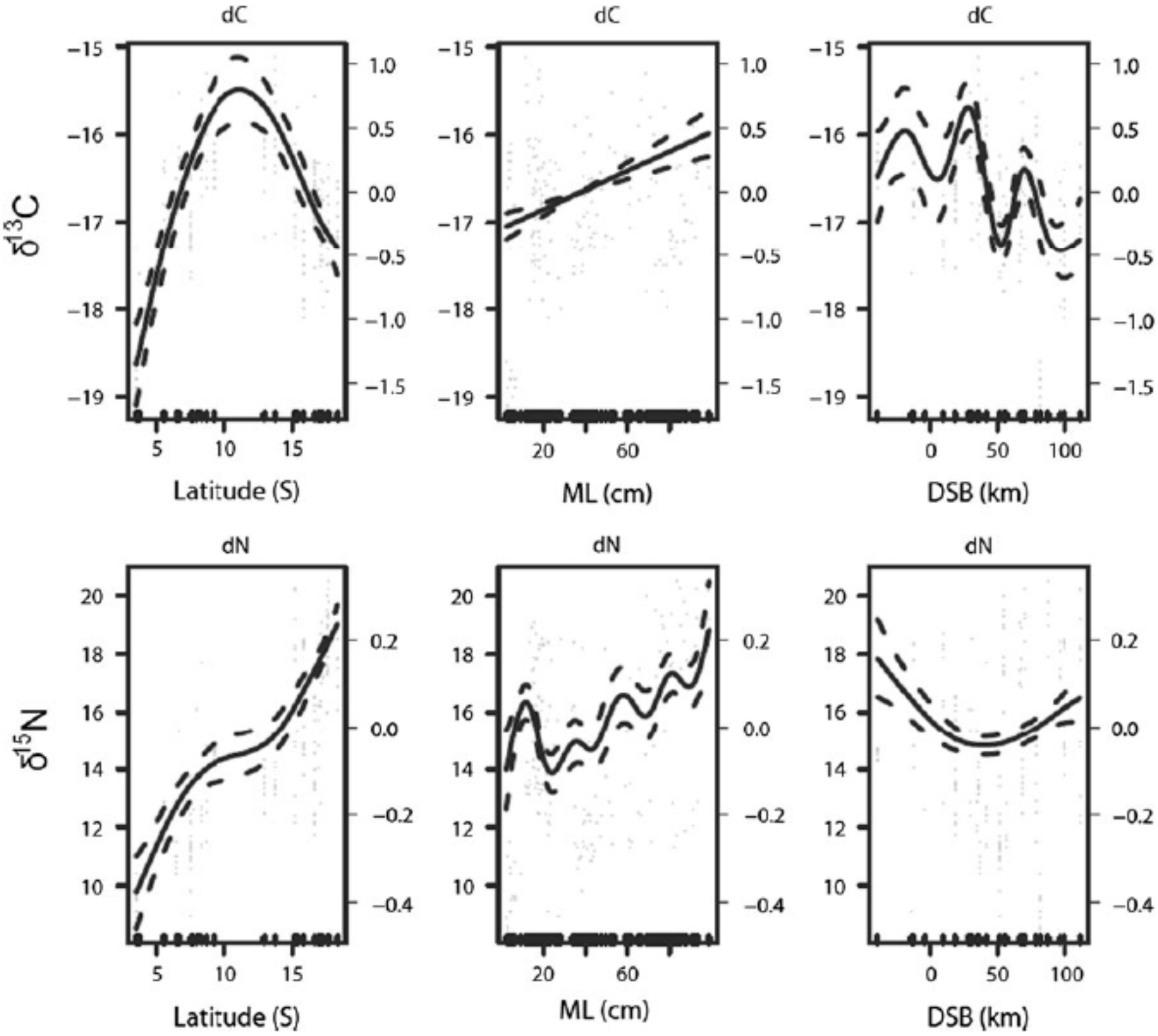

Figure 5.3. GAMs of muscle δ13C and δ15N values as a function of latitude, mantle length (ML) and distance to shelf break (DSB) (Source: Argüelles et al. 2012).

Besides Argüelles *et al.* (2012) shows an overall increase in δ^{15}N values with ML greater than 20 cm (Figure 5.3), suggesting that there is an increase in trophic level with ontogeny for this species. These results agree with those of Ruiz-Cooley *et al.*, (2010, 2006) who found a significant increasing trend of δ^{15}N with mantle length. This is also associated with a very high variability of d^{15}N values with mantle length. As already proposed (Lorrain *et al.*, 2011; Ruiz-Cooley *et al.*, 2010), this work suggest that this is due to highly opportunistic foraging strategies in jumbo squid. This is consistent with Lorrain *et al.*, (2011) who reported the first results on jumbo squid trophic isotope ecology off Peru using sequential stable isotope values along the *gladius* of five large individuals. Even if the trophic level increases with squid size; this trend was not systematic. Indeed, analyzing the most recent part of two large individuals, the authors hypothesized that their similar proximal δ^{13}C value indicated that they foraged in similar habitats, and their very different nitrogen isotopic values indicated feeding on distinct trophic levels (i.e. euphausiids vs. fish). This is also corroborated by stomach content data that show that large and small jumbo squid forage on the same prey spectra and can feed from euphausiids or mesopelagic fish at any size (Figure 5.4 A and B). Intra-individual δ^{13}C variations on *gladius* isotopic profiles were interpreted as reflecting either migrations or more resident periods. Flat lying (invariant) sections of the carbon isotope profiles are assumed to represent resident locations or spatially limited movements (i.e., habitat 1, 2, 3 on Figure 5.4 A and B), while sections where the δ^{13}C profiles vary (grey symbols) represent a migration between habitats. With resident and migration period defined, intra-individual δ^{15}N variations during resident periods (i.e., within habitats 1, 2 or 3; Figure 5.4 A and B) was interpreted as a change in trophic position. Variability in δ^{15}N profiles during migrations (changing δ^{13}C), however, could not be interpreted since baseline d^{15}N variations may occur during squid migrations.

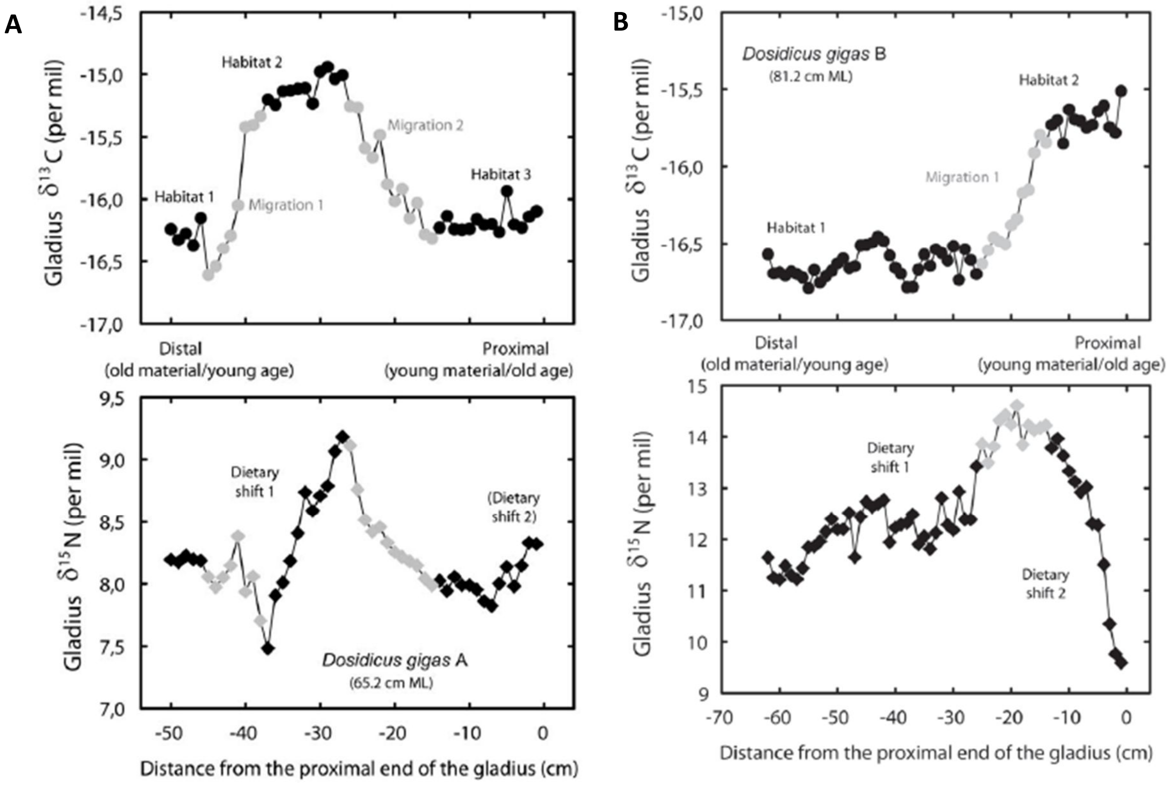

Figure 5.4. High resolution isotopic profile along individual A gladius. δ13C (filled circles) and δ15N (filled diamonds) values along the length of the gladius of a 65.2 cm ML(A) and 81.2 cm ML(B) jumbo squid. Grey symbols represent periods of migration, while black symbols illustrate a more fixed isotopic habitat (Source: Lorrain et al., 2011).

Size effect on diet composition of the jack mackerel and chub mackerel (Chapter IV) was not obvious. However, the sampling was heterogeneous in terms of size during the covered time period. For instance, jack mackerel large individuals (from 15 to 70 cm) were sampled during the 1970s only, i.e. during the first years of the period. With global data for jack mackerel (1973-2013), we have observed that Copepoda is the dominant group in the small-size. The euphausiids, Zoea larvae and *Pleuroncodes monodon*, increased for medium-size individuals and the percentage of anchovy was important in large individuals. This diet shift with predator size has already been indicated by others authors (Muck and Sanchez 1987; Ermolovich and Gardina, 1994). This change in diet composition with fish size can be attributed to the predator's ability to capture and handle the prey (Christensen, 1996; Lundvall et al., 1999).

Interestingly, we observed an important contribution of anchovy in the diet of large jack mackerel (>41 cm FL) during the 1970s when the average fish size was higher (Díaz, 2013). During this period, large jack mackerel had access to highly energetic prey such as the Peruvian anchovy *Engraulis ringens*, because the jack mackerel could enter of coastal waters due to a deepen oxycline (Bertrand et al., 2011; Flores et al., 2013). However, since the late 1990s, overfishing removed these large jack mackerel from the system (Gerlotto *et al*., 2012). This could explain why high fish proportion in the diet was only observed in the first years of our time series, before great commercial fishing development (Figure 4.5D).

Chub mackerel did not present clear pattern in the diet composition with size,. This predator foraged on small zooplankton (Copepoda) at all size class. This pattern was already mentioned by Konchina (1982) but not by Muck and Sanchez (1987). In this study the zooplankton contribution was even greater in chub mackerel, while small chub mackerel could paradoxically consume more fishes than large chub mackerel (Figures 4.5A, 4.11). Castro, (1993)mentioned the chub mackerel juvenile foraged mainly fishes (42%) in Canarias.

In summary, we indicated that individual size is strongly linked to ontogenetic migration for jumbo squid. Whereas continental shelf constitutes an important biogeographic barrier (Bakun, 1996; Genin, 2004; Zhu et al., 2009) for feeding jack mackerel and chub mackerel. The contribution of prey is higher in the border of the shelf break, especially the euphausiids (Figure 4.5). These results are in agreement with the proposal by Ballón et al., (2011), who showed the macrozooplankton biomass increase over the continental shelf break.

The latitudinal pattern trend seems more related to the geography of the Peruvian coast than to genuine latitudinal effects. We hypothesized that the lack of effect was explained by the geomorphology of the coast and the width of the continental shelf. There is a trend for euphausiids that dominated in the north part (3º-10ºS) and decreased to the south where the continental shelf is wide. On the contrary, the squat lobster *Pleuroncodes monodon* increased in the diet with the latitude southward where the continental shelf is narrow. Gutiérrez et al. (2008) indicates that the squat lobster is distributed mainly in high latitudes in the Peruvian coast (between 9-12ºS).

5.4. The overlap between jumbo squid and *Vinciguerria lucetia*

With the results of this work, we know that changes in prey composition according to squid size and spatiotemporal features were more related to prey accessibility rather than to specific/size-related preferences.

Jumbo squid perform ontogenetic migration with small individuals distributed far from the coast than larger jumbo squid (Arguelles *et al.,* 2001). Prey composition in the stomach contents matches this distribution, mesopelagic fish (*V. lucetia* and myctophiids) recovered mainly in the small jumbo squids stomachs, confirmed the structuring role of spatial matching in the jumbo squid-prey interactions, because small jumbo squids consumed more mesopelagic fish than larger individuals. This prey group contributed more during spring and far from the coast, when jumbo squid was more offshore.

This pattern is in accordance with our results in Rosas-Luis *et al*. (2011). We worked with acoustic surveys for assessing the biomass and distribution of the jumbo squid and the mesopelagic fish *V. lucetia* that were carried out in the Northern Humboldt Current System in 2007 and 2008. Besides, 937 stomach contents of jumbo squid were analyzed. In this work the main group in the diet of the jumbo squid was mesopelagic fish and inside this group, the principal prey was V. lucetia. The acoustic biomass estimates made for *D. gigas* and *V. lucetia* are considered realistic, however, in order to correctly estimate biomass the values obtained with the acoustic method can be contrasted with net trawls, in which the collected organisms are identified and analyzed. This method provides a tool for verifying the fish composition in the water column (Cornejo and Koppelmann, 2006).

With the acoustic method, we detected *D. gigas* and *V. lucetia* form aggregations, supported the hypothesis of a strong relationship between these two species, which is reflected in the jumbo squid's feeding activity and the vertical migrations shown in the echograms. Trophic relationships between *D. gigas* and *V. lucetia* are evident during the day and night and *D. gigas* probably feeds on *V. lucetia* in deeper waters. Alarcón *et al.* (2004) carried out experimental fishing with semipelagic trawls for lightfish and recorded large catches of jumbo squid. The acoustic biomass estimates and echogram signals of *D. gigas* and *V. lucetia* in the water column suggest a close relationship between prey and predator, as the estimated distribution of jumbo squid near and offshore the continental shelf break overlapped with that of *V lucetia*. Similar pattern is reflected in the stomach content analysis of the squid, in which *V. lucetia* was the main component. Evidently, jumbo squid prey on other species, which were present in the stomach contents at the same time as *V. lucetia*. However, their abundance in the ecosystem is probably lower than that of *V. lucetia*. Moreover that *V. lucetia* and *D. gigas* migrate to deeper waters during the day (migratory behaviour: Gilly et al., 2006; Markaida *et al*., 2005) and it is the factor that determines the dominance of *V. lucetia* in the squid's stomach contents.

The acoustic biomass estimates show that there is a relation between the two species, the importance of *V. lucetia* lies in its ability to support jumbo squid predation, this is a species with dynamic development that promotes rapid population growth, which is reflected in a high abundance and wide distribution in the ocean (Ahlstrom *et al*., 1976). These characteristics are evident in *V. lucetia*, one of the most important fishes in the Northern Humboldt Current System. It is found between 5° and 18°S and can dominate the total catch in up to 68% of scientific cruises (Cornejo and Koppelmann, 2006). Based on the stomach content analysis of *D. gigas* and the acoustic detection we can infer that *V. lucetia* was the main component of the jumbo squid's diet in 2007 and 2008 in the Humboldt Current System off Peru. When there is a high biomass of *V. lucetia*, *D. gigas* has been observed to focus its feeding on this species (Table 5.1) (Rosas-Luis *et al.* 2011).

