Trophic dynamics in the northern Humboldt Current system: insights from stable isotopes and stomach content analyses

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Pepe Espinoza

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JURY **Arnaud Bertrand** IRD Directeur
Anne Lorrain IRD Co-directrice
Frédéric Jean
Hervé Lebris
Frédéric Ménard
Yves Cherel

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Pepe Espinoza

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Thèse soutenue le
devant le jury composé de :

Hervé LEBRIS
PR, Agrocampus ouest / *Rapporteur*

Frédéric MENARD
DR, IRD / *Rapporteur*

Yves CHEREL
DR, CNRS / *Examinateur*

Frédéric JEAN
MCF, UBO / *Président*

Arnaud BERTRAND
DR, IRD / *Directeur de thèse*

Anne LORRAIN
CR, IRD / *Co-directrice de thèse*

Abstract

The northern Humboldt Current system (NHCS) off Peru is one of the most productive world marine regions. It represents less than 0.1% of the world ocean surface but presently sustains about 10% of the world fish catch, with the Peruvian anchovy or anchoveta *Engraulis ringens* as emblematic fish resource. Compared with other eastern boundary upwelling systems, the higher fish productivity of the NHCS cannot be explained by a corresponding higher primary productivity. On another hand, the NHCS is the region where El Niño, and climate variability in general, is most notable. Also, surface oxygenated waters overlie an intense and extremely shallow Oxygen Minimum Zone (OMZ). In this context, the main objective of this study is to better understand the trophic flows in the NHCS using both stomach content and stable isotope analyses. The study focuses on a variety of organisms from low trophic levels such as zooplankton to top predators (seabirds and fur seals). The approach combines both long-term and specific studies on emblematic species such as anchoveta, and sardine *Sardinops sagax* and a more inclusive analysis considering the 'global' food web in the recent years (2008 – 2012) using stable isotope analysis.

Revisiting anchovy and sardine we show that whereas phytoplankton largely dominated anchoveta and sardine diets in terms of numerical abundance, the carbon content of prey items indicated that zooplankton was by far the most important dietary component. Indeed for anchovy euphausiids contributed 67.5% of dietary carbon, followed by copepods (26.3%). Selecting the largest prey, the euphausiids, provide an energetic advantage for anchoveta in its ecosystem where oxygen depletion imposes strong metabolic constrain to pelagic fish. Sardine feed on smaller zooplankton than do anchoveta, with sardine diet consisting of smaller copepods and fewer euphausiids than anchoveta diet. Hence, trophic competition between sardine and anchovy in the northern Humboldt Current system is minimized by their partitioning of the zooplankton food resource based on prey size, as has been reported in other systems. These results suggest an ecological role for pelagic fish that challenges previous understanding of their position in the foodweb (zooplanktophagous instead of phytophagous), the functioning and the trophic models of the NHCS.

Finally to obtain a more comprehensive vision of the relative trophic position of NHCS main components we used stable isotope analyses. For that purpose we analyzed the $\delta^{13}C$ and $\delta^{15}N$ stable isotope values of thirteen taxonomic categories collected off Peru from 2008 - 2011, i.e., zooplankton, fish, squids and air-breathing top predators. The $\delta^{15}N$ isotope signature was strongly impacted by the species, the body length and the latitude. Along the Peruvian coast, the OMZ get more intense and shallow south of ~7.5ºS impacting the baseline nitrogen stable isotopes. Employing a linear mixed-effects modelling approach taking into account the latitudinal and body length effects, we provide a new vision of the relative trophic position of key ecosystem components. Also we confirm stomach content-based results on anchoveta *Engraulis ringens* and highlight the potential remarkable importance of an often neglected ecosystem component, the squat lobster *Pleuroncodes monodon*. Indeed, our results support the hypothesis according to which this species forage to some extent on fish eggs and larvae and can thus predate on the first life stages of exploited species. However, the $\delta^{13}C$ values of these two species suggest that anchoveta and squat lobster do not exactly share the same habitat. This would potentially reduce some direct competition and/or predation.

Key words: Northern Humboldt Current system, trophic ecology, oxygen minimum zone, anchoveta *Engraulis ringens*, sardine *Sardinops sagax*, jumbo squid *Dosidicus gigas*, squat lobster *Pleuroncodes monodon*, stable isotope analysis, stomach content.

Résumé en Français

Le nord du système du Courant de Humboldt (NHCS), le long des côtes péruviennes, est l'une des régions océanique les plus productives au monde. Il représente moins de 0.1% de la surface des océans mondiaux mais contribue actuellement à plus de 10% des captures mondiales en poissons, avec l'anchois *Engraulis ringens* comme espèce emblématique. Comparé aux autres systèmes d'upwelling de bord Est, la forte productivité en poissons ne peut être expliquée par une productivité primaire plus élevée. Par contre, le NCHS est la région où El Niño, et la variabilité climatique en général est la plus notable. D'autre part, les eaux de surface oxygénées recouvrent une zone de minimum d'oxygène extrêmement intense et superficielle. L'objectif principal de ce travail est de mieux comprendre les relations trophiques au sein du NHCS en combinant l'analyse de contenus stomacaux et d'isotopes stables. Cette étude se focalise sur une variété d'organismes allant des bas niveaux trophiques comme le zooplancton aux prédateurs supérieurs (oiseaux et les otaries à fourrure). Elle combine des études de contenus stomacaux ponctuelles et sur le long terme d'espèces clés telles que l'anchois et la sardine *Sardinops sagax* et une analyse plus globale, basée sur l'utilisation d'isotopes stables et considérant l'ensemble du réseau trophique dans les années récentes (2008 – 2012).