Table 5.1. Acoustic biomass estimation of jumbo squid and V. lucetia, and estimated consumption of V. lucetia by D. gigas between 2007 and 2008. Q/B of jumbo squid= 5.8, taken from Alarcón-Muñoz et al. (2008) (Source: Rosas-Luis et al. 2011).

Fishing cruiser prospecting	***DCij***	**Hydroacoustic biomass *D. gigas* (t)**	***D.gigas* predation on *V. lucetia* (t)**	**Hydroacoustic biomass *V. lucetia* (t)**	**Estimation of predation by *D. gigas* on *V. lucetia* (%)**
2007 02-04	0.09	1231713.3	625390.1	5948499.9	10.51
2008 05-07	0.15	717086.8	570084.0	2445635.2	23.31
2008 11-12	0.59	154047.0	481704.9	8317821.4	5.79

5.5. Long-term diet data of fish predators provide information on temporal changes of the forage fauna in the NHCS

The analyses of the diet of jack mackerel between 1973 and 2013 (Chapter IV) highlighted the occurrence of at least two temporal scenarios in the NHCS: (1) from 1973 to around 2000, a period with strong dominance of euphausiids; (2) after 2000 the squat lobster *P. monodon* and Zoea larvae increased in the diet, while the occurrence and abundance of Engraulidae in stomachs was moderate (Alegre *et al.*, 2013, 2015). Temporal patterns for chub mackerel were blurred because data were missing for several years. For jack mackerel these scenarios matched with warm and cold periods proposed by Chavez et al. (2003, 2008). The increase of *P. monodon* in the diet was in concordance with the abundance of this prey along the Peruvian coast since the mid-1990s, and particularly after the El Niño in 1997– 1998 (Gutiérrez et al., 2008). Even before this surge in abundance, Elliot and Paredes (1996) reported great biomass of *P. monodon* in the south of Peru in late 1995. Furthermore, the dominance of euphausiids in the jack mackerel diet increased from the late 1970 to the late 1990s and dropped after. This trend is contradictory with the trend in euphausiids abundance off Peru (Ayón et al., 2011) that presented lower biomasses in the late 1970-1990s and increased then after.

Therefore the following paradox appears: if jack mackerel and chub mackerel are opportunistic foragers (Konchina et al. 1981; Konchina, 1982; Muck & Sanchez 1987; in this study), changes in their diet should indicate changes in the species assemblage of the ecosystem. In Chapter IV we indicated that changes in prey contribution actually correspond to observed changes in the ecosystem in the case of *P. monodon* but not in the case of Euphausiidae. The explanation we propose for this paradox is that the *P. monodon* is an "easy" prey to get. They congregated in dense patches within a thin surface layer above the oxycline (Bertrand et al., 2011, 2014). In addition, they are accessible during the complete diel cycle (i.e., day and night) while most Euphausiidae perform diel vertical migration, and are therefore inaccessible during the day (Ballón et al., 2011). Besides *P. monodon* has a high nutritional content (Gutierrez, 2002). Aurioles-Gamboa et al. (2004) showed that the fatty acid composition of a close species, *P. planipes*, depended of the available food quality. In the highly productive NHCS, *P. monodon* is no food limited and has high protein and fatty acid content (Gutierrez, 2002). A close pattern occurred with the diet data of chub mackerel. However, many years were missing, which did not allow us to draw conclusions about temporal changes in the diet of this species. Our results refuted the use of opportunistic foragers as real indicators of ecosystem changes. Indeed the decadal changes in JM diet point out that the foraging behaviour depends on prey abundance but also on prey accessibility and the prey energetic content.

The NHCS is a region particularly affected by El Niño southern oscillation (Chavez et al. 2008). Exceptional El Niño events, such as those that occurred in 1982-83 and 1997-98, affect all marine ecosystems components (Barber and Chavez 1983; Arntz and Tarazona 1990; Fiedler 2002) including jack mackerel and chub mackerel populations (Arcos *et al.*, 2001; Bertrand *et al.*, 2004b; Gerlotto *et al.*, 2012). The paradox is that, contrary to previous studies (Muck and Sanchez 1987; Sánchez de Benites and Muck, 1987), prey diversity was significantly lower during El Niño (Chapter IV). We did not detect strong differences in diet composition between El Niño, La Niña and neutral periods (Figure 4.9). Comparable results were observed on anchovy diet (Espinoza and Bertrand, 2008). The reason for such a weak effect of ENSO events on pelagic fish trophic ecology is puzzling. Euphausidae are the main prey group for pelagic fishes (this study, Espinoza and Bertrand, 2008; Espinoza et al., 2009). Their occurrence and abundance seem highly resilient to El Niño events (Brinton 1967; Ballón et al., 2008; Aronés et al., 2009).

5.6. Patterns of prey diversity

The selection of food is an important factor to consider in the dynamics of fish stocks, because stocks production probably depending on the type, quality and abundance of prey (Ursin, 1979). However, one must consider prey size, prey composition and prey abundance in the diet as well as prey availability in the environment.

We obtained unexpected results in this work when studying the prey richness in the jumbo squid diet (Chapter III). The results of multinomial model indicate that jumbo squid fullness increased with the number of prey taxa. This result has an opposite pattern than expected. We therefore question the usual hypothesis that top predators can seek locally dense aggregations of monospecific prey. For example tuna forage on dense and monospecific prey aggregations, they can feed on this concentration until satiation (Bard et al., 2002; Bertrand et al., 2002; Ménard and Marchal, 2003; Potier et al., 2008). On the contrary, when prey are scattered (Auster et al., 1992), tunas forage on a higher diversity of prey but with a lesser efficiency (Potier et al., 2007).

The comparison of the diet of both jack and chub mackerels (Chapter IV) investigated using Multivariate Regression Tree analysis CART (Figure 4.11) argues that there are significant differences in the diet of these two pelagic fishes. Although both species are preferably zooplanktophagus, it should be noted more proportion of fish in the diet of chub mackerel. There are anatomical differences in the mouthparts of both species, which would differentiate the type of diet. The jack mackerel, has protrusible mouth, during feeding shoots their lips to suck the prey (Mapukata, 2002). The type of the mouth in adult chub mackerel is a transitional form between the types of fish "planktophagous" and "ichtyophagus" but closer to the latter type. The pharyngeal plates are provided with sharp teeth and directed into the esophagus; its function is to retain the prey caught in the mouth and further contribute to the mechanism of swallowing food (Angelescu, 1980). Then, chub mackerel feed by filtering small particles from suspension and besides engulfing large individually prey (O'Connell and Zweifel, 1972) and jack mackerel used only particulate feed (Mapukata, 2002). In this work we found a highest proportion of fish in chub mackerel diet, than jack mackerel. This finding also contradicts the work of Medina and Arancibia (1998), who found that jack mackerel selects prey 11.8 times larger than prey of chub mackerel, in relation with predator bodyweight. The explanation of this paradox in the NHCS could be based on the occupation of space in both species. The chub mackerel inhabits most coastal areas and have more access to the anchovy and their larvae, the jack mackerel inhabits the ocean areas for their sensitivity to the shallow OMZ. But in the oceanic area there are huge amounts of mesopelagics, especially *V. lucetia* (Cornejo and Koppelmann, 2006); and our results indicate that jack mackerel consume low amounts of mesopelagic, contrary to what was found for Chilean waters (Medina and Arancibia, 1992, 1998, 2002).

5.7. Concluding remarks and perspectives

This study provided a new vision of the trophic ecology of the main predators in the NHCS. Several paradoxes were deciphered (e.g. the jumbo squid - anchovy - Oxygen) and some surprises came out (e.g. the preference of jack and chub mackerel over squat lobster than Euphausiidae). This work that is based on a considerable number of stomach samples and with great spatiotemporal coverage, allowed us to understand the feeding behavior of important resources in the NHCS. In many cases the diet could indicate spatio-temporal changes in the environment. However, we cannot infer entirely on the presence of organisms in the environment through the analyses of stomach contents of predators. Other processes inherent to predators such as livelihood strategies, competition and opportunism need to be considered. The global patterns that we described in this work, illustrate the opportunistic foraging behaviour, life strategies and the high degree of plasticity of these species. Such behavior allows adaptation to changes in the environment.

The main limitation of this study was the inability to work with more environmental variables, particularly physicochemical variables. This problem resided mainly in the amount of biological information that is handled in this study and the lack of time to also handle other environmental time series. Therefore, further studies should take into account more environmental variables to better understand the feeding behavior of these species. In addition, the methodological framework developed during this work should be applied to other important species such as Bonito, Dolphin fish and Tuna, allowing us to complement the picture of the feeding behavior of the main resources of NHCS spatially and of the food supply. Finally, our findings should help to improve monitoring protocols by applying methods of minimum sample size in order to have balanced sampling scheme in time and space.

Besides, the highly variability in time and space of predators' diet shows that trophic models with fixed diet (e.g. Ecopath) can have major drawbacks. In the NHCS, trophic models should definitively consider adaptive trophic behaviours, and we propose to work with people who developed a Humboldt version of the OSMOSE End-to-End model (Oliveros, 2014) to develop a reliable model of oceanic ecosystem in Peru.

References

Abramov, A.A., Kotlyar, A.N., 1980. Some biological features of the Peruvian jack mackerel, Trachurus symmetricus murphyi. J. Ichthyol. 80, 25–31.

Ahlstrom, E.H., 1969. Mesopelagics and bathypelagics fishes in the California current region. CalCOFI Rept. 13, 39–44.

Ahlstrom, H., Moser, H.G., O'Toole, M.J., 1976. Development and distribution of larvae and early juveniles of the commercial lanternfish, Lampanyctodes hectoris (Günther), off the west coast of southern Africa, with a discussion of phylogenetic relationships of the genus. Bull. South. Calif. Acad. Sci. 75, 138–152.

Alamo, A., Espinoza, P., 1998. Variaciones alimentarias en engraulis ringens y otros recursos pelágicos durante invierno-primavera de 1997. Inf. Inst. del Mar del Perú 130, 45–52.

Alamo, A., Navarro, I., Espinoza, P., Zubiate, P., 1996. Relaciones tróficas, espectro alimentario y ración de alimentación de las principales especies pelágicas en el verano 1996. Inf. Inst. del Mar del Perú 122, 36–46.

Alamo, V., Valdivieso, V., 1997. Lista sistemática de moluscos marinos del Perú, Segunda Ed. ed. Instituto del Mar del Perú, Callao.

Alarcón, J.C., Salazar, F., Ganoza, G., Chacon, J., Calderon, M., TakHIA, O., 2004. Efectos del incremento del tamaño de malla del copo de la red semipelágica en la captura de Vinciguerria lucetia, in: Reunión Cientifica Internacional. Instituto Del Mar Del Peru-Japan Deep Sea Trawler Association. Callao, Peru.

Alarcón-Muñoz, R., Cubillos, L.A., Gatica, C., 2008. Jumbo squid (Dosidicus gigas) biomass off central Chile effects on Chilean Hake (Merluccius gayi). Calif. Coop. Ocean. Fish. Investig. Reports 49, 157–166.

Albert, a., Echevin, V., Lévy, M., Aumont, O., 2010. Impact of nearshore wind stress curl on coastal circulation and primary productivity in the Peru upwelling system. J. Geophys. Res. 115, C12033. doi:10.1029/2010JC006569

Alegre, A., Bertrand, A., Espino, M., Espinoza, P., Dioses, T., Ñiquen, M., Navarro, I., Simier, M., Ménard, F., 2015. Diet diversity of jack and chub mackerels and ecosystem changes in the northern Humboldt Current system: A long-term study. Prog. Oceanogr. 137, 299–313. doi:10.1016/j.pocean.2015.07.010

Alegre, A., Espinoza, P., Espino, M., 2013. Trophic ecology of Jack mackerel Trachurus murphyi in Peru, 1977 – 2011. Rev. peru. biol Vol. Ext., 75–82.

Alegre, A., Ménard, F., Tafur, R., Espinoza, P., Argüelles, J., Maehara, V., Flores, O., Simier, M., Bertrand, A., 2014. Comprehensive model of Jumbo squid Dosidicus gigas trophic ecology in the Northern Humboldt current system. PLoS One 9, e85919. doi:10.1371/journal.pone.0085919

Alheit, J., Niquen, M., 2004. Regime shifts in the Humboldt Current ecosystem. Prog. Oceanogr. 60, 201–222. doi:10.1016/j.pocean.2004.02.006

Allauca, S., 1990. Presencia de la Corriente Costanera Ecuatoriana. Acta Ocean. del Pacífico 6, 1–17.

Amaratunga, T., 1983. The role of cephalopods in the marine ecosystem., in: Caddy, J.F. (Ed.), Advances in Assessment of World Cephalopod Resources. FAO Fish Tech Pap, Rome, pp. 379–415.

Angelescu, V., 1980. Ecologia trófica de la caballa del atlantico sudoccidental. Bol. do Inst. Ocean. 29, 41–47.

Anon, 1984. Report of survey for the development of new distant water trawling grounds in 1983. Kaihatsu News.

Anon, 1985. Report of survey for the development of new distant water trawling grounds in 1984. Kaihatsu News.

Antezana, T., 2009. Species-specific patterns of diel migration into the Oxygen Minimum Zone by euphausiids in the Humboldt Current Ecosystem. Prog. Oceanogr. 83, 228–236. doi:10.1016/j.pocean.2009.07.039

Antezana, T., 2010. Euphausia mucronata: A keystone herbivore and prey of the Humboldt Current System. Deep Sea Res. Part II Top. Stud. Oceanogr. 57, 652–662. doi:10.1016/j.dsr2.2009.10.014

Arcos, D.F., Cubillos, L.A., Núñez, S.P., 2001. The jack mackerel fishery and El Niño 1997–98 effects off Chile. Prog. Oceanogr. 49, 597–617.

Argüelles, J., Lorrain, A., Cherel, Y., Graco, M., Tafur, R., Alegre, A., Espinoza, P., Taipe, A., Ayón, P., Bertrand, A., 2012a. Tracking habitat and resource use for the jumbo squid Dosidicus gigas: a stable isotope analysis in the Northern Humboldt Current System. Mar. Biol. 159, 2105–2116.

Argüelles, J., Lorrain, A., Cherel, Y., Graco, M., Tafur, R., Alegre, A., Espinoza, P., Taipe, A., Ayón, P., Bertrand, A., 2012b. Tracking habitat and resource use for the jumbo squid Dosidicus gigas: a stable isotope analysis in the Northern Humboldt Current System. Mar. Biol. 159, 2105–2116. doi:10.1007/s00227-012-1998-2

Arguelles, J., Rodhouse, P.G., Villegas, P., Castillo, G., 2001. Age, growth and population structure of the jumbo flying squid Dosidicus gigas in Peruvian waters. Fish. Res. 54, 51–61.

Arntz, W., Tarazona, J., 1990. Effects of El Niño on benthos, fish and fisheries off the South American Pacific coast, in: Glynn, P.W. (Ed.), Global Ecological Consequences of the 1982-83 El Niño- Southern Oscillation. Elsevier Oceanography Series, Amsterdan, pp. 323–360.

Arntz, W.E., Fahrbach, E., 1996. No Title, First Edit. ed. Fondo de Cultura Económica, Mexico.

Arntz, W.E., Tarazona, J., Gallardo, V., Flores, L., Salzwedel, H., 1991. Benthos communities in oxygen deficient shelf and upper slope areas of the Peruvian and Chilean Pacific coast, and changes caused by El Niño, in: Tyson, R.V., Pearson, T.H. (Eds.), Modern and Ancient Continental Shelf Anoxia. Geological Society Special Publications, London, pp. 131–154.