Les analyses des contenus stomacaux d'anchois et de sardine ont permis de revisiter l'écologie de ces espèces. En effet, bien que le phytoplancton domine largement les contenus stomacaux en termes d'abondance numérique, le zooplancton est de loin la composante alimentaire la plus importante pour ces deux espèces en termes de carbone. Dans le cas de l'anchois, les euphausiacés contribuent à plus de 67.5% du carbone ingéré, suivis par les copépodes (26.3%). Sélectionner les proies les plus grandes telles que les euphausiacés procure un avantage énergétique pour l'anchois dans cet écosystème où les carences en oxygène imposent de fortes contraintes métaboliques aux poissons pélagiques. La sardine se nourrit de zooplancton plus petit que l'anchois (copépodes plus petits et moins d'euphausiacés). Ainsi, la compétition trophique entre les sardines et les anchois est minimisée dans le NSCH par le partage de la ressource zooplancton selon sa taille, comme cela a déjà été montré dans d'autres écosystèmes. Ces résultats remettent en question la compréhension première de la position des petits poissons pélagiques (zooplanctonophage et non phytoplanctonophage) dans la chaine trophique ce qui implique de reconsidérer le fonctionnement et les modèles trophiques du NCHS.

Afin d'obtenir une compréhension plus globale de la position trophique relative des principaux composants du NHCS une approche basée sur des analyses d'isotopes stables (δ^{13}C et δ^{15}N) a été utilisée. Pour ce faire, la signature isotopique d'échantillons de 13 groupes taxonomiques (zooplancton, poissons, calmars et prédateurs supérieurs) prélevés entre 2008 et 2011 a été déterminée. Les valeurs de δ^{15}N obtenues sont fortement impactées par l'espèce, la taille et la latitude. Le long de la cote péruvienne, la zone de minimum d'oxygène devient en effet plus intense et plus superficielle au sud de ~7.5ºS impactant fortement la valeur de δ^{15}N de la ligne de base. Nous avons donc utilisé un modèle linéaire à effet mixte prenant en compte les effets latitude et taille afin de prédire la position trophique relative des composants clés de l'écosystème. Ces analyses isotopiques confirment les résultats issus des contenus stomacaux sur le régime alimentaire de l'anchois et mettent en évidence l'importance potentielle d'une composante souvent négligée de l'écosystème, la galathée pélagique *Pleuroncodes monodon.* En effet, nos résultats supportent l'hypothèse selon laquelle cette espèce s'alimenterait en partie sur les œufs et larves d'anchois, menaçant ainsi les premiers stades de vie des espèces exploitées. Les valeurs différentes de δ^{13}C suggèrent cependant que les anchois et les galathées pélagiques ne partageraient pas exactement le même habitat, ce qui réduirait potentiellement la compétition directe et/ou la prédation.

Mots clés: Système Nord du Courant de Humboldt, écologie trophique, zone de minimum d'oxygène, anchois *Engraulis ringens*, sardine *Sardinops sagax*, calmar géant *Dosidicus gigas*, *Pleuroncodes monodon*, isotopes stables, contenus stomacaux.

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Those whose names are not on these lines, do not worry you are in a place where no one can delete, in my mind.

Well, sorry, but I hear some voices of stomachs, tissues and numbers, telling me we want to world know us, please, you must to make it possible. I leave you so far, I will keep in touch.

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CHAPTER 1

General Introduction

Eastern boundary upwelling systems (EBUS), i.e., Benguela, California, Canary and the Humboldt Current systems support ~20% of worldwide fish harvests (Fréon *et al.*, 2009). The landings are mostly based on two heavily exploited fish resources, anchovy (the genus *Engraulis*) and sardine (the genera *Sardinops* and *Sardina*). The northern Humboldt Current system (NHCS) off Peru produces more fish per unit area than any other oceanic region. It represents less than 0.1% of the world ocean surface but presently sustains about 10% of the world fish catch, with the Peruvian anchovy or anchoveta *Engraulis ringens* as emblematic fish resource (Chavez *et al.*, 2008). Compared with other EBUS, the higher fish productivity of the NHCS cannot be explained by a corresponding higher primary productivity (Fig. 1.1) (Chavez *et al.*, 2008). On another hand, the NHCS is the region where El Niño, and climate variability in general, is most notable (Chavez *et al.*, 2008). Also, as a result of sinking and decay of primary production and poor ventilation, surface oxygenated waters overlie an intense and extremely shallow Oxygen Minimum Zone (OMZ). The OMZ affects global nutrient budgets, as nitrate instead of oxygen is used by bacteria as a terminal electron acceptor (Chavez *et al.*, 2008). A series of hypothesis based on the characteristics of the NHCS were proposed to explain the secret of its productivity but the ultimate reasons are still not clear.

In this introduction we will briefly present the main characteristics of the NHCS and explain why trophic dynamics are important processes that should be considered to better understand ecosystem functioning. We will then expose the main objectives of this thesis before presenting a short summary of each chapter.

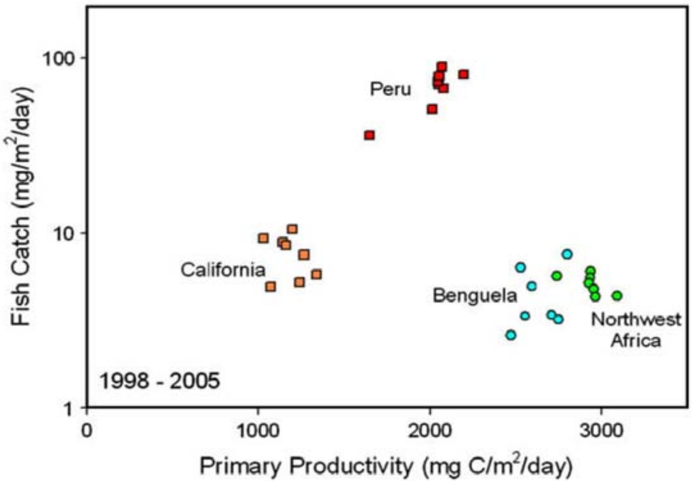

Figure 1.1: Fish catch versus primary productivity for the four main eastern boundary coastal upwelling ecosystems for the years 1998–2005. Source: Chavez et al. (2008).

1.1. Circulation and dynamics in the Northern Humboldt Current system

The NHCS is mostly wind-driven by the South Pacific subtropical anticyclone (Strub *et al.*, 1998) forcing the South Pacific gyre (see Figure 1.2 for a schematic representation of the circulation in the NHCS). Near the Peruvian coast, the dominant alongshore equatorward winds and cyclonic wind-stress curl produce offshore Ekman transport of surface water generating an intense upwelling characterized by an alongshore narrow strip of cold (Fig. 1.2b, color shading) and highly productive water and a current system composed of equatorward surface and mainly poleward subsurface flows. Upwelling of cool waters brings phytoplankton nutrients to the surface, dramatically increasing biological productivity. Upwelling intensity is generally high during most of the year with a maximum during austral winter (Gunther, 1936; Strub *et al.*, 1998), which results in year-round high nutrient concentrations in the surface waters (Pennington *et al.*, 2006; Echevin *et al.*, 2008). The Peruvian coastal upwelling region is thus characterised by extremely high rates of primary productivity (Thiede and Suess 1983; Berger *et al.*, 1989; Pennington *et al.*, 2006) even if lower than in the Canaria and Benguela Current systems (Carr, 2002; Chavez *et al.*, 2008). Note that in surface waters along the shelf region, nutrient concentrations, especially of nitrate, phosphate and iron, are very high and are not limiting for blooming diatoms (Bruland *et al.*, 2005; Franz *et al.*, 2012). Large diatoms tend to dominate in phytoplankton biomass (Rojas de Mendiola, 1981; Wilkerson *et al.*, 2000). However, the dinoflagellates are other key phytoplankton component. They are associated with warm events such as El Niño (Rojas de Mendiola 1979; Delgado *et al.*, 2001). Also these organisms are motile and capable to migrate vertically (Forward *et al.*, 1986) to take up nitrate below the thermocline (Dortch and Maske 1982; Franz *et al.*, 2012). Therefore, if stratification increases but a shallow thermocline/nutricline persists, coastal dinoflagellates will increase by swimming to shallow depths to take up nutrients at night and return to the surface to photosynthesize during the day (Chavez *et al.*, 2011).

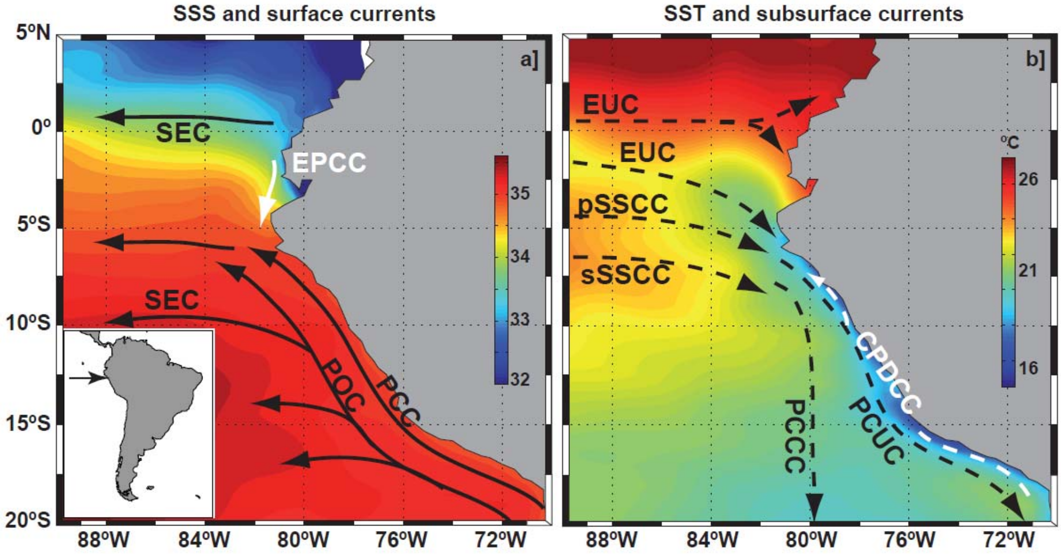

Figure 1.2: Sea surface properties and oceanic circulation scheme. (a) Sea-Surface Salinity (SSS, color shading) and surface circulation. (b) Sea-Surface Temperature (SST, colour shading in °C) and subsurface circulation. The Ecuador-Peru Coastal Current (EPCC) and Chile-Peru Deep Coastal Current (CPDCC) are indicated by white arrows. SEC: South Equatorial Current; EPCC: Ecuador-Peru Coastal Current; POC: Peru Oceanic Current; PCC: Peru Coastal Current. EUC: Equatorial Undercurrent; pSSCC: primary (northern branch) Southern Subsurface Countercurrent; sSSCC: secondary (southern branch) Southern Subsurface Countercurrent; PCCC: Peru-Chile Countercurrent; PCUC: Peru-Chile Undercurrent; CPDCC: Chile-Peru Deep Coastal Current. Source: Chaigneau et al. (2013).

Because of the constant upwelling of subsurface cold water, a wide region off the Peruvian coast is dominated by relatively cold, highly productive water mass, the Cold Coastal Water (CCW). The oligotrophic Subtropical Surface Water (SSW) is located offshore the CCW. The Surface Tropical Water (STW) is found north of the equator and characterized by higher temperatures and lower salinities than the other water masses present off Peru. The Surface Equatorial Water (SEW) is found between the CCW and the STW (Fig. 1.3). The main characteristics of the mater masses can be found in Table 1.1.