Aronés, K., Ayón, P., Hirche, H.J., Schwamborn, R., 2009. Hydrographic structure and zooplankton abundance and diversity off Paita, northern Peru (1994 to 2004) - ENSO effects, trends and changes. J. Mar. Syst. 78, 582–598. doi:10.1016/j.jmarsys.2009.01.002

Ashok, K., Behera, S.K., Rao, S. a., Weng, H., Yamagata, T., 2007. El Niño Modoki and its possible teleconnection. J. Geophys. Res. 112, 1–27. doi:10.1029/2006JC003798

Aurioles-Gamboa, D., Castro-González, M.I., Perez-Gil-Romo, F., Barita, J.L.S., 2004. Quality differences in feeding areas of the red crab, Pleuroncodes planipes Stimpson, as reflected from their lipid, fatty acids, and astaxanthin composition. Crustac. Int. 77, 163–176.

Auster, P.J., Griswold, C.A., Youngbluth, M.J., Bailey, T.G., 1992. Aggregations of myctophid fishes with other pelagic fauna. Environ. Biol. Fishes 35, 133–139.

Ayón, P., Correa, J., 2013. Spatial and temporal variability of Jack mackerel Trachurus murphyi larvae in Peru between 1966 – 2010. Rev. Peru. Biol. 20, 83–86.

Ayón, P., Criales-hernandez, M.I., Schwamborn, R., Hirche, H., 2008a. Zooplankton research off Peru: A review. Prog. Oceanogr. 79, 238–255. doi:10.1016/j.pocean.2008.10.020

Ayón, P., Swartzman, G., Bertrand, A., Gutiérrez, M., Bertrand, S., 2008b. Zooplankton and forage fish species off Peru: Large-scale bottom-up forcing and local-scale depletion. Prog. Oceanogr. 79, 208–214. doi:10.1016/j.pocean.2008.10.023

Ayón, P., Swartzman, G., Espinoza, P., Bertrand, A., 2011. Long-term changes in zooplankton size distribution in the Peruvian Humboldt Current System: conditions favouring sardine or anchovy. Mar. Ecol. Prog. Ser. 422, 211–222. doi:10.3354/meps08918

Bahamonde, R., 1978. Distribución y abundancia relitiva de los principales recursos demersales entre Corral (40ºS) y el Cabo de Hornos (57ºS). Valparaiso.

Bakun, A., 1996. Patterns in the Ocean: Ocean Processes and Marine Population Dynamics., First Edit. ed. NOAA, California.

Bakun, A., Weeks, S.J., 2008. The marine ecosystem off Peru: What are the secrets of its fishery productivity and what might its future hold? Prog. Oceanogr. 79, 290–299. doi:10.1016/j.pocean.2008.10.027

Ballón, M., Bertrand, A., Lebourges-Dhaussy, A., Gutiérrez, M., Ayón, P., Grados, D., Gerlotto, F., 2011. Is there enough zooplankton to feed forage fish populations off Peru? An acoustic (positive) answer. Prog. Oceanogr. 91, 360–381. doi:10.1016/j.pocean.2011.03.001

Ballón, M., Wosnitza-Mendo, C., Guevara-Carrasco, R., Bertrand, A., 2008. The impact of overfishing and El Niño on the condition factor and reproductive success of Peruvian hake, Merluccius gayi peruanus. Prog. Oceanogr. 79, 300–307. doi:10.1016/j.pocean.2008.10.016

Barange, M., Pillar, S.C., 1992. Cross-shelf circulation, zonation and maintenance mechanisms of Nyctiphanes capensis and Euphausia hanseni (Euphausiacea) in the northern Benguela upwelling system. Cont. Shelf Res. 12, 1027–1042.

Barber, R.T., Chavez, F.P., 1983. Biological consequences of El Niño. Science (80-.). 222, 1203–1210.

Barber, R.T., Chavez, F.P., 2008. Biological Consequences of El Ninio. Science (80-.). 222, 1203–1210.

Barbieri, M.A., Silva, C., Larouche, P., Nieto, K., Yáñez, E., 2004. Detection of mesoscale oceanic fea tures using radarsat-1 avhrr and seawifs images and the possible link with Jack mackerel (Trachurus murphyi) distribution in central Chile. ISSN 29–39.

Bard, F.-X., Kouamé, B., Hervé, A., 2002. Schools of large yellowfin (Thunnus albacares) concentrated by foraging on a monospecific layer of Cubiceps pauciradiatus , observed in the eastern tropical Atlantic. Col. Vol. Sci. Pap. ICCAT 96, 33–41.

Bazzino, G., Gilly, W.F., Markaida, U., Salinas-Zavala, C. a., Ramos-Castillejos, J., 2010. Horizontal movements, vertical-habitat utilization and diet of the jumbo squid (Dosidicus gigas) in the Pacific Ocean off Baja California Sur, Mexico. Prog. Oceanogr. 86, 59–71. doi:10.1016/j.pocean.2010.04.017

Benites, C., Valdivieso, V., 1986. Resultados de la pesca exploratoria de 1979/80 y desembarque de cefalópodos pelágicos en el litoral peruano. Boletín del Inst. del Mar del Perú 10, 108–139.

Benoit-Bird, K.J., Au, W.W.L., 2003. Prey dynamics affect foraging by a pelagic predator (Stenella longirostris) over a range of spatial and temporal scales. Behav. Ecol. Sociobiol. 53, 364–373. doi:10.1007/s00265-003-0585-4

Bertrand, A., Ballón, M., Chaigneau, A., 2010. Acoustic observation of living organisms reveals the upper limit of the oxygen minimum zone. PLoS One 5, e10330. doi:10.1371/journal.pone.0010330

Bertrand, A., Barbieri, M.A., Cordova, J., Hernandez, C., Gomez, F., Leiva, F., 2004a. Diel vertical behaviour, predator-prey relationships, and occupation of space by jack mackerel (Trachurus murphyi) off Chile. ICES J. Mar. Sci. 61, 1105–1112. doi:10.1016/j.icesjms.2004.06.010

Bertrand, A., Barbieri, M.A., Gerlotto, F., Leiva, F., Córdova, J., 2006. Determinism and plasticity of fish schooling behaviour as exemplified by the South Pacific jack mackerel Trachurus murphyi. Mar. Ecol. Prog. Ser. 311, 145–156. doi:10.3354/meps311145

Bertrand, A., Bard, F.X., Josse, E., 2002a. Tuna food habits related to the micronekton distribution in French Polynesia. Mar. Biol. 140, 1023–1037. doi:10.1007/s00227-001-0776-3

Bertrand, A., Chaigneau, A., Peraltilla, S., Ledesma, J., Graco, M., Monetti, F., Chavez, F.P., 2011. Oxygen: a fundamental property regulating pelagic ecosystem structure in the coastal southeastern tropical Pacific. PLoS One 6, e29558. doi:10.1371/journal.pone.0029558

Bertrand, A., Gerlotto, F., Bertrand, S., Gutiérrez, M., Alza, L., Chipollini, A., Díaz, E., Espinoza, P., Ledesma, J., Quesquén, R., Peraltilla, S., Chavez, F., 2008. Schooling behaviour and environmental forcing in relation to anchoveta distribution: An analysis across multiple spatial scales. Prog. Oceanogr. 79, 264–277. doi:10.1016/j.pocean.2008.10.018

Bertrand, A., Grados, D., Colas, F., Bertrand, S., Capet, X., Chaigneau, A., Vargas, G., Mousseigne, A., Fablet, R., 2014. Broad impacts of fine-scale dynamics on seascape structure from zooplankton to seabirds. Nat. Commun. 5, 6239. doi:10.1038/ncomms6239

Bertrand, A., Josse, E., Bach, P., Gros, P., Dagorn, L., 2002b. Hydrological and trophic characteristics of tuna habitat : consequences on tuna distribution and longline catchability. Can. J. Fish. Aquat. Sci 59, 1002–1013. doi:10.1139/F02-073

Bertrand, A., Segura, M., Gutiérrez, M., Vásquez, L., 2004b. From small-scale habitat loopholes to decadal cycles : a habitat-based hypothesis explaining fluctuation in pelagic fish populations off Peru. Fish Fish. 5, 296–316.

Bertrand, A., Segura, M., Gutiérrez, M., Vásquez, L., 2004c. From small-scale habitat loopholes to decadal cycles: a habitat-based hypothesis explaining fluctuation in pelagic fish populations off Peru. Fish Fish. 5, 296–316.

Bertrand, S., Dewitte, B., Tam, J., Díaz, E., Bertrand, A., 2008. Impacts of Kelvin wave forcing in the Peru Humboldt Current system: Scenarios of spatial reorganizations from physics to fishers. Prog. Oceanogr. 79, 278–289. doi:10.1016/j.pocean.2008.10.017

Blaskovic, V., Fernández, C., Alegre, A., Navarro, I., 2009. Food caracteristics of the main pelagic species (pisces) in the Northern Humboldt Current System, 2009.

Bouchon, M., Cahuin, S., Diaz, E., Niquen, M., 2000. Captura y esfuerzo pesquero de la pesquería de anchoveta peruana (Engraulis ringens). Boletín del Inst. del Mar del Perú 19, 109–116.

Boyle, P., Rodhouse, P.G., 2005. Ecology and Fisheries, First Edit. ed. Blackwell Science Ltd., Oxford.

Breiman, L., Friedman, J., Olshen, R., Stone, C., 1984. Classification and Regression Trees. Wadsworth & Brooks/Cole Advanced Books & Software, Pacific Grove, California.

Budelmann, B., 1994. Cephalopod sense organs, nerves and the brain: adaptations for high performance and life style. Mar. Freshw. Behav. Physiolgy 25, 13–33.

Caddy, J.F., 1983. The cephalopods: factors relevant to their population dynamics and to the assessment and management of stocks, in: Caddy, J.F. (Ed.), Advanced in Assessment of World Cephalopods Resources. FAO Fish Tech Pap, pp. 416–449.

Calienes, R., Guillén, O., Lostaunau, N., 1985. Variabilidad Espacio-Temporal de Clorófila, Producción Primaria y Nutrientes Frente a la Costa Peruana. Boletín del Inst. del Mar del Perú 10, 1–44.

Carr, M., Kearns, E., 2003. Production regimes in four Eastern Boundary Current systems. Deep Sea Res. Part II Top. Stud. Oceanogr. 50, 3199–3221. doi:10.1016/j.dsr2.2003.07.015

Carr, M.-E., 2002. Estimation of potential productivity in Eastern Boundary Currents using remote sensing. Deep Sea Res. Part II Top. Stud. Oceanogr. 49, 59–80.

Castillo, R., Gutiérrez, M., Peraltilla, S., Herrera, N., 1998. Biomasa de recursos pesqueros a finales del invierno 1998. Crucero BIC Humboldt y BIC Jose Olaya Balandra 9808-09, de Paita a Tacna. Inf. Inst. del Mar del Perú 141, 136–155.

Castro Hernández, J., 1991. Ecología Trófica de la Caballa (Scomber japonicus Houttuyn, 1780), en Aguas del Archipiélago Canario. Universidad de las Palmas de Gran Canaria.

Castro Hernández, J., Santana Ortega, A., 2000. Sinopsis of biological data on the Chub mackerel (Scomber japonicus Houttuyn, 1782), First Edit. ed. FAO Fish Synop, Rome.

Castro, J.J., 1993. Feeding preferences of Scomber japonicus in the Canary Islands area. Sci. Mar. 13, 323–328.

Castro, J.J., Hernández-García, V., 1993. Ontogenetic changes in mouth structures , foraging behaviour and habitat use of Scomber japonicus and Illex coindetii. Sci. Mar. 59, 347–355.

Celik, M., 2008. Seasonal changes in the proximate chemical compositions and fatty acids of chub mackerel (Scomber japonicus) and horse mackerel (Trachurus trachurus) from the north eastern Mediterranean Sea. Int. J. Food Sci. Technol. 43, 933–938. doi:10.1111/j.1365-2621.2007.01549.x

Chaigneau, A., Dominguez, N., Eldin, G., Vasquez, L., Flores, R., Grados, C., Echevin, V., 2013. Near-coastal circulation in the Northern Humboldt Current System from shipboard ADCP data. J. Geophys. Res. Ocean. 118, 5251–5266. doi:10.1002/jgrc.20328

Chavez, F., Ryan, J., Lluch-Cota, S., Ñiquen, M., 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. Science 299, 217–21. doi:10.1126/science.1075880

Chavez, F.P., Bertrand, A., Guevara-Carrasco, R., Soler, P., Csirke, J., 2008. The northern Humboldt Current System: Brief history, present status and a view towards the future. Prog. Oceanogr. 79, 95–105. doi:10.1016/j.pocean.2008.10.012

Chavez, F.P., Messié, M., 2009. A comparison of Eastern Boundary Upwelling Ecosystems. Prog. Oceanogr. 83, 80–96. doi:10.1016/j.pocean.2009.07.032

Chavez, F.P., Messié, M., Pennington, J.T., 2011. Marine primary production in relation to climate variability and change. Ann. Rev. Mar. Sci. 3, 227–60. doi:10.1146/annurev.marine.010908.163917

Checkley, D.M., Oozeki, Y., Roy, C., 2009. Climate Change and Small Pelagic Fish Edited by.

Cherel, Y., Hobson, K. a, 2005. Stable isotopes, beaks and predators: a new tool to study the trophic ecology of cephalopods, including giant and colossal squids. Proc. Biol. Sci. 272, 1601–7. doi:10.1098/rspb.2005.3115

Chernyshkov, P., Timokhin, E., Glubokov, A., 2008. Interannual and seasonal variability of oceanological conditions in the Southern Pacific Ocean in connection with the pelagic ecosystem structure. Santiago.

Chipps, S.R., Garvey, J.E., 2007. Assessment of diets and feeding patterns. In: Analysis and interpretation of freshwater fisheries data, American Fisheries Society., in: Guy, C.S., Brown, M.L. (Eds.), Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society, Maryland, pp. 473–514.

Chirichigno, N., Cornejo, R., 2001. Catálogo comentado de los peces marinos del Perú.

Chong, J., Oyarzún, C., Galleguillos, R., Tarifeño, E., Sepúlveda, R., Ibáñez, C., 2005. Fishery biology parameters of jumbo squid, Dosidicus gigas (Orbigny, 1835) (Cephalopoda: Ommastrephidae), in central Chile coast (29^{o}S-40^{o}S) during 1993-1994. Gayana Zool. 69, 319–328.

Christensen, B., 1996. Predator foraging capabilities and prey antipredator behaviours: pre- versus postcapture constraints on size-dependent predator–prey interactions. OIKOS 76, 368–380.

Clarke, A., Gaston, K.J., 2006. Climate, energy and diversity. Biol. Sci. 273, 2257–2266.

Clarke, R., Paliza, O., Aguayo, A., 1988. Sperm whales of the southeast Pacific. Part IV: Fatness, food and feeding. Investig. Cetacea 21, 52–195.

Codispoti, L.A., 1981. Temporal nutrient variability in three different upwelling regions. Coast. Estuar. Sci. 1, 209–220.

Coker, R.E., 1910. Condiciones de la pesquería de Mollendo. Boletín del Minist. Fom. 8, 64–114.

Collette, B.B., Nauen, C.E., 1983. FAO Species Catalogue Vol . 2 Scombrids of the world an annotated and illustrated catalogue of Tunas, Mackerels, Bonitos and related species know to date. FAO Fish. Synopsis 2, 137.

Collins, C., Mascarenhas, A., Martinez, R., 2013. Structure of ocean circulation between the Galápagos Islands and Ecuador. Adv. Geosci. 33, 3–12. doi:10.5194/adgeo-33-3-2013

Córdova, 1998. Evaluación hidroacústica del recurso jurel en la ZEE de Chile. Valparaiso.

Cornejo, R., Koppelmann, R., 2006. Distribution patterns of mesopelagic fishes with special reference to Vinciguerria lucetia Garman 1899 (Phosichthyidae: Pisces) in the Humboldt Current Region off Peru. Mar. Biol. 149, 1519–1537. doi:10.1007/s00227-006-0319-z

Cosgrove, J.A., 2005. The first specimens of Humboldt squid in British Columbia. PICES 13, 30–31.

Croker, R.S., 1937. Further notes on the jumbo squid, Dosidicus gigas. Fish. Bull. 23, 246–247.

Csirke, J., 2013. The Jack mackerel Trachurus murphy in Peru. Rev. Peru. Biol. 20, 5–8.

Csirke, J., Guevara-Carrasco, R., Cárdenas, G., Niquen, M., Chipollini, A., 1996. Situación de los recursos Anchoveta (Engraulis Ringens) y Sardina (Sardinops sagax) a principios de 1994 y perspectivas para la pesca en el Perú, con particular preferencia a las regiones norte y centro de la costa peruana. Boletín del Inst. del Mar del Perú 15, 1–23.

Cubillos, L., Ibáñez, C., González, C., Sepúlveda, A., 2004. Pesca de investigación: Pesca de jibia (Dosidicus gigas) con red de cerco entre la V y X regiones, año 2003. Talcahuano.

Cury, P., Bakun, A., Crawford, R., Jarre, A., Quiñones, R., Shannon, L., Verheye, H., 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. ICES J. Mar. Sci. 57, 603–618. doi:10.1006/jmsc.2000.0712

Cury, P., Roy, C., 1989. Optimal Environmental Window and Pelagic Fish Recruitment Success in Upwelling Areas. Can. J. Fish. Aquat. Sci. 46, 670–680.

Cushing, D.H., 1971. Upwelling and the Production of Fish, in: Russell, F.S., Yonge, M. (Eds.), Advances in Marine Biology. Elsevier, London, pp. 255–300, 300a,301–334.

Czeschel, R., Stramma, L., Schwarzkopf, F.U., Giese, B.S., Funk, A., Karstensen, J., 2011. Middepth circulation of the eastern tropical South Pacific and its link to the oxygen minimum zone. J. Geophys. Res. 116, 1–13. doi:10.1029/2010JC006565

Daneri, G., Dellarossa, V., Quiñones, R., Jacob, B., Montero, P., Ulloa, O., 2000. Primary production and community respiration in the Humboldt Current System off Chile and associated oceanic areas. Mar. Ecol. Prog. Ser. 197, 41–49.

Dewitte, B., Vazquez-Cuervo, J., Goubanova, K., Illig, S., Takahashi, K., Cambon, G., Purca, S., Correa, D., Gutierrez, D., Sifeddine, A., Ortlieb, L., 2012. Change in El Niño flavours over 1958–2008: Implications for the long-term trend of the upwelling off Peru. Deep Sea Res. Part II Top. Stud. Oceanogr. 77-80, 143–156. doi:10.1016/j.dsr2.2012.04.011

Díaz, E., 2013. Estimation of growth parameters of Jack mackerel Trachurus murphyi caught in Peru , from length frequency analysis. Rev. Peru. Biol. 20, 61–66.

Diaz, R.J., Rosenberg, R., 2008. Spreading dead zones and consequences for marine ecosystems. Science 321, 926–9. doi:10.1126/science.1156401

Dioses, T., 1985. Influencia del Fenómeno "El Niño" 1982-83 en el Peso Total Individual de los Peces Pelágicos: Sardina, Jurel y Caballa. Boletín del Inst. del Mar del Perú Volumen Ex, 129–134.

Dioses, T., 2013. Age and growth of Jack mackerel Trachurus murphyi in Peru. Rev. Peru. Biol. 20, 45–52.

Dioses, T., Alarcon, V.H., Nakama, M.H., Echevarria, A., 1989. Oocyte development, partial fecundity and vertical distribution of the spawning schools of jack mackerel, Trachurus murphyi N., Revista de la Comision Permanente del Pacifico Sur.

Echevin, V., Aumont, O., Ledesma, J., Flores, G., 2008. The seasonal cycle of surface chlorophyll in the Peruvian upwelling system: A modelling study. Prog. Oceanogr. 79, 167–176. doi:10.1016/j.pocean.2008.10.026

Echevin, V., Aumont, O., Tam, J., Pasapera, J., 2004. The seasonal cycle of surface chlorophyll along the Peruvian coast: comparison between seawifs satellite observations and dynamical/biogeochemical coupled model simulations. Gayana 68, 325–326.

Ehrhardt, N.M., Jacquemin, P.S., García, B.F., Gonzáles, D.G., López, B.J.M., Ortiz, C.J., Solís, N.A., 1983. On the fishery and biology of the giant squid Dosidicus gigas in the Gulf of California, in: Caddy, J.F. (Ed.), Advances in Assessment of World Cephalopod Resources. FAO Fish Tech Pap, Rome, pp. 306–340.

Elizarov, A.. A., Grechina, A.S., Kotenev, B.N., Kuzetsov, A.N., 1993. Peruvian jack mackerel, Trachurus symmetricus murphyi, in the open waters of the South Pacific. J. Ichthyol. 33, 86–104.

Elliot, W., Paredes, F., 1996. Estructura especiológica del subsistema costero E/P San Jacinto I9512-9601. Inf. Inst. del Mar del Perú 121, 14–26.

Ermolovich, C.I., Gardina, L., 1994. Alimentación del Jurel, in: Arcos, D.F., Grechina, A.S. (Eds.), Biología Y Pesca Comercial Del Jurel En El Pacífico Sur. Instituto de Investigación Pesquera, Talcahuano, pp. 55–60.

Escribano, R., Hidalgo, P., Krautz, C., 2009. Zooplankton associated with the oxygen minimum zone system in the northern upwelling region of Chile during March 2000. Deep Sea Res. Part II Top. Stud. Oceanogr. 56, 1083–1094. doi:10.1016/j.dsr2.2008.09.009

Espino, M., 2013. The Jack mackerel Trachurus murphyi and the environmental macro-scale variables. Rev. Peru. Biol. 20, 9–20.

Espino, M., Yamashiro, C., 2012. Climate Variability and Fisheries in the southeastern Pacific. Lat. Am. J. Aquat. Res. 40, 705–721.

Espinoza, P., 2014. Trophic dynamics in the northern Humboldt Current system: insights from stable isotopes and stomach contents. L'UNIVERSITÉ DE BRETAGNE OCCIDENTALE.

Espinoza, P., Bertrand, a, 2014. Ontogenetic and spatiotemporal variability in anchoveta Engraulis ringens diet off Peru. J. Fish Biol. 84, 422–35. doi:10.1111/jfb.12293

Espinoza, P., Bertrand, A., 2008. Revisiting Peruvian anchovy (Engraulis ringens) trophodynamics provides a new vision of the Humboldt Current system. Prog. Oceanogr. 79, 215–227. doi:10.1016/j.pocean.2008.10.022

Espinoza, P., Bertrand, A., van der Lingen, C.D., Garrido, S., Rojas de Mendiola, B., 2009. Diet of sardine (Sardinops sagax) in the northern Humboldt Current system and comparison with the diets of clupeoids in this and other eastern boundary upwelling systems. Prog. Oceanogr. 83, 242–250. doi:10.1016/j.pocean.2009.07.045

Evseenko, S.A., 1987. Reproduction of the Peruvian jack mackerel Trachurus symmetricus murphyi in the South Pacific. J. Ichthyol. 27, 151–160.

FAO, 2014a. Global capture production 1950-2012 [WWW Document]. URL http://www.fao.org/figis/servlet/SQServlet?file=/work/FIGIS/prod/webapps/figis/temp/hqp_223624599080030770.xml&outtype=html (accessed 11.4.14).

FAO, 2014b. National fisheries sector overview Peru [WWW Document]. URL ftp://ftp.fao.org/Fi/DOCUMENT/fcp/en/FI_CP_PE.pdf (accessed 11.4.14).

Fiedler, P.C., 2002. Environmental change in the eastern tropical Pacific Ocean: review of ENSO and decadal variability. Mar. Ecol. Prog. Ser. 244, 265–283.

Field, J.C., Baltz, K.E.N., Walker, W.A., 2007. Range expansion and trophic interactions of the jumbo squid, Dosidicus gigas, in the California current. Calif. Coop. Ocean. Fish. Investig. Reports 48, 131–146.

Field, J.C., Elliger, C., Baltz, K., Gillespie, G.E., Gilly, W.F., Ruiz-Cooley, R.I., Pearse, D., Stewart, J.S., Matsubu, W., Walker, W. a., 2013. Foraging ecology and movement patterns of jumbo squid (Dosidicus gigas) in the California Current System. Deep Sea Res. Part II Top. Stud. Oceanogr. 95, 37–51. doi:10.1016/j.dsr2.2012.09.006

Fitch, J.E., Brownell, R.L., 1968. Fish Otoliths in Cetacean Stomachs and Their Importance in Interpreting Feeding Habits. Fish. Res. 25, 2561–2574.

Flores, R., Espino, M., Luque, G., 2013. Environmental variability patterns in the Peruvian waters. Rev. Peru. Biol. 20, 21–28.

Frank, K.T., Petrie, B., Shackell, N.L., 2007. The ups and downs of trophic control in continental shelf ecosystems. Trends Ecol. Evol. 22, 236–242.

Frank, T., Widder, E., 2002. Effects of a decrease in downwelling irradiance on the daytime vertical distribution patterns of zooplankton and micronekton. Mar. Biol. 140, 1181–1193.

Fréon, P., Barange, M., Arístegui, J., 2009. Eastern Boundary Upwelling Ecosystems: Integrative and comparative approaches. Prog. Oceanogr. 83, 1–14. doi:10.1016/j.pocean.2009.08.001

Fréon, P., Bouchon, M., Mullon, C., García, C., Ñiquen, M., 2008. Interdecadal variability of anchoveta abundance and overcapacity of the fishery in Peru. Prog. Oceanogr. 79, 401–412. doi:10.1016/j.pocean.2008.10.011

Fréon, P., Cury, P., Shannon, L., Roy, C., 2005. Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: a review 76, 385–462.

Fuenzalida, R., Schneider, W., Garcés-Vargas, J., Bravo, L., Lange, C., 2009. Vertical and horizontal extension of the oxygen minimum zone in the eastern South Pacific Ocean. Deep Sea Res. Part II Top. Stud. Oceanogr. 56, 992–1003. doi:10.1016/j.dsr2.2008.11.001

Gallardo, V.A., 1977. Large benthic microbial communities in sulphide biota under Peru—Chile subsurface countercurrent. Nature 268, 331–332.

García-Godos Naveda, I., 2001. Patrones morfológicos del otolito sagitta de algunos peces óseos del mar peruano. Boletín del Inst. del Mar del Perú 20, 1–84.

Genin, A., 2004. Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. J. Mar. Syst. 50, 3–20. doi:10.1016/j.jmarsys.2003.10.008

Gerlotto, F., Bertrand, S., Bez, N., Gutierrez, M., 2006. Waves of agitation inside anchovy schools observed with multibeam sonar: a way to transmit information in response to predation. ICES J. Mar. Sci. 63, 1405–1417. doi:10.1016/j.icesjms.2006.04.023

Gerlotto, F., Gutiérrez, M., Bertrand, A., 2012. Insight on population structure of the Chilean jack mackerel (Trachurus murphyi). Aquat. Living Resour. 25, 341–355. doi:10.1051/alr/2012036

Gilly, W., Markaida, U., Baxter, C., Block, B., Boustany, A., Zeidberg, L., Reisenbichler, K., Robison, B., Bazzino, G., Salinas, C., 2006. Vertical and horizontal migrations by the jumbo squid Dosidicus gigas revealed by electronic tagging. Mar. Ecol. Prog. Ser. 324, 1–17. doi:10.3354/meps324001

Gilly, W.F., 2005. Spreading and stranding of jumbo squid. Ecosystems Observations for the Monterrey Bay National Marine Sanctuary 2005 [WWW Document]. URL http://www.montereybay.noaa.gov/reports/2005/eco/harvestedsp.html (accessed 11.12.14).

Gilly, W.F., Zeidberg, L.D., Booth, J.A.T., Stewart, J.S., Marshall, G., Abernathy, K., Bell, L.E., 2012. Locomotion and behavior of Humboldt squid, Dosidicus gigas, in relation to natural hypoxia in the Gulf of California, Mexico. J. Exp. Biol. 215, 3175–90. doi:10.1242/jeb.072538

Graco, M., Ledesma, J., Flores, G., Girón, M., Calienes, R., Guillén, O., Lostaunau, N., 2007. Nutrients, oxygen and biogeochemical processes in the Humboldt upwelling current system off Peru Nutrientes , oxígeno y procesos biogeoquímicos en el sistema de surgencias de la corriente de Humboldt frente a Perú. Rev. peru. biol 14, 117–128.

Grechina, F.A., 1998. Historia de investigaciones y aspectos básicos de la ecología del jurel Trachurus symmetricus murphyi (Nichols) en alta mar del Pacífico Sur, in: Arcos, D. (Ed.), Biología Y Ecología Del Jurel En Aguas Chilenas. Instituto de Investigación Pesquera, Concepción, pp. 11–34.

Guillén, O., Calienes, R., De Roldán, R., 1977. Medio Ambiente y Producción Primaria frente al Área Pimentel - Chimbote. Boletín del Inst. del Mar del Perú 3-4, 108–159.

Gutiérrez, D., Arónes, K., Chang, F., Quipúzcoa, L., Villanueva, P., 2005. Impacto de la variación oceanográfica estacional e interanual sobre los ensambles de microfitoplancton, mesozooplancton, ictioplancton y macrozoobentos de dos áreas costeras del norte del Perú entre 1994 y 2002. Boletín del Inst. del Mar del Perú 22, 3–60.

Gutiérrez, D., Bertrand, A., Wosnitza-mendo, C., Dewitte, B., Purca, S., Peña, C., Chaigneau, A., Graco, M., Echevin, V., Grados, C., 2011. Climate change sensitivity of the Peruvian upwelling system and ecological implications. Rev. Peru. Geo-Atmosférica 3, 1–26.

Gutiérrez, D., Enríquez, E., Purca, S., Quipúzcoa, L., Marquina, R., Flores, G., Graco, M., 2008. Oxygenation episodes on the continental shelf of central Peru: Remote forcing and benthic ecosystem response. Prog. Oceanogr. 79, 177–189. doi:10.1016/j.pocean.2008.10.025

Gutiérrez, D., Sifeddine, A., Field, D., Ortlieb, L., Vargas, G., Chávez, F., Velazco, F., Ferreira, V., Tapia, P., Salvatteci, R., Boucher, H., Morales, M.C., Valdés, J., Reyss, J.L., Campusano, A., Boussafir, M., Mandeng-Yogo, M., García, M., Baumgartner, T., 2009. Rapid reorganization in ocean biogeochemistry off Peru towards the end of the Little Ice Age. Biogeosciences 6, 835–848.

Gutierrez, M., 2002. A technical and scientific approach about needs of new sustainable fisheries. Callao.

Gutiérrez, M., Bertrand, A., Ballón, M., Espinoza, P., Alegre, A., Gerlotto, F., 2008a. Distribution changes and interactions of Jack Mackerel off Peru as observed using acoustics (1983-2008). Santiago de Chile.