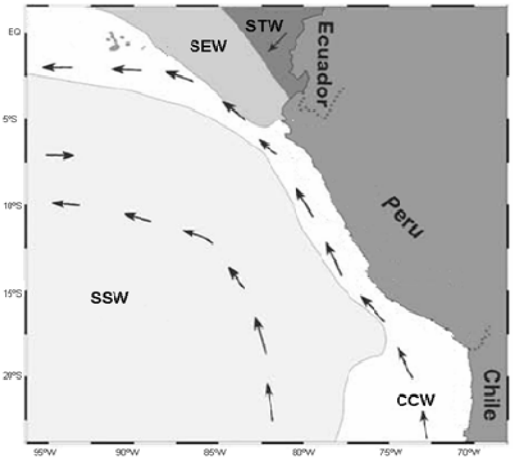

Figure 1.3: Distribution of the main water masses in the HCS: Cold coastal water (CCW), Surface subtropical water (SSW), Surface equatorial water (SEW), Surface tropical water (STW). Source: Ayón et al. (2008a).

Table 1.1 Main characteristics of the water masses presents in the Humboldt Current System (source: Bertrand et al. 2004a).

Water mass	Abbreviation	Main characteristics
Cold coastal water	CCW	Salinity: 34.80–35.05; superficial temperature: 15–17ºC in winter and 15–19ºC in summer. Influenced by upwelling, very productive
Surface subtropical water	SSW	Salinity >35.10; superficial temperature: 17–25ºC in winter and 20–25ºC in summer. Oceanic characteristics, oligotrophic water mass
Surface equatorial water	SEW	Salinity: 34.00–34.80; superficial temperature: 20–26ºC in winter and 21–26ºC in summer. Mesotrophic water mass
Surface tropical water	STW	Salinity <34.00; superficial temperature: >23ºC in winter and >26ªC in summer.

The Peruvian upwelling system is subjected to bottom-up forcing at intraseasonal (Bertrand *et al.*, 2008b) interannual (Barber and Chavez, 1983), multidecadal (Chavez *et al.*, 2003; Alheit and Ñiquen, 2004; Ayón *et al.*, 2008b) and centennial time scales (Gutiérrez *et al.*, 2009; Siffedine *et al.*, 2008; Valdés *et al.*, 2008; Salvatteci, 2013).

The most remarkable expressions of the interannual variability of the Humboldt Current system are the warm and cold phases of the El Niño Southern Oscillation (ENSO), El Niño and La Niña, respectively. During El Niño conditions the thermocline deepens, which makes the coastal upwelling ‘inefficient’ in terms of nutrient enrichment (Barber and Chavez, 1983). Conversely, during La Niña conditions the thermocline rises, which allow coastal upwelling to bring cold and nutrient-rich water toward the surface. As a consequence, the cold coastal water (CCW) mass expands. These two sets of conditions also affect the spatial organization of living organisms by modifying the volume of the favourable pelagic habitat, or the surface of the oxygenated bottom areas, due to the along-coast propagation of the KWs (Bertrand *et al.*, 2008b; Gutiérrez *et al.*, 2008).

In the short term, the ENSO-related changes in the physical and biological conditions could have some negative effects, like reducing the abundance of the anchoveta and its predators (Arntz and Fahrbach, 1996). However, in the long term, it might contribute to maintaining the high fish production of the system by favouring fast-growing fish species like anchovy, which take advantage of the low predation pressure and rapidly increase their population and dominate the system (Bakun and Weeks, 2008). Still, each El Niño is different and has different effect on the ecosystem. Strong El Niño Events such as the events of 1982-83 and 1997-98 dramatically impact the coastal ecosystem, while others do not (Bertrand *et al.*, 2004a). Recent studies showed that the extraordinary warm events such as the 1982-83 and 1997-98 El Niño are distinct from the others (e.g. 1992–93, 2002–03, 2004-05, 2009-10), which correspond to "El Niño Modoki" or "Central Pacific" (Takahashi *et al.*, 2011). Indeed when Central Pacific El Niño occurs, the conditions can even be slightly cooler off Peru (Dewitte *et al.*, 2012), far from the archetypal El Niño effects on the Peruvian ecosystem (Barber and Chavez, 1983; Alheit and Niquen, 2004; Bertrand *et al.*, 2004a).

1.2. Oxygen minimum zone

Oxygen depletion is widespread in the world oceans (Kamykowski and Zentara, 1990), occurring as permanent, seasonal and episodic features. Where upwelling is most intense in the world ocean there is high phytoplankton production. This material sinks and is decomposed in midwater, consuming dissolved oxygen. When high oxygen demand occurs in combination with low ventilation, a massive midwater oxygen minimum develops (Wyrtki, 1962). Since it combines high productivity and low ventilation, a prominent feature of the NHCS is the presence of a permanent oxygen minimum zone (OMZ, Fig. 1.4). OMZ are defined as regions where oxygen concentrations are <0.5 ml.l-1 (or about 7.5% saturation; <22 μM) (Levin, 2003). In the NHCS, the OMZ is thickest (>600 m) between 5 and 13ºS and to about 1 000 km offshore (Fuenzalida *et al.*, 2009). Because of the coastal upwelling, which lifts the coastal hypoxic layer closer to the sea surface (Fuenzalida *et al.*, 2009), the OMZ upper boundary is shallowest at the coast (25-50 m) off Peru and northern Chile (e.g., Morales *et al.*, 1996; Strub *et al.*, 1998). These OMZs contribute to 25–75% of oceanic N2O production (Nevison *et al.*, 2004), a potent greenhouse gas, which influences the Earth's heat budget and depletes stratospheric ozone (Prather *et al.*, 1995)]. OMZs are generally the site of intense denitrification (Naqvi *et al.*, 2000). Actually in OMZ, both intense denitrification and anaerobic ammonium oxidation (anammox) occur (Kuypers *et al.*, 2005; Lam *et al.*, 2009; Lam and Kuypers, 2011), which has strong impact on nitrogen cycling and organic matter remineralisation, subsequently limiting the biological production (Lam *et al.*, 2009).

In response to global warming and direct anthropogenic influences, OMZs of the World Ocean are expanding (Oschlies *et al.*, 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. Indeed, the OMZ strongly influences the distribution and mortality of marine organisms (Levin, 2003; Prince and Goodyear, 2006; Diaz and Rosenberg, 2008; Bertrand *et al.*, 2011). Although a few species of zooplankton (e.g. the euphausiid *Euphausia mucronata*), mesopelagic fish, and squids (e.g. the jumbo squid *Dosidicus gigas*) have adapted their metabolism to temporarily (through diel vertical migration) or permanently inhabit OMZs, most marine species limit their distribution to the surface oxygenated layer. Intensification of oxygen-poor and acidic conditions could severely impact marine communities e.g. by (i) shrinking the available habitat, (ii) diminishing the capacity of plankton to develop calcium carbonate skeletons, (iii) eliminating species from metazoans to fish predators or (iv) hampering the spawning success of fish resources (Levin, 2003; Orr *et al.*, 2005; Diaz and Rosenberg, 2008; Bertrand *et al.*, 2011).

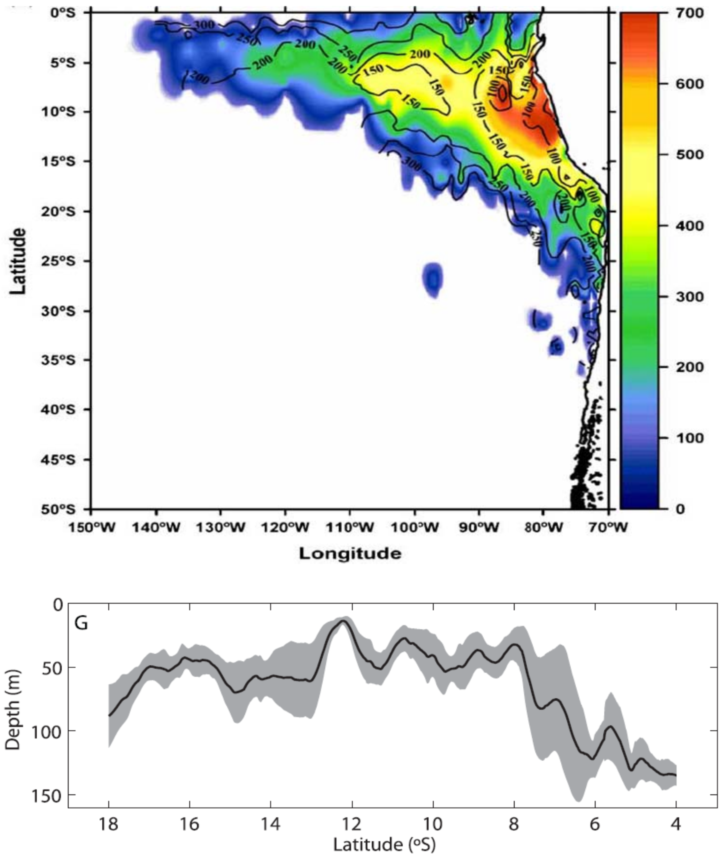

Figure 1.4: Upper plot: OMZ thickness and upper boundary in the Eastern South Pacific. Thickness is colour-coded according to the colour bar on the right-hand side of the figure; units are in m. The upper boundary of the OMZ is shown in black contour lines with 50 m intervals; Source: Fuenzalida et al. (2009). Lower plot: Meridional variation of the upper OMZ averaged between the coast and 200 km offshore during a survey performed in 2005 (black solid line) and corresponding ± standard deviation (grey shaded area). Source: Bertrand et al. (2010).

1.3. The marine ecosystem with more fish production

As previously indicated, the NHCS is the "heavyweight champion of the world" in terms of fish productivity although it generates considerably less primary production than the Northern Benguela Current System (Bakun and Weeks, 2008).

Different hypotheses have been proposed to explain this paradox:

(i) The proximity to the equator, unique among the EBUSs, allows strong upwelling with relatively weak winds so a weak turbulence (Parrish *et al.*, 1983), which may increase the occurrence of the optimal environmental windows for fish reproduction (Cury and Roy, 1989);
(ii) Differences in the trophic structure within EBUSs (Carr and Kearns, 2003);
(iii) The strong influence of ENSO inter-annual variability might 're-set' the ecosystem and could favour fast-growing populations like small pelagic fishes in the NHCS (Bakun and Weeks, 2008);
(iv) In opposition with other EBUS, the main spawning periods match the season of maximal shelf retention of ichthyoplankton and food concentration in the NHCS for both anchovy and sardine (Brochier *et al.*, 2011).

Despite numerous studies the paradox is still not fully understood and trophic dynamics play probably an important role. Indeed, trophic dynamics greatly influence population dynamics, species coexistence and the organization of communities (Pimm, 1982; Polis and Winemiller, 1996). Species are linked through trophic relationships which denote transfers of energy and nutrients (Odum, 1969; Holt and Loreau, 2002; Link, 2002). Such interactions are commonly called trophic structure or “food web” or “food chain”, and is referred to the way in which organisms use food resources (Shackell *et al.*, 2010). Of this way, a healthy marine ecosystem has a food web with highly interconnected linkages, which can denote the complexity of the ecosystem (Menge, 1995). Thus, the trophic dynamics goals is defining nodes (predator and prey), understand these and the relation with the environment (Latour *et al.*, 2003; Link, 2002; Pikitch *et al.*, 2004).