Gutiérrez, M., Castillo, R., Segura, M., Peraltilla, S., Flores, M., 2012. Trends in spatio-temporal distribution of Peruvian anchovy and other small pelagic fish biomass from 1966-2009 Tendencias espacio-temporales en la distribución de la biomasa de anchoveta peruana y de otros peces pelágicos pequeños entre 1966 y 2009. J. Aquat. Res 40, 633–648.

Gutiérrez, M., Peraltilla, S., 2008. Evaluación acústica de la distribución y abundancia de especies pelágicas y mesopelágicas en invierno 2004. Inf. Inst. del Mar del Perú 35, 129–140.

Gutiérrez, M., Ramirez, A., Bertrand, S., Móron, O., Bertrand, A., 2008b. Ecological niches and areas of overlap of the squat lobster "munida" (Pleuroncodes monodon) and anchoveta (Engraulis ringens) off Peru. Prog. Oceanogr. 79, 256–263. doi:10.1016/j.pocean.2008.10.019

Guzman, O., Castillo, J., Lillo, S., Pineda, P., Rodriguez, Giakoni, I., 1983. Estudio de recursos pelágicos. Programa monitoreo de los recursos pelágicos. I. Prospección zona Arica–Coquimbo. (18°30′–30°00′S). Valparaiso.

Helly, J.J., Levin, L. a, 2004. Global distribution of naturally occurring marine hypoxia on continental margins. Deep Sea Res. Part I Oceanogr. Res. Pap. 51, 1159–1168. doi:10.1016/j.dsr.2004.03.009

Hernández, J., 1991. Ecología trófica de la caballa (Scomber japonicus, Houttuyn, 1780) en aguas del archipiélago canario. Universidad de Las Palmas de Gran Canaria.

Herzka, S.Z., 2005. Assessing connectivity of estuarine fishes based on stable isotope ratio analysis. Estuar. Coast. Shelf Sci. 64, 58–69. doi:10.1016/j.ecss.2005.02.006

Huyer, A., Knoll, M., Paluszkiewicz, T., Smith, R.L., 1991. The Peru Undercurrent: a study in variability. Deep Sea Res. Part A. Oceanogr. Res. Pap. 38, S247–S271. doi:10.1016/S0198-0149(12)80012-4

Huyer, A., Smith, R.L., Paluszkiewicz, T., 1987. Coastal Upwelling off Peru During Normal and E1 Nifio Times, 1981-1984. J. Geophys. Res. 92, 1981–1984.

Hyslop, E.J., 1980. Stomach contents analysis-a review of methods and their application. J. Fish Biol. 17, 411–429. doi:10.1111/j.1095-8649.1980.tb02775.x

Ibáñez, C.M., 2013. Ecological impact of Dosidicus gigas over hake populations in the eastern Pacific Ocean. Amici Molluscarum 21, 7–16.

Ibáñez, C.M., Arancibia, H., Cubillos, L. a., 2008. Biases in determining the diet of jumbo squid Dosidicus gigas (D′ Orbigny 1835) (Cephalopoda: Ommastrephidae) off southern-central Chile (34°S–40°S). Helgol. Mar. Res. 62, 331–338. doi:10.1007/s10152-008-0120-0

Ibáñez, C.M., Keyl, F., 2009. Cannibalism in cephalopods. Rev. Fish Biol. Fish. 20, 123–136. doi:10.1007/s11160-009-9129-y

Jereb, P., Roper, C., 2010. Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Vol. 2, Myopsid and Oegopsid Squids. FAO Fish. Synop, Rome.

Kao, H.-Y., Yu, J.-Y., 2009. Contrasting Eastern-Pacific and Central-Pacific Types of ENSO. J. Clim. 22, 615–632. doi:10.1175/2008JCLI2309.1

Kawahara, S., Uozumi, Y., Yamada, H., 1988. Fisrt record of a carangid fish,Trachurus murphyi from New Zealand. Japanese J. Ichthyol. 35, 212–214.

Kessler, W.S., 2006. The circulation of the eastern tropical Pacific: A review. Prog. Oceanogr. 69, 181–217. doi:10.1016/j.pocean.2006.03.009

Keyl, F., Argüelles, J., Tafur, R., 2010. Interannual variability in size structure , age , and growth of jumbo squid (Dosidicus gigas) assessed by modal progression analysis. ICES J. Mar. Sci. 68, 507–518.

Kinzer, J., Schulz, K., 1985. Vertical distribution and feeding patterns of midwater fish in the central equatorial Atlantic. Mar. Biol. 85, 313–322.

Konchina, Y. V, 1982. Feeding of the Pacifie Mackerel , Scomber japonicus (Scombridae), Near the Peruviah Coast, Marine Fisheries and oceanography Research Institute. Moscow.

Konchina, Y. V, 1990. Feeding Ecology of Pseudoneritic Fishes on the Nasca Ridge. Vopr. ikhtiologii 30, 983–993.

Konchina, Y. V, 1993. Trophic Status of Peruvian Pseudoneritic Fish in Oceanic Epipelagic Water. Vopr. ikhtiologii 32, 67–82.

Konchina, Y. V., 1981. The Peruvian jack mackerel, Trachurus symmetricus murphyi, a facultative predator in the coastal upwelling ecosystem. J. Ichthyol. 21, 46–59.

Konchina, Y. V., 1992. Trophic status of Peruvian pseudoneritic fish in oceanic epipelagic water. J. Ichthyol. 32, 20–39.

Konchina, Y., Nesin, A., Onishchik, N., Pavlov, Y., 1996. On the Migration and Feeding of the Jack Mackerel Trachurus symmetricus murphyi in the Eastern Pacific. J. Ichthyol. 36, 793–803.

Kotenev, B.N., Kukhorenko, K.G., Glubokov, A.I., 2006. Main results of the Russian multidisciplinary ecosystem research, and exploratory fish-finding of concentrations of hydrobionts and their fisheries development in the south Pacific. Moscow.

Kug, J.-S., Jin, F.-F., An, S.-I., 2009. Two Types of El Niño Events: Cold Tongue El Niño and Warm Pool El Niño. J. Clim. 22, 1499–1515. doi:10.1175/2008JCLI2624.1

Kuhnert, P.M., Duffy, L.M., Young, J.W., Olson, R.J., 2011. Predicting fish diet composition using a bagged classification tree approach: a case study using yellowfin tuna (Thunnus albacares). Mar. Biol. 159, 87–100. doi:10.1007/s00227-011-1792-6

Le Cren, E.D., 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (Perca fluviatilis). J. Anim. Ecol. 20, 201–219.

Levin, L.A., 2003. Oxygen minimum zone benthos: adaptations and community response to hypoxia. Ocean. Mar. Biol. Ann. Rev 41, 1–45.

Liu, B., Chen, X., Lu, H., Chen, Y., Qian, W., 2010. Fishery biology of the jumbo flying squid *Dosidicus gigas* off the Exclusive Economic Zone of Chilean waters. Sci. Mar. 74, 687–695. doi:10.3989/scimar.2010.74n4687

Lorrain, A., Argüelles, J., Alegre, A., Bertrand, A., Munaron, J.-M., Richard, P., Cherel, Y., 2011. Sequential Isotopic Signature Along Gladius Highlights Contrasted Individual Foraging Strategies of Jumbo Squid (Dosidicus gigas). PLoS One 6, e22194.

Lukas, R., 1986. The termination of the equatorial undercurrent in the eastern Pacific. Prog. Ocean. 16, 63–90.

Lundvall, D., Svanbäck, R., Persson, L., Byström, P., 1999. Size-dependent predation in piscivores: interactions between predator foraging and prey avoidance abilities. Can J Fish Aquat Sci 56, 1285–1292.

Lundvall, D., Svanbäck, R., Persson, L., Byström, P., 1999. Size-dependent predation in piscivores: interactions between predator foraging and prey avoidance abilities. Can. J. Fish. Aquat. Sci. 56, 1285–1292. doi:10.1139/cjfas-56-7-1285

Mackas, D.L., Kieser, R., Saunders, M., Yelland, D.R., Brown, R.M., Moore, D.F., 1997. Aggregation of euphausiids and Pacific hake (Merluccius productus) along the outer continental shelf off Vancouver Island. Can. J. Fish. Aquat. Sci. 54, 2080–2096. doi:10.1139/f97-113

Mangold, K., 1987. Reproduction, in: Boyle, P.R. (Ed.), Cephalopod Life Cycles, Comparative Reviews. Springer, London, pp. 157–200.

Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., Francis, R.C., 1997. A Pacific Interdecadal Climate Oscillation with Impacts on Salmon Production. Bull. Am. Meteorol. Soc. 78, 1069–1079.

Mapukata, T., 2002. Laboratory studies on the feeding behaviour of juvenile cape horse mackerel Trachurus trachurus capensis. University of Cape Town.

Maridueña, L.S., Menz, A., 1986. Caballa, Scomber japonicus Houttuyn, 1780. En: Bases Biológicas y Marco Conceptual para el Manejo de los Recursos Pelágicos en el Pacífico Suroriental, in: Bases Biológicas Y Marco Conceptual Para El Manejo de Los Recursos Pelágicos En El Pacífico Suroriental.

Markaida, U., 2001. Biología del calamar gigante Dosidicus gigas Orbigny, 1835 (cephalopoda: ommastrephidae) en el Golfo de California, México.

Markaida, U., 2006. Food and feeding of jumbo squid Dosidicus gigas in the Gulf of California and adjacent waters after the 1997–98 El Niño event. Fish. Res. 79, 16–27. doi:10.1016/j.fishres.2006.02.016

Markaida, U., Gilly, W.F., Salinas-Zavala, C.A., Rosas-Luis, R., Booth, J.A.T., 2008. Food and feeding of jumbo squid Dosidicus gigas in the central gulf of California during 2005 – 2007. CalCOFI Rep. 49, 90–103.

Markaida, U., Rosenthal, J.J.C., Gilly, W.F., 2005. Tagging studies on the jumbo squid (Dosidicus gigas) in the Gulf of California , Mexico. Fish. Bull. 103, 219–226.

Markaida, U., Sosa-Nishizaki, O., 2003. Food and feeding habits of jumbo squid Dosidicus gigas (Cephalopoda: Ommastrephidae) from the Gulf of California, Mexico. J. Mar. Biol. Assoc. UK 83, 507–522. doi:10.1017/S0025315403007434h

Martinez, C., Bohm, G., Cerna, F., Días, E., Muñóz, P., Aranis, A., Caballero, L., Aravena, R., Ossa, L., 2006. Estudio biológico-pesquero de la caballa entre la I-X Regiones.

Matsui, T., 1967. Review of the mackerel genera Scomber and Rastrelliger with description of a new species of Rastrelliger. Copeia 1, 71–83.

McClatchie, S., Dunford, A., 2003. Estimated biomass of vertically migrating mesopelagic fish off New Zealand. Deep. Res. Part I 50, 1263–1281.

McCullagh, P., Nelder, J.A., 1989. Generalized Linear Models, Second Edi. ed. Chapman and Hall, London.

Medina, M., Arancibia, H., 1992. Trophic interactions between horse mackerel (Trachurus murphyi) and mackerel (Scomber japonicus) in the pelagic environment off north Chile. Invest. Cient. y Tec. 2, 67–78.

Medina, M., Arancibia, H., 1998. Prey size selection in horse mackerel (Trachurus symmetricus murphyi) and mackerel (Scomber japonicus) off northern Chile. Rev. Investig. en Cienc. y Tecnol. 4, 35–41.

Medina, M., Arancibia, H., 2002. Dinámica trófica del jurel (Trachurus symmetricus murphyi) en el norte de Chile. Investig. Mar. Valparaiso 30, 45–55.

Menard, F., Marchal, E., 2003. Foraging behaviour of tuna feeding on small schooling Vinciguerria nimbaria in the surface layer of the equatorial Atlantic Ocean. Aquat. Living Resour. 16, 231–238. doi:10.1016/S0990-7440(03)00040-8

Mendo, J., 1984. Edad, crecimiento y algunos aspectos reproductivos y alimentarios de la caballa (Scomber japonicus peruanus). Boletín del Inst. del Mar del Perú 8, 105–144.

Michel, G.E., Klett, A., Ochoa, R.I., 1986. Estudio preliminar para la determinación gonádica del calamar gigante Dosidicus gigas (D'Orbigny 1835). Cienc. Pesq. 5, 77–89.

Miller, T.W., Brodeur, R.D., Rau, G.H., 2008. Carbon stable isotopes reveal relative contribution of shelf-slope production to the Northern California Current pelagic community. Limnol. Oceanogr. 53, 1493–1503. doi:10.4319/lo.2008.53.4.1493

Miranda, L., Hernández, A.F., Sepúlveda, A.O., Landaeta, M., 1998. Alimentación del jurel y análisis de la selectividad en la zona centro - sur de Chile, in: Arcos, D.F. (Ed.), Biología Y Ecología Del Jurel En Aguas Chilenas. Instituto de Investigación Pesquera, Talcahuano, pp. 173–187.

Mollier-Vogel, E., Ryabenko, E., Martinez, P., Wallace, D., Altabet, M., Schneider, R., 2012. Nitrogen isotope gradients off Peru and Ecuador related to upwelling , productivity, nutrient uptake and oxygen deficiency. Deep Sea Res. Part I Oceanogr. Res. Pap. 70, 14–25.

Montes, I., Colas, F., Capet, X., Schneider, W., 2010. On the pathways of the equatorial subsurface currents in the eastern equatorial Pacific and their contributions to the Peru-Chile Undercurrent. J. Geophys. Res. 115, 1–16. doi:10.1029/2009JC005710

Muck, P., Sánchez, G., 1987. The importance of mackerel and horse mackerel predation for the Peruvian anchoveta stock (a population and feeding model)., in: Pauly, D., Tsukayama, I. (Eds.), The Peruvian Anchoveta and Its Upwelling Ecosystem: Three Decades of Change. ICLARM Studies and Reviews, p. 351.

Nesis, K.N., 1970. The biology of the giant squid of Perú and Chile, Dosidicus gigas. Oceanology 10, 108–118.

Nesis, K.N., 1979. Squids of the family Ommastrephidae in the Australian–New Zealand region. Tr. Instituta Okeanol. im. P.P. Shirshova Akad. Nauk SSSR 106, 140–146.

Nesis, K.N., 1983. Dosidicus gigas. Cephalopod Life Cycles. Academic Press, London.

Nesis, K.N., 1985. Oceanic cephalopods: Distribution, life forms, evolution. Nauka, Moscow.

Newel, 1963. Marine plankton a practical guide. Hutchison Biological Monographs.

Nigmatullin, C.M., 1979. Main stages of the evolutionof the squid family Ommastrephidae (Cephalopoda, Oegopsida), in: Wagin, Ed. Problems of Evolutionary Morphology, Kazan. University Press, Kazan, pp. 210–219.

Nigmatullin, C.M., Nesis, K.N., Arkhipkin, A.I., 2001. A review of the biology of the jumbo squid Dosidicus gigas (Cephalopoda : Ommastrephidae). Fish. Res. 54, 9–19.

Ñiquen, M., Bouchon, M., Cahuin, S., Díaz, E., 2000. Pesquería de anchoveta en el mar peruano 1950 - 1999. Boletín del Inst. del Mar del Perú 19, 117–124.

Ñiquen, M., Bouchon, M., Ulloa, D., Medina, A., 2013. Analysis of the Jack mackerel Trachurus murphyi fishery in Peru. Rev. Peru. Biol. 20, 97–106.

Ñiquen, M., Peña, C., 2008. Distribution and Concentration of Jack Mackerel (Trachurus Murphyi) Related to Oceanographical Features between North Peru to North Chile.