1.4. A brief history of trophic studies in the NHCS

The search for a quantitative understanding of the dynamics of interactions between the biotic and abiotic components of marine ecosystems, and their effects on the dynamics of fish populations constitutes the foundation of modern fisheries oceanography (Dower *et al.*, 2000). The foundation for fisheries management on an ecosystem-basis must lie in appropriate modelling of the ecosystems. Furthermore, as stated by Denman (2000), “it is almost axiomatic to state that confidence in forecast will increase with the increased use of observations”. Therefore a model (qualitative or quantitative) is constructed according to the available knowledge and hypotheses. So models changes with time when new information are available. In this sense the vision of the trophic dynamics evolved with time in the NHCS so our vision of ecosystem functioning and dynamics.

The first ecosystem perspective of the NHCS was published by Vogt (1948) (Fig. 1.5). The vision was mostly land-based with the seabirds occupying a central role and other land-related organisms (from condor to house fly!) also playing an important position. Indeed at that time, fish were virtually not exploited. On the contrary, seabirds excrement (guano – derived of an Inca word: guanay, the common name of the cormorant *Phalacrocorax bougainvillii* in Peru) was extracted to be used as fertilizer and generated an important role in the Peruvian economy, mainly at 19th century and beginning of the 20th (Chavez *et al.*, 2008). The guano was exported worldwide and in particular in Europe. The importance of guano justified the development of the first marine biology scientific research entity in Peru, the Marine Biology Laboratory (Laboratorio de Biología Marina) of the Compañia Administradora de Guano, which aim was to study and preserve the guanay (Chavez *et al.*, 2008).

During the 1940s a fishery developed on Pacific Eastern bonito (*Sarda chiliensis*) and tuna (primarily *Thunnus albacore*) due to a high demand of the liver oil of these species in the US market during World War II and later the Korean War. The later increased demand for guano and coincidentally the strong El Niño of 1957–1958 led to a dramatic decrease in seabird populations (Chavez *et al.*, 2008). Around 1955 the anchoveta fishery started. The catches were first used as fertilizer and then for producing fish meal.

To accompany the development of the anchovy fishery, the Peruvian government and United Nations established in 1960 the Instituto de Recursos Marinos (IREMAR), which began under the leaderships of FAO. Then, in 1964, was created the Instituto del Mar del Peru (IMARPE), fusioning IREMAR with the Consejo de Investigaciones Hidrobiológicas (CIH). The anchoveta fishery continued to grow during the 1960s to a peak harvest of 12 million tonnes per year in 1970 (actually probably 18 million tonnes when considering for unregistered catches, see Castillo and Mendo, 1987) accounting for 20% of the world catch, and the anchoveta population collapsed in early 1970s due to the combination of the El Niño 1972, the beginning of an unfavourable decadal climatic regime, and overfishing.

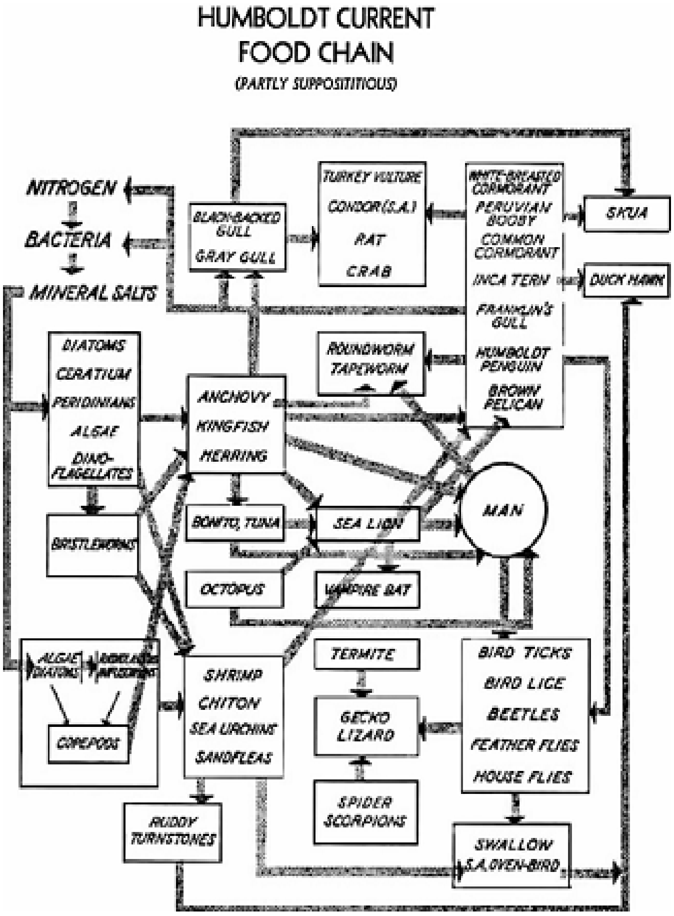

Figure 1.5: First "ecosystem-based" diagram for the Northern Humboldt Current system. Source: Vogt (1948).

Just before the anchoveta collapse, Ryther (1969) published a seminal article considering that anchoveta feed directly on phytoplankton, and this very short and efficient food chain explain the large population of this species (and then is transferred to the top predators. This paper had a considerable impact during decades.

The anchoveta crash led to develop intense scientific studies and an important advance was synthesized by IMARPE in conjunction with ICLARM (now World Fish Center) and the Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) during the mid 1980s (Pauly and Tsukayama, 1987; Pauly *et al.*, 1989a,b).The anchoveta became the centre of the system (Fig. 1.6) but important links and feedbacks between climate, ocean circulation, biogeochemical cycles, trophic webs and fish production were also taken into account (Fig. 1.7).