O'Connell, C.P., Zweifel, J.R., 1972. A laboratory study of particulate and filter feeding of the pacific mackerel, Scomber japonicus. Fish. Bull. 70, 973–981.

Ochoa-Báez, R.I., 1982. Estudio preliminar del sistema reproductor del "calamar gigante" del Golfo de Baja California Dosidicus gigas (D'Orbigny, 1835) Mollusca: Cephalopoda. CIBCASIO 6, 187–198.

Oliveros, R., 2014. End to end modelling for an ecosystem approach to fisheries in the Northern Humboldt Current Ecosystem. l'Université de Montpellier.

Pardo, A.S., Oliva, J.L., 1992. Estimación de la talla de primera madurez de caballa (Scomber japonicus peruanus) en la zona norte de Chile durante el período de máxima actividad reproductiva. Invest. Pesq. 37, 97–106.

Paulmier, a., Ruiz-Pino, D., 2009. Oxygen minimum zones (OMZs) in the modern ocean. Prog. Oceanogr. 80, 113–128. doi:10.1016/j.pocean.2008.08.001

Pauly, D., 2012. Gasping Fish and Panting Squids: Oxygen, Temperature and the Growth of Water-Breathing Animals. Fish Fish. 13, 359–359. doi:10.1111/j.1467-2979.2012.00461.x

Pauly, D., Muck, P., Mendo, J., Tsukayama, I., 1989. The Peruvian Upwelling Ecosystem Dynamics and Interactions. Callao.

Pennington, J.T., Mahoney, K.L., Kuwahara, V.S., Kolber, D.D., Calienes, R., Chavez, F.P., 2006. Primary production in the eastern tropical Pacific: A review. Prog. Oceanogr. 69, 285–317. doi:10.1016/j.pocean.2006.03.012

Penven, P., Echevin, V., Passapera, J., Colas, F., Tam, J., 2005. Average circulation, seasonal cycle, and mesoscale dynamics of the Peru Current System: A modeling approach. J. Geophys. Res. 110, C10021. doi:10.1029/2005JC002945

Perea, Á., Mori, J., Buitrón, B., Sánchez, J., 2013. Reproductive aspects of Jack mackerel Trachurus murphy. Rev. Peru. Biol. 20, 29–34.

Philander, S.G.H., 1973. Equatorial Undercurrent : Measurements and theories. Rev. Geophys. 11, 513–570.

Pikitch, E.K., Rountos, K.J., Essington, T.E., Santora, C., Pauly, D., Watson, R., Sumaila, U.R., Boersma, P.D., Boyd, I.L., Conover, D.O., Cury, P., Heppell, S.S., Houde, E.D., Mangel, M., Plagányi, É., Sainsbury, K., Steneck, R.S., Geers, T.M., Gownaris, N., Munch, S.B., 2014. The global contribution of forage fish to marine fisheries and ecosystems. Fish Fish. 15, 43–64. doi:10.1111/faf.12004

Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methos, and assumptions. . Ecology 83, 703–718. doi:Doi 10.2307/3071875

Potier, M., Marsac, F., Cherel, Y., Lucas, V., Sabatié, R., Maury, O., Ménard, F., 2007. Forage fauna in the diet of three large pelagic fishes (lancetfish, swordfish and yellowfin tuna) in the western equatorial Indian Ocean. Fish. Res. 83, 60–72. doi:10.1016/j.fishres.2006.08.020

Potier, M., Romanov, E., Cherel, Y., Sabatié, R., Zamorov, V., Ménard, F., 2008. Spatial distribution of Cubiceps pauciradiatus (Perciformes : Nomeidae) in the tropical Indian Ocean and its importance in the diet of large pelagic fishes. Aquat. Living Resour. 21, 123–134.

Rahm, G., 1937. Zoologische Probleme an der südamerikanischen westküste besonders über das Massensterber em Pazifik, Cong Int Zool. Lisboa.

Rasero, M., Gonzáles, A.F., Castro, B.G., Guerra, A., 1996. Predatory relationship of two sympatric squid, Todaropsis eblanae and Illex coindetti (Cephalopoda: Ommastrephidae) in Galician waters. J. Mar. Biol. Assoc. UK 76, 73–87.

Rasmusson, E.M., Carpenter, T.H., 1982. Variations in Tropical Sea Surface Temperature ans Surface Wind Fields Associated with the Sourthern Oscillation/El Niño. Mon. Weather Rev. 110, 354–384.

Reynolds, R.W., Smith, T.M., Liu, C., Chelton, D.B., Casey, K.S., Schlax, M.G., 2007. Daily High-Resolution Blended Analyses for Sea Surface Temperature. J. Clim. 20, 5473–5496.

Ridgway, K.R., Dunn, J.R., Wilkin, J.L., 2002. Ocean Interpolation by Four-Dimensional Weighted Least Squares — Application to the Waters around Australasia. J. Atmos. Ocean. Technol. 19, 1357–1375.

Rocha, F., Vega, M.A., 2003. Overview of cephalopod fisheries in Chilean waters. Fish. Res. 60, 151–159. doi:10.1016/S0165-7836(02)00080-2

Rodhouse, P.G., Nigmatullin, C.M., 1996. Role as consumers. Philos. Trans. R. Soc. London Brithany 351, 1003–1022.

Rojas de Mendiola, B., 1981. Seasonal phytoplankton distribution along the Peruvian coast. Coast. Estuar. Sci. 1, 348–356.

Rojas de Mendiola, B., Ochoa, N., Calienes, R., Gómez, O., 1969. Contenido Estomacal de Anchoveta en Cuatro Áreas de la Costa Peruana. Inf. Inst. del Mar del Perú 27, 1–30.

Roper, C., Sweeney, M., Nauen, C., 1984. Cephalopods of the World. An annotated and illustrated catalogue of especies of interest to fisheries. FAO Fish. Synopsis 125, 277.

Rosa, R., Seibel, B. a, 2008. Synergistic effects of climate-related variables suggest future physiological impairment in a top oceanic predator. Proc. Natl. Acad. Sci. U. S. A. 105, 20776–80. doi:10.1073/pnas.0806886105

Rosa, R., Seibel, B.A., 2010. Metabolic physiology of the Humboldt squid, Dosidicus gigas: Implications for vertical migration in a pronounced oxygen minimum zone. Prog. Oceanogr. 86, 72–80.

Rosas-Luis, R., 2007. Descripción de la alimentación del calamar gigante Dosidicus gigas d´Orbigny, 1835 en la costa occidental de la península de Baja California. Centro de Investigaciones Biológicas del Noroeste, S. C.

Rosas-Luis, R., Salinas-Zavala, C. a., Koch, V., Luna, P.D.M., Morales-Zárate, M.V., 2008. Importance of jumbo squid Dosidicus gigas (Orbigny, 1835) in the pelagic ecosystem of the central Gulf of California. Ecol. Modell. 218, 149–161. doi:10.1016/j.ecolmodel.2008.06.036

Rosas-Luis, R., Tafur-Jimenez, R., Alegre-Norza, A.R., Castillo-Valderrama, P.R., Cornejo-Urbina, R.M., Salinas-Zavala, C.A., Sánchez, P., 2011. Trophic relationships between the jumbo squid (Dosidicus gigas) and the lightfish (Vinciguerria lucetia) in the Humboldt Current System off Peru. Sci. Mar. 75, 549–557.

Ruiz-Cooley, R., Villa, E., Gould, W., 2010. Ontogenetic variation of δ13C and δ15N recorded in the gladius of the jumbo squid Dosidicus gigas: geographic differences. Mar. Ecol. Prog. Ser. 399, 187–198. doi:10.3354/meps08383

Ruiz-Cooley, R.I., Markaida, U., Gendron, D., Aguíñiga, S., 2006. Stable isotopes in jumbo squid (Dosidicus gigas) beaks to estimate its trophic position: comparison between stomach contents and stable isotopes. J. Mar. Biol. Assoc. United Kingdom 86, 437–445.

Russell, R.W., Hunt, G.L., Coyle, K.O., Cooney, R.T., 1992. Foraging in a fractal environment: Spatial patterns in a marine predator-prey system. Landsc. Ecol. 7, 195–209. doi:10.1007/BF00133310

Ryther, J.H., 1969. Photosynthesis and fish production in the sea. Science 166, 72–6.

Salvatteci, R., 2013. Multi-decadal to millennial scale variability in Oxygen Minimum Zone intensity, export production and pelagic fish abundances from marine laminated sediments off Pisco, Peru during the last 25 000 years. l'UNIVERSITÉ PIERRE ET MARIE CURIE.

Salvatteci, R., Gutiérrez, D., Field, D., Sifeddine, A., Boussafir, M., Ortlieb, L., 2011. Multi-decadal to centennial-scale changes in fish scale deposition from marine laminated sediments off Pisco, Peru. Búzios.

Sánchez de Benites, G., Alamo, A., Fuentes, H., 1985. Alteraciones en la Dieta Alimentaria de Algunos Peces Comerciales por el Efecto del Fenómeno "El Niño." Boletín del Inst. del Mar del Perú Volumen Ex, 135–142.

Sánchez de Benites, G., Muck, P., 1987. La situacion alimentaria del Jurel Trachurus murphry Nichols en un año normal (1979) y en el niño 1982/83. Boletín del Inst. del Mar del Perú 11, 152–177.

Sánchez, J., Perea, Á., Buitrón, B., Romero, L., 2013. Scale of gonad maturity stages of Jack mackerel Trachurus murphyi Nichols 1920. Rev. Peru. Biol. 20, 35–44.

Sánchez, J.A., 2011. Escala de madurez gonadal y fecundidad de Dosidicus gigas (D'Orbigny; 1835) (Mollusca: Cephalopoda) "calamar gigante" o "pota." Universidad Nacional Federico Villarreal.

Sánchez, S., 2000. Variación estacional e interanual de la biomasa fitoplanctónica y concentraciones de clorofila A, frente a la costa peruana durante 1976 -2000. Boletín del Inst. del Mar del Perú 19, 29–44.

Santander, H., 1981. Patrones de distribución y fluctuaciones de desoves de anchoveta y sardina. Boletín del Inst. del Mar del Perú Vol. Extr., 180–192.

Santander, H., Flores, R., 1983. Los desoves y distribución larval de ciertas especies pelágicas y sus relaciones con las variaciones del ambiente marino frente al Perú, in: Sharp, G.D., Csirke, J. (Eds.), Actas de La Consulta de Expertos Para Examinar Los Cambios En La Abundancia Y Composición Por Especies de Recursos de Peces Neríticos. FAO Fish. Rep., San José de Costa Rica, p. 553.

Sassa, C., Kawaguchi, K., Kinoshita, T., Watanabe, C., 2002. Assemblages of vertical migratory mesopelagic fish in the transitional region of the western North Pacific. Fish. Oceanogr. 11, 193–204.

Scharf, F.S., Juanes, F., Rountree, R. a., 2000. Predator size - Prey size relationships of marine fish predators: Interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Mar. Ecol. Prog. Ser. 208, 229–248. doi:10.3354/meps208229

Schmiede, P., Acuña, A., 1992. Regreso de las jibias (Dosidicus gigas) a Coquimbo. Rev. Chil. Hist. Nat. 65, 389–390.

Seibel, B. a, 2011. Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones. J. Exp. Biol. 214, 326–36. doi:10.1242/jeb.049171

Seibel, B. a., 2013. The jumbo squid, Dosidicus gigas (Ommastrephidae), living in oxygen minimum zones II: Blood–oxygen binding. Deep Sea Res. Part II Top. Stud. Oceanogr. 95, 139–144. doi:10.1016/j.dsr2.2012.10.003

Serra, R., 1991. Important life history aspects of the Chilean jack mackerel, Trachurus symmetricus murphyi. Invest. Pesq. 36, 67–83.

Serra, R., Rojas, O., Aguayo, M., 1982. Caballa, Scomber japonicus peruanus Jordan y Hubbs, in: Estado Actual de Las Principales Pesquerías Nacionales. Bases Para Un Desarrollo Pesquero. IFOP, Santiago de Chile.

Shchetinnikov, A.S., 1989. Food spectrum of Dosidicus gigas (Oegopsida) in the ontogenesis. Zool. Zhu. 68, 28–39.

Sifeddine, a., Gutiérrez, D., Ortlieb, L., Boucher, H., Velazco, F., Field, D., Vargas, G., Boussafir, M., Salvatteci, R., Ferreira, V., García, M., Valdés, J., Caquineau, S., Mandeng Yogo, M., Cetin, F., Solis, J., Soler, P., Baumgartner, T., 2008. Laminated sediments from the central Peruvian continental slope: A 500 year record of upwelling system productivity, terrestrial runoff and redox conditions. Prog. Oceanogr. 79, 190–197. doi:10.1016/j.pocean.2008.10.024

Silva, N., Neshybat, S., 1979. On the southernmost extension of the Peru-Chile Undercurrent. Deep Sea Res. 26, 1387–1393.

Simard, Y., Mackas, D.L., 1989. Mesoscale Aggregations of Euphausiid Sound Scattering Layers on the Continental Shelf of Vancouver Island. Can. J. Fish. Aquat. Sci. 46, 1238–1249.

Sobarzo, M., Figueroa, M., Djurfeldt, L., 2001. Upwelling of subsurface water into the rim of the Biobio submarine canyon as a response to surface winds. Cont. Shelf Res. 21, 279–299. doi:10.1016/S0278-4343(00)00082-0

Sokal, R.R., Rohlf, F.J., 1995. Biometry. The Principles and Practice of Statistics in Biological Research, Third Edit. ed. Freeman and Company, New York.

Spencer, P.D., Collie, J.S., 1997. Patterns of population variability in marine fish stocks. Fish. Oceanogr. 6, 188–204.

Stramma, L., Johnson, G.C., Sprintall, J., Mohrholz, V., 2008. Expanding oxygen-minimum zones in the tropical oceans. Science 320, 655–8. doi:10.1126/science.1153847

Stramma, L., Prince, E.D., Schmidtko, S., Luo, J., Hoolihan, J.P., Visbeck, M., Wallace, D.W.R., Brandt, P., Körtzinger, A., 2011. Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. Nat. Clim. Chang. 2, 33–37. doi:10.1038/nclimate1304

Stramma, L., Schmidtko, S., Levin, L. a., Johnson, G.C., 2010. Ocean oxygen minima expansions and their biological impacts. Deep Sea Res. Part I Oceanogr. Res. Pap. 57, 587–595. doi:10.1016/j.dsr.2010.01.005

Strub, P.T., Mesías, J., Montecino, V., Rutllant, J., Salinas, S., 1998. Coastal ocean circulation off western South America, in: Robinson, A.R., Brink, K.H. (Eds.), The Sea. John Wiley & Sons, Inc., New Jersey, pp. 273–313.

Swartzman, G., Bertrand, A., Gutiérrez, M., Bertrand, S., Vasquez, L., 2008. Progress in Oceanography The relationship of anchovy and sardine to water masses in the Peruvian Humboldt Current System from 1983 to 2005. Prog. Oceanogr. 79, 228–237. doi:10.1016/j.pocean.2008.10.021

Swartzman, G., Hickey, B., Michael Kosro, P., Wilson, C., 2005. Poleward and equatorward currents in the Pacific Eastern Boundary Current in summer 1995 and 1998 and their relationship to the distribution of euphausiids. Deep Sea Res. Part II Top. Stud. Oceanogr. 52, 73–88. doi:10.1016/j.dsr2.2004.09.028

Tafur, R., Keyl, F., Argüelles, J., 2010. Reproductive biology of jumbo squid Dosidicus gigas in relation to environmental variability of the northern Humboldt Current System. Mar. Ecol. Prog. Ser. 400, 127–141. doi:10.3354/meps08386

Tafur, R., Rabí, M., 1997. Reproduction of the jumbo flying squid , Dosidicus gigas (Orbigny , 1835) (Cephalopoda: Ommastrephidae) off Peruvian coasts. Sci. Mar. 61, 33–37.

Tafur, R., Villegas, P., Rabí, M., Yamashiro, C., 2001. Dynamics of maturation , seasonality of reproduction and spawning grounds of the jumbo squid Dosidicus gigas (Cephalopoda: Ommastrephidae) in Peruvian waters. Fish. Res. 54, 33–50.

Taipe, A., Yamashiro, C., Mariategui, L., Rojas, P., Roque, C., 2001. Distribution and concentrations of jumbo flying squid (Dosidicus gigas) off the Peruvian coast between 1991 and 1999. Fish. Res. 54, 21–32.

Takahashi, K., Montecinos, A., Goubanova, K., Dewitte, B., 2011. ENSO regimes: Reinterpreting the canonical and Modoki El Niño. Geophys. Res. Lett. 38, n/a–n/a. doi:10.1029/2011GL047364

Taylor, M.H., Tam, J., Blaskovic, V., Espinoza, P., Michael Ballón, R., Wosnitza-Mendo, C., Argüelles, J., Díaz, E., Purca, S., Ochoa, N., Ayón, P., Goya, E., Gutiérrez, D., Quipuzcoa, L., Wolff, M., 2008. Trophic modeling of the Northern Humboldt Current Ecosystem, Part II: Elucidating ecosystem dynamics from 1995 to 2004 with a focus on the impact of ENSO. Prog. Oceanogr. 79, 366–378. doi:10.1016/j.pocean.2008.10.008

Tilic, I., 1963. Material estadístico sobre la industria peruana de harina de pescado. Callao.

Toggweiler, J.R., Dixon, K., Broecker, W.S., 1991. The Peru upwelling and the ventilation of the south Pacific thermocline. J. Geophys. Res. Ocean. 96, 20467–20497.

Trégouboff, G., Rosse, M., 1957. Manuel de planctonologie mediterraneénne. Tomes I & II.

Trübenbach, K., Pegado, M.R., Seibel, B. a, Rosa, R., 2013. Ventilation rates and activity levels of juvenile jumbo squid under metabolic suppression in the oxygen minimum zone. J. Exp. Biol. 216, 359–68. doi:10.1242/jeb.072587

Trübenbach, K., Teixeira, T., Diniz, M., Rosa, R., 2012. Hypoxia tolerance and antioxidant defense system of juvenile jumbo squids in oxygen minimum zones. Deep Sea Res. Part II Top. Stud. Oceanogr. 1–9. doi:10.1016/j.dsr2.2012.10.001

Tsuchiya, M., Talley, L.D., 1998. A Pacific hydrographic section at 88°W: Water-property distribution. J. Geophys. Res. 103, 12899–12918.

Valdés, J., Ortlieb, L., Gutierrez, D., Marinovic, L., Vargas, G., Sifeddine, A., 2008. 250 years of sardine and anchovy scale deposition record in Mejillones Bay, northern Chile. Prog. Oceanogr. 79, 198–207. doi:10.1016/j.pocean.2008.10.002

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S, Fourt Edit. ed. Springer.

Villegas, P., 2001. Growth, life cycle and fishery biology of Loligo gahi (d'Orbigny, 1835) off the Peruvian coast. Fish. Res. 54, 123–131.

Waluda, C.M., Yamashiro, C., Elvidge, C.D., Hobson, V.R., Rodhouse, P.G., 2004. Quantifying light-fishing for Dosidicus gigas in the eastern Pacific using satellite remote sensing. Remote Sens. Environ. 91, 129–133. doi:10.1016/j.rse.2004.02.006

Waluda, C.M., Yamashiro, C., Rodhouse, P.G., 2006. Influence of the ENSO cycle on the light-fishery for Dosidicus gigas in the Peru Current: An analysis of remotely sensed data. Fish. Res. 79, 56–63. doi:10.1016/j.fishres.2006.02.017

Williams, A., Koslow, J., Terauds, A., Haskard, K., 2001. Feeding ecology of five fishes from the mid-slope micronekton community off southern Tasmania, Australia. Mar. Biol. 139, 1177–1192.

Willig, M.R., Kaufman, D.M., Stevens, R.D., 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annu. Rev. Ecol. Evol. Syst. 34, 273–309.

Wing, B.L., 2006. Unusual invertebrates and fish observed in the Gulf of Alaska, 2004–2005. PICES 14, 26–28.

Wolff, G.A., 1984. NOAA Technical Report NMFS 17 Identification and Estimation of Size From the Beaks of 18 Species of Cephalopods From the Pacific Ocean.

Wormuth, J., 1976. The biogeography and numerical taxonomy of the oegopsid squid family Ommastrephidae in the Pacific Ocean. Bull. Scripps. Inst. Ocean. 23, 90.

Wyrtky, K., 1966. Ocean Mar Biol Ann Rev Oceano Equat Pacif.pdf. Ocean. Mar. Biol. Ann. Rev 4, 33–68.

Wyrtky, K., 1967. Circulation and Water Masses in the Eastern Equatorial Pacific Ocean. Int. J. Oceanol. Limnol. 1, 117–147.

Yamashiro, C., Mariátegui, L., Rubio, J., Argüelles, J., Tafur, R., Taipe, A., Rabí, M., 1998. Jumbo flying squid fishery in Perú, in: Okutani, T. (Ed.), Contributed Papers to International Symposium on Large Pelagic Squid. Japan Marine Fishery Resources Research Center. Tokyo, pp. 119–125.

Yatsu, A., Tafur, R., Maravi, C., 1999. Embryos and Rhynchoteuthion Paralarvae of Jumbo Flying Squid Dosidicus gigas (Cephalopoda) Obtained through Artificial Fertilization from Peruvian Waters. Fish. Sci. 65, 904–908.

Yeh, S.-W., Kug, J.-S., Dewitte, B., Kwon, M.-H., Kirtman, B.P., Jin, F.-F., 2009. El Niño in a changing climate. Nat. Lett. 461, 511–514.

Zeidberg, L.D., Robison, B.H., 2007. Invasive range expansion by the Humboldt squid, Dosidicus gigas, in the eastern North Pacific. Proc. Natl. Acad. Sci. U. S. A. 104, 12948–50. doi:10.1073/pnas.0702043104

Zhu, Y., Tande, K.S., Zhou, M., 2009. Mesoscale physical processes and zooplankton transport-retention in the northern Norwegian shelf region. Deep Sea Res. Part II Top. Stud. Oceanogr. 56, 1922–1933. doi:10.1016/j.dsr2.2008.11.019

Zuev, G., Nesis, K., Nigmatullin, C., 1975. System and evolution of the squid genera Ommastrephes and Symplectoteuthis (Cephalopoda, Ommastrephidae). Zool. Zhurnal. 54, 1468–1479.

Zuta, S., Guillén, O., 1970. Oceanografía de las Aguas Costeras del Perú. Boletín del Inst. del Mar del Perú 2, 161–245.

Appendix A

Chapter III

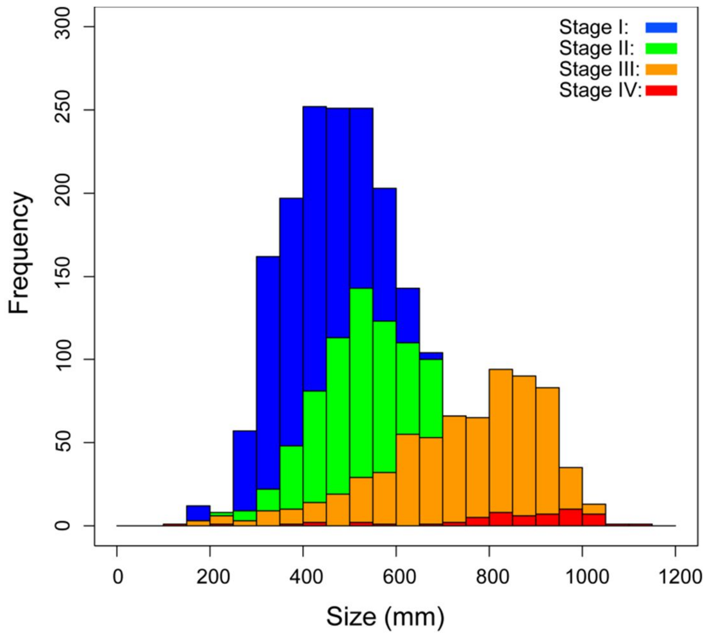

Figure A3.1. Distribution frequency of jumbo squid maturity stages (I: immature; II: in maturing; III: mature; and IV: spawning) according to mantle size.

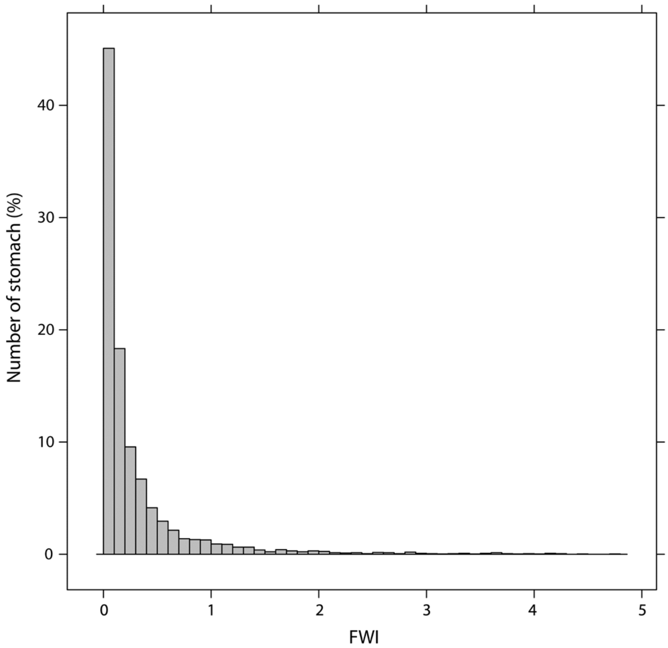

Figure A3.2. Distribution of the fullness weight index (FWI) of non-empty jumbo squid stomach.

Table A3.1. Overall description of the 55 prey taxa observed in jumbo squid stomach sampled off Peru during 2004–2011. Are indicated, the taxonomic information, the mean value (±standard deviation) of the proportion by weight (%Weight) and by number (%Number) as well as the frequency of occurrence (%Occurrence).

Phylum	**Class**	**Order**	**Family**	**Species**	**Dietary groups**	**% Weight**	**% Number**	**% Occurrence**
Mollusca	Gastropoda	Thecosomata	Cavoliniidae	*Cavolinia uncinata*	Other	0.07 (± 2.16)	0.19 (± 3.49)	0.44
				Diacria spp.	Other	1.03 (± 9.13)	2.39 (± 13.17)	4.56
			Thecosomata n/i		Other	0.00 (± 0.01)	0.03 (± 1.02)	0.08
		Littorinimorpha	Atlantidae	*Atlanta* spp.	Other	0.00 (± 0.02)	0.11 (± 1.38)	1.08
			Naticidae	*Natica* spp.	Other	0.01 (± 0.83)	0.18 (± 2.37)	1.44
		Gastropoda n/i			Other	0.00 (± 0.05)	0.03 (± 0.91)	0.19
	Bivalvia	Solemyoida larvae			Other	0.00 (± 0.00)	0.01 (± 0.36)	0.17
	Cephalopoda	Octopoda	Argonautidae	*Argonauta* sp.	Other Cephalopoda	1.21 (± 10.25)	1.06 (± 8.41)	2.65
		Myopsida	Loliginidae		Other Cephalopoda	0.21 (± 4.47)	0.21 (± 4.45)	0.25
		Oegopsida	Enoploteuthidae	*Abraliopsis affinis*	Other Cephalopoda	3.65 (± 17.51)	3.19 (± 15.49)	6.63
			Ommastrephidae	*Dosidicus gigas*	*Dosidicus gigas*	8.57 (± 25.49)	3.41 (± 11.69)	13.21
		Paralarve of Cephalopoda			Other Cephalopoda	0.00 (± 0.01)	0.00 (± 0.12)	0.03
		Eggs of Cephalopoda			Other Cephalopoda	0.03 (± 1.66)	0.03 (± 1.66)	0.03
		Cephalopods n/i			Other Cephalopoda	26.11 (± 42.21)	21.95 (± 37.72)	35.74
Arthropoda	Crustacea n/i				Other	0.37 (± 5.67)	0.44 (± 5.87)	0.72
	Maxillopoda	Calanoida	Aetididae	*Aetideus* sp.	Other	0.00 (± 0.00)	0.00 (± 0.18)	0.03
			Oncaeidae	*Oncaea* sp.	Other	0.00 (± 0.00)	0.02 (± 0.81)	0.11
			Calanoida n/i		Other	0.00 (± 0.06)	0.02 (± 0.99)	0.03
	Ostracoda				Other	0.01 (± 0.45)	0.03 (± 1.50)	0.08
	Malacostraca	Amphipoda	Gammaridea		Other	0.06 (± 2.33)	0.08 (± 2.63)	0.11
			Amphipoda n/i		Other	0.00 (± 0.02)	0.01 (± 0.55)	0.03
		Decapoda	Galatheidae	*Pleuroncodes monodon*	*Pleuroncodes monodon*	1.66 (± 12.36)	1.74 (± 12.47)	2.29
			Euphausiidae		Euphausiidae	6.44 (± 23.63)	7.75 (± 26.25)	8.26
			Zoea larvae		Other	0.08 (± 2.42)	0.09 (± 2.60	0.17
			Decapods n/i		Other	0.03 (± 1.66)	0.06 (± 1.48)	0.25
		Stomatopoda	Squillidae	*Squilla panamensis*	Other	0.14 (± 3.61)	0.24 (± 4.27)	0.41
			Stomatopods n/i		Other	0.05 (± 1.87)	0.09 (± 2.33)	0.19
Teleosteii	Actinopterygii	Stomiiformes	Phosichthyidae	*Vinciguerria lucetia*	*Vinciguerria lucetia*	19.68 (± 37.64)	24.43 (± 37.64)	35.90
		Osmeriformes	Bathylagidae	*Leuroglossus* sp.	Teleosteii	0.26 (± 4.39)	0.48 (± 4.72)	1.91
			Argentinidae	*Argentina* sp.	Teleosteii	0.00 (± 0.00)	0.00 (± 0.21)	0.03
		Myctophiformes	Myctophidae	*Benthosema panamense*	Other Myctophidae	0.00 (± 0.00)	0.01 (± 0.83)	0.03
				Diogenichthys laternatus	Other Myctophidae	2.50 (± 14.25)	3.62 (± 15.78)	7.79
				Lampanyctus sp.	*Lampanyctus* sp.	4.58 (± 19.57)	5.13 (± 17.76)	13.57
				Myctophum aurolaternatum	*Myctophum* spp.	1.40 (± 11.07)	1.01 (± 7.94)	2.76
				Myctophum nitidulum	*Myctophum* spp.	1.21 (± 10.20)	1.25 (± 9.49)	2.87
				Myctophum sp.	*Myctophum* spp.	1.00 (± 9.25)	1.26 (± 9.10)	3.40
				Myctophids n/i	Other Myctophidae	4.47 (± 19.57)	6.06 (± 19.75)	14.10
		Perciformes	Sphyraenidae	*Sphyraena* spp.	Teleosteii	0.70 (± 8.04)	0.52 (± 5.50)	1.60
			Nomeidae	*Cubiceps* spp.	Teleosteii	1.85 (± 12.60)	1.28 (± 9.55)	2.76
				Psenes sio	Teleosteii	0.30 (± 5.31)	0.34 (± 5.00)	0.75
			Carangidae	*Trachurus murphyi*	Teleosteii	0.22 (± 4.43)	0.15 (± 3.40)	0.28
			Scombridae	Scombrids n/i	Teleosteii	0.03 (± 1.66)	0.01 (± 0.83)	0.03
		Gadiformes	Moridae	*Physiculus* spp.	Teleosteii	0.03 (± 1.62)	0.00 (± 0.22)	0.03
			Macrouridae	Macrourids n/i	Teleosteii	0.15 (± 3.70)	0.05 (± 1.60)	0.19
			Merlucciidae	*Merluccius gayi peruanus*	Teleosteii	0.14 (± 3.59)	0.07 (± 2.19)	0.19
		Clupeiformes	Engraulidae	*Engraulis ringens*	Engraulidae	1.91 (± 12.95)	1.39 (± 10.17)	2.63

Table A3.2. Yearly description of the 55 prey taxa observed in jumbo squid stomach sampled off Peru during 2004–2011. Proportion by weight: %W; proportion by number: %N; frequency of occurrence: %O.