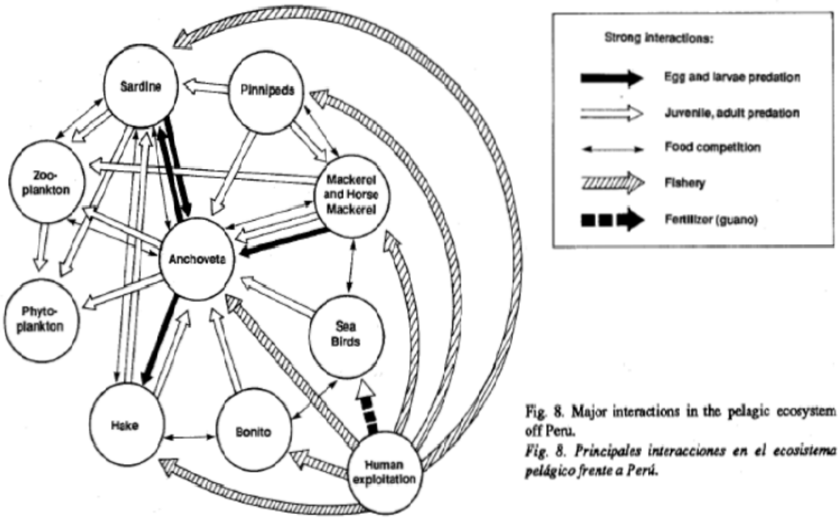

Figure 1.6: Major interaction in the pelagic ecosystem off Peru. Source: Muck (1989).

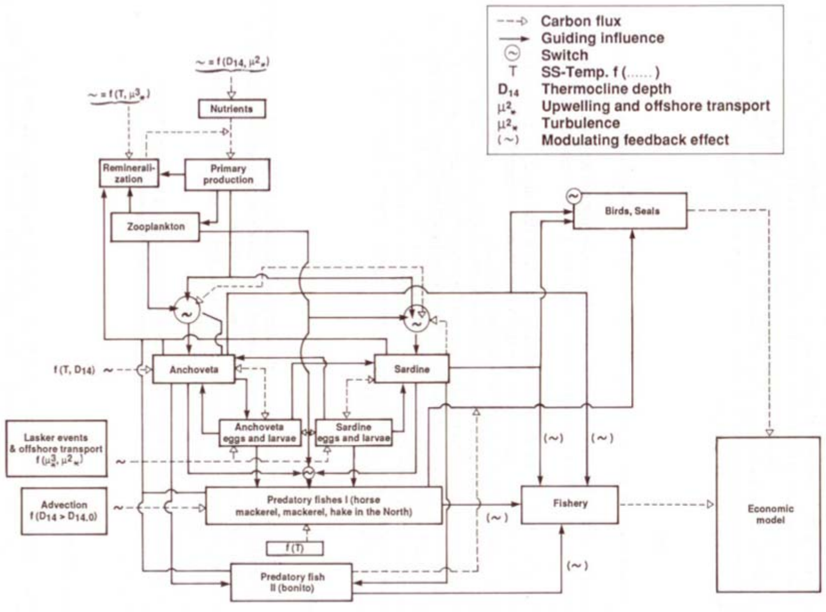

Figure 1.7: Elements to be considered in a simulation model of the Peruvian upwelling ecosystem. Source: Csirke et al. (1989).

In these syntheses and the works later developed from this basis, the anchoveta was considered as mostly filter-feeder and phytoplanktivorous in agreement with Ryther (1969). In this way Jarre-Teichmann (1998) focused on different biological regimes in the 1960s and 1980s with emphasis to set the basis for more sophisticated modelling approaches of the species interactions and how the fisheries impact the ecosystem functioning (Fig. 1.8).

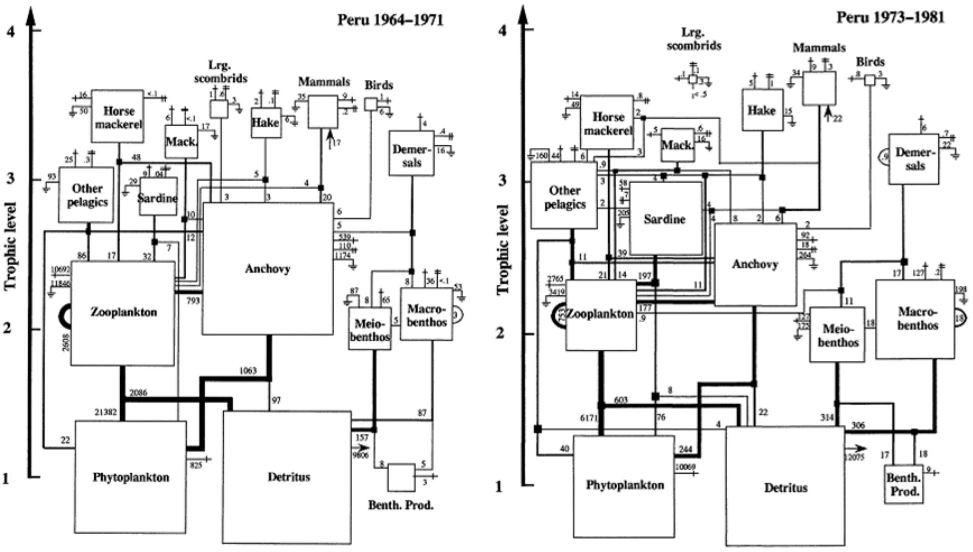

Figure 1.8: Trophic flows average in the Northern Humboldt Current System, from the periods 1964-1971 and 1973-1981. Flows of wet mass are in units of 10^3 $kg.km^{-2}.yr^{-1}$. Flows leave boxes on the upper half and enter them on the lower half. The width of the line indicates the order of magnitude of trophic flows. Biomass of detritus is a rough estimate. Source: Jarre et al. (1991) and Jarre-Teichmann (1998).