					2004			**2005**			**2006**			**2007**			**2008**			**2009**			**2010**			**2011**		
Phylum	**Class**	**Order**	**Family**	**Species**	**%W**	**%N**	**%O**	**%W**	**%N**	**%O**	**%W**	**%N**	**%O**	**%W**	**%N**	**%O**	**%W**	**%N**	**%O**	**%W**	**%N**	**%O**	**%W**	**%N**	**%O**	**%W**	**%N**	**%O**
Mollusca	Gastropoda	Thecosomata	Cavoliniidae	*Cavolinia uncinata*	0.00	0.00	0.00	0.85	1.41	4.02	0.12	0.76	1.46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
				Diacria spp.	4.16	8.71	13.46	0.00	0.00	0.00	0.34	0.89	1.25	0.43	0.73	0.84	0.24	0.47	2.21	1.01	2.40	4.46	0.64	1.33	3.63	0.25	2.22	6.55
			Thecosomata n/i		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.19	0.63	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Littorinimorpha	Atlantidae	*Atlanta* spp.	0.01	0.52	5.00	0.00	0.00	0.00	0.00	0.10	1.25	0.00	0.11	0.84	0.00	0.00	0.00	0.00	0.05	0.27	0.00	0.02	0.38	0.00	0.01	0.28
			Naticidae	*Natica* spp.	0.10	0.51	2.88	0.00	0.24	1.34	0.00	0.32	2.71	0.00	0.05	0.84	0.00	0.05	0.92	0.00	0.14	1.49	0.00	0.02	0.19	0.00	0.04	0.57
		Gastropoda n/i			0.00	0.03	0.19	0.00	0.00	0.00	0.00	0.01	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.18	0.96	0.00	0.00	0.00
	Bivalvia	Solemyoida larvae			0.00	0.03	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.41	0.00	0.00	0.00	0.00	0.04	0.28
	Cephalopoda	Octopoda	Argonautidae	*Argonauta* sp.	1.75	1.49	2.69	4.61	2.24	7.59	0.00	0.00	0.00	0.00	0.00	0.00	0.37	0.36	0.74	2.27	1.95	3.92	0.65	0.82	2.49	0.59	1.36	5.41
		Myopsida	Loliginidae		1.43	1.41	1.54	0.10	0.11	0.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Oegopsida	Enoploteuthidae	*Abraliopsis affinis*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.17	0.98	3.87	5.59	4.58	10.27	11.15	9.60	17.97	7.44	7.40	13.96
			Ommastrephidae	*Dosidicus gigas*	10.67	4.22	15.96	11.13	3.79	14.73	7.60	2.75	11.48	22.68	8.53	31.80	5.84	2.22	11.07	7.48	3.65	11.89	8.02	2.93	12.05	2.87	1.39	5.70
		Paralarve of Cephalopoda			0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.28
		Eggs of Cephalopoda			0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.28	0.28	0.28
		Cephalopods n/i			20.06	16.38	35.58	16.09	11.88	29.46	24.98	21.90	35.49	19.47	17.81	30.13	21.97	19.26	29.34	33.33	27.42	40.54	29.06	25.26	34.61	34.31	27.18	45.58
Arthropoda	Crustacea n/i				0.79	1.03	1.92	0.45	0.52	1.34	0.00	0.00	0.00	0.00	0.00	0.00	0.26	0.45	0.74	0.40	0.34	0.41	0.71	0.82	1.15	0.00	0.00	0.00
	Maxillopoda	Calanoida	Aetididae	*Aetideus* sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.19	0.00	0.00	0.00
			Oncaeidae	*Oncaea* sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.16	0.76	0.00	0.00	0.00
			Calanoida n/i		0.00	0.00	0.00	0.01	0.27	0.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Ostracoda				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.18	0.38	0.00	0.01	0.28
	Malacostraca	Amphipoda	Gammaridea		0.19	0.35	0.58	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.18	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
			Amphipoda n/i		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.28
		Decapoda	Galatheidae	*Pleuroncodes monodon*	0.01	0.10	0.38	3.58	3.77	4.02	0.00	0.05	0.21	0.00	0.00	0.00	3.80	3.50	4.98	1.07	1.30	1.76	1.92	2.25	2.68	3.81	3.78	4.84
			Euphausiidae		10.49	12.71	13.27	2.51	4.29	4.46	7.64	8.76	9.19	5.04	6.10	6.28	9.32	11.14	12.18	6.03	7.10	7.70	4.14	4.95	5.16	2.14	2.71	3.13
			Zoea larvae		0.00	0.00	0.00	0.15	0.33	0.89	0.51	0.53	0.84	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
			Decapods n/i		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.31	1.22	0.00	0.00	0.00	0.00	0.00	0.00
		Stomatopoda	Squillidae	*Squilla panamensis*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.69	1.19	2.03	0.00	0.00	0.00	0.00	0.00	0.00
			Stomatopods n/i		0.02	0.07	0.38	0.00	0.22	0.45	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.15	0.37	0.20	0.20	0.27	0.00	0.00	0.00	0.00	0.00	0.00
Teleosteii	Actinopterygii	Stomiiformes	Phosichthyidae	*Vinciguerria lucetia*	19.16	20.32	35.58	18.92	23.50	46.88	27.82	31.95	44.05	14.84	21.93	31.38	27.61	31.22	41.88	13.57	17.88	26.49	17.70	26.40	35.18	16.74	22.95	33.05
		Osmeriformes	Bathylagidae	*Leuroglossus* sp.	0.19	0.14	0.38	0.43	0.24	0.89	0.02	0.24	1.67	0.69	0.85	2.09	0.24	0.70	3.69	0.34	0.46	1.89	0.10	0.54	1.53	0.34	0.78	2.85
			Argentinidae	*Argentina* sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.19	0.00	0.00	0.00
		Myctophiformes	Myctophidae	*Benthosema panamense*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.19	0.00	0.00	0.00
				Diogenichthys laternatus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.50	6.59	15.31	4.17	5.65	9.86	4.29	6.10	12.81	3.60	6.13	16.81
				Lampanyctus sp.	2.13	3.50	11.92	6.25	7.62	25.00	8.06	8.06	20.88	8.60	11.12	18.41	3.85	3.73	13.10	5.10	5.58	12.16	3.36	3.32	8.03	1.47	1.84	7.41
				Myctophum aurolaternatum	0.19	0.23	2.12	0.75	0.81	1.34	0.01	0.10	0.21	0.00	0.00	0.00	0.00	0.05	0.74	0.89	0.73	1.76	3.70	2.02	5.74	6.24	4.83	10.83
				Myctophum nitidulum	0.16	0.17	0.96	0.94	1.92	4.91	2.43	2.18	4.38	4.22	4.94	5.86	0.91	0.94	2.58	0.23	0.38	1.08	2.04	1.65	4.59	0.53	0.36	1.99
				Myctophum sp.	3.31	4.36	13.27	0.86	2.07	7.59	1.61	1.94	3.34	0.00	0.17	0.42	0.00	0.00	0.00	0.27	0.28	0.54	0.00	0.00	0.00	2.07	1.83	4.56
				Myctophids n/i	4.83	6.82	20.77	6.34	9.92	25.45	4.63	6.31	21.29	9.40	13.58	23.01	2.30	3.02	7.38	6.16	7.61	12.43	2.34	2.93	7.46	2.16	3.10	4.84
		Perciformes	Sphyraenidae	*Sphyraena* spp.	0.35	0.41	1.92	1.27	0.76	3.57	0.74	0.48	1.67	0.42	0.47	1.67	0.74	0.55	0.92	0.40	0.20	0.41	0.95	0.71	2.29	1.19	0.92	2.28
			Nomeidae	*Cubiceps* spp.	0.00	0.00	0.00	1.82	0.54	2.23	1.35	0.49	2.51	1.62	1.96	4.18	2.17	1.71	2.77	1.18	0.78	1.62	1.47	1.23	3.25	6.94	4.76	8.26
				Psenes sio	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.73	0.81	2.16	0.63	0.80	1.72	0.57	0.57	0.57
			Carangidae	*Trachurus murphyi*	0.00	0.00	0.00	0.00	0.00	0.00	0.94	0.63	1.04	0.00	0.00	0.00	0.61	0.48	0.92	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
			Scombridae	Scombrids n/i	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.07	0.14	0.00	0.00	0.00	0.00	0.00	0.00
		Gadiformes	Moridae	*Physiculus* spp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.02	0.14	0.00	0.00	0.00	0.00	0.00	0.00
			Macrouridae	Macrourids n/i	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.03	0.37	1.34	0.00	0.00	0.00
			Merlucciidae	*Merluccius gayi peruanus*	0.27	0.29	0.38	0.00	0.00	0.00	0.21	0.01	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.52	0.21	0.76	0.00	0.00	0.00
		Clupeiformes	Engraulidae	*Engraulis ringens*	0.69	0.34	1.54	3.70	2.36	6.70	0.41	0.26	0.42	5.19	4.07	6.69	5.11	3.64	6.46	1.53	1.29	2.03	0.19	0.10	0.19	0.80	0.66	0.85
				Engraulids n/i	0.67	0.67	1.92	4.38	3.65	5.36	0.77	0.66	1.25	0.75	0.84	1.26	0.74	0.72	1.11	0.35	0.35	1.08	0.20	0.11	0.57	0.28	0.28	0.28
		Pleuronectiformes	Cynoglossidae	Cynoglossids n/i	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.55	0.22	1.14
		Syngnathiformes	Syngnathidae	*Hippocampus* sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.03	0.19	0.00	0.00	0.00
				Syngnathids n/i	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.62	0.52	0.76	0.00	0.00	0.00
		Beloniformes	Exocoetidae	*Exocoetus* spp.	0.15	0.16	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Teleosteii n/i				18.20	15.06	28.27	14.85	17.55	33.93	9.74	10.39	15.66	6.61	6.34	10.88	7.91	7.83	13.47	6.59	7.25	12.03	4.51	4.31	6.31	4.82	4.20	9.69
	Eggs of Teleosteii n/i				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.42	0.42	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Urochordata			Salpidae		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.00
Algae			Laminariaceae		0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.05	0.21	0.00	0.00	0.00	0.16	0.04	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table A3.3. Result of the Kruskal-Wallis test performed on the 11 dietary groups according to Size, Distance to the shelf-break, Season and SSTA. Significant differences are in bold.

	Size (df=3)		**Distance to the shelf (df=3)**		**Season (df=3)**		**SSTA (df=3)**	
Dietary group	**H**	**p-value**	**H**	**p-value**	**H**	**p-value**	**H**	**p-value**
Dosidicus gigas	55.78	**<0.001**	2.78	0.42	3.31	0.35	30.21	**<0.001**
Others Cephalopoda	66.12	**<0.001**	12.92	**0.01**	21.47	**<0.001**	28.52	**<0.001**
Euphausiidae	73.26	**<0.001**	8.69	**0.03**	45.86	**<0.001**	75.1	**<0.001**
Pleuroncodes monodon	4.73	0.19	10.67	**0.01**	7.47	0.06	44.79	**<0.001**
Vinciguerria lucetia	140.42	**<0.001**	46.09	**<0.001**	163.19	**<0.001**	78.52	**<0.001**
Lampanyctus sp.	41.16	**<0.001**	4.92	0.18	37.78	**<0.001**	18.41	**<0.001**
Myctophidae	32.61	**<0.001**	11.09	**0.01**	36.55	**<0.001**	24.99	**<0.001**
Myctophum spp.	57.89	**<0.001**	34.09	**<0.001**	31.78	**<0.001**	43.97	**<0.001**
Engraulidae	4.56	0.21	29.89	**<0.001**	37.62	**<0.001**	15.92	**<0.001**
Teleosteii	6.77	0.08	7.01	0.07	5.33	**p<0.001**	2.57	0.46

Appendix B

List of publications during the thesis

Journal articles *indexed (ISI,* Scielo)

Alegre, A., Bertrand A., Espino M., Espinoza P., Dioses T., Ñiquen M., Navarro I., Simier M., Ménard F. 2015. Diet diversity of jack and chub mackerels and ecosystem changes in the northern Humboldt Current system: A long-term study. Progress in Oceanography 137: 299–313. http://www.sciencedirect.com/science/article/pii/S0079661115001627 .

Alegre, A., Ménard, F., Tafur, R., Espinoza, P., Argüelles, J., Maehara, V., Flores, O, Simier, M, Bertrand, A. (2014) Comprehensive model of jumbo squid Dosidicus gigas trophic ecology in the northern Humboldt Current system. *Plos ONE.* Retrieved from http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3896428/pdf/pone.0085919.pdf

Alegre, A., Espinoza, P., & Espino, M. (2013) Trophic ecology of Jack mackerel Trachurus murphyi in Peru, 1977 – 2011. *Rev. peru. biol, Vol. Ext.*, 75–82. Retrieved from http://revistasinvestigacion.unmsm.edu.pe/index.php/rpb/article/view/2622/2295

Argüelles, J., Lorrain, A., Cherel, Y., Graco, M., Tafur, R., **Alegre, A**., … Bertrand, A. (2012) Tracking habitat and resource use for the jumbo squid Dosidicus gigas: a stable isotope analysis in the Northern Humboldt Current System. *Marine Biology*, 159(9), 2105–2116. Retrieved from http://download.springer.com/static/pdf/993/art%253A10.1007%252Fs00227-012-1998-2.pdf?auth66=1411305936_3b969f196ef4a7d35e0ceda29ea948f4&ext=.pdf

Lorrain, A., Argüelles, J., **Alegre, A.**, Bertrand, A., Munaron, J.-M., Richard, P., & Cherel, Y. (2011) Sequential Isotopic Signature Along Gladius Highlights Contrasted Individual Foraging Strategies of Jumbo Squid (*Dosidicus gigas*). *Plos ONE*, *6*(7), e22194. Retrieved from http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3136502/pdf/pone.0022194.pdf

Rosas-Luis, R., Tafur-Jimenez, R., **Alegre-Norza, A**. R., Castillo-Valderrama, P. R., Cornejo-Urbina, R. M., Salinas-Zavala, C. A., & Sánchez, P. (2011) Trophic relationships between the jumbo squid (*Dosidicus gigas*) and the lightfish (Vinciguerria lucetia) in the Humboldt Current System off Peru. *Scientia Marina*, *75*(3), 549–557. Retrieved from http://www.icm.csic.es/scimar/index.php/secId/6/IdArt/4012/