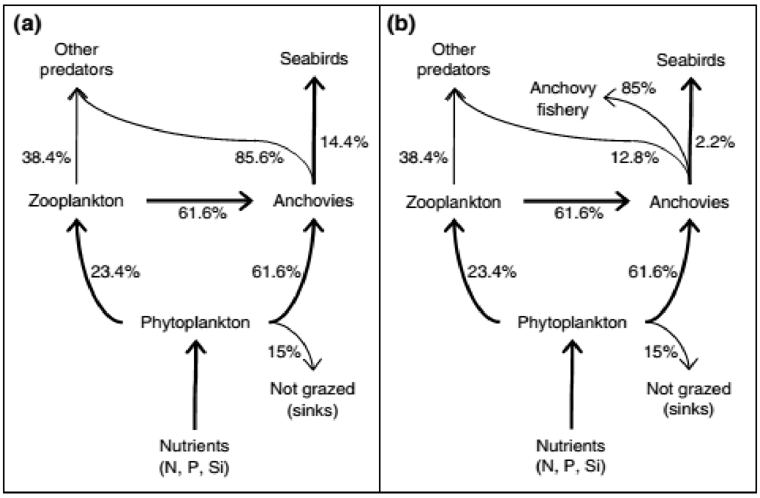

Figure 1.9: Schematic representation of the food web in the Peruvian upwelling system without (a) and with (b) the industrial fishery for anchoveta included in the model. The numbers correspond to the proportion of productivity available at one trophic level consumed by the next trophic level at any given time. Source Jahncke et al. (2004).

Following the efforts to model the trophic dynamics of the NHCS, Jahncke *et al.* (2004) constructed a model from environment to seabirds covering the period 1925-2000 (Fig. 1.9). The model indicates that the growth of seabird populations from 1925 to 1955 was likely a response to increased productivity of the Peruvian upwelling system and that the subsequent drastic decline in seabird abundance was likely due to competition for food with the fishery, which caught 85% of the anchovies, which otherwise would have been available for the seabirds. In this model also the main energetic flux towards anchoveta pass directly through phytoplankton (61.6% of the carbon come directly from phytoplankton, while 61.6% of 23.4%, i.e. 14.4% come from zooplankton; see Fig. 9).

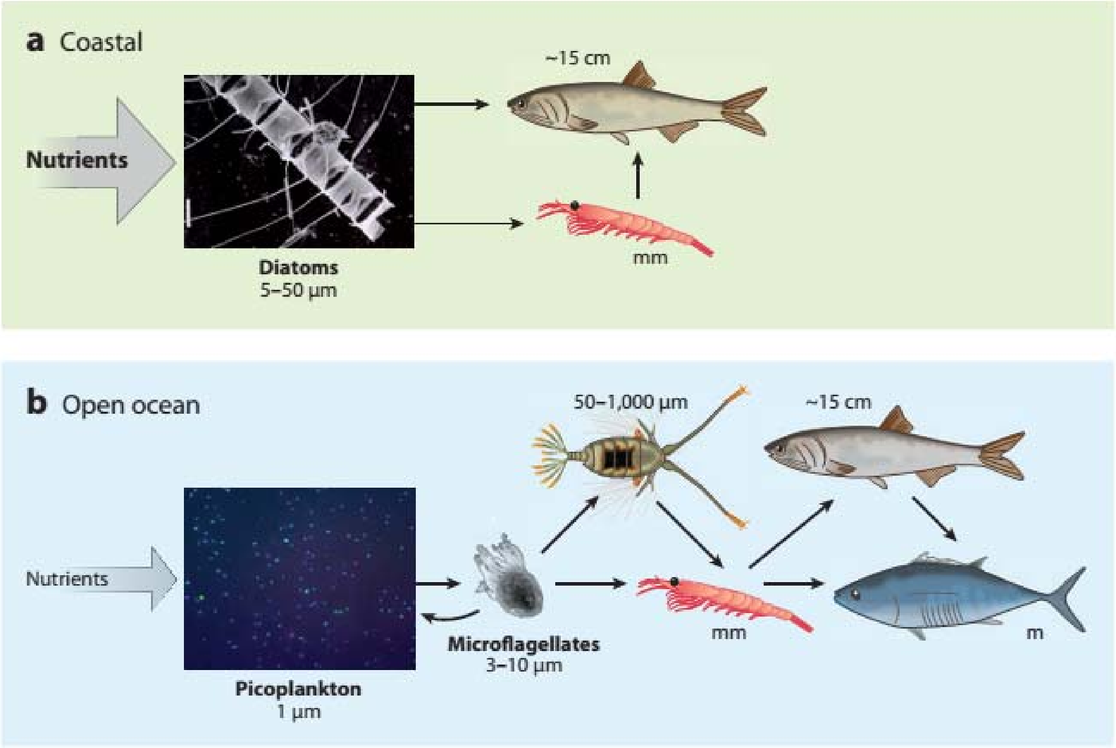

Figure 1.10: Conceptual model of (a) coastal and (b) open ocean pelagic ecosystems. Near coasts the nutrients are abundant, dense, colonial, centric diatom blooms form. The primary production can be transferred rapidly to small plentiful fish and the food chain is short and efficient. In the open ocean, under low nutrient input, photosynthetic picoplanktonic organisms dominate. The consumers of picoplankton are also very small and have growth rates similar to their prey. Scarce nutrients are recycled and retained in the upper layer. Modified from Chavez et al. (2011).

Finally a recent conceptual model, separating the coastal and open pelagic ecosystems (Fig. 1.10), indicated that nutrients were abundant and dense near coasts with the development of transient blooms of colonial centric diatoms. Diatoms accumulate biomass, which can be transferred rapidly from to plentiful small fish (Ryther, 1969). This coastal food chain is short and efficient, but also leaky in the sense that a relatively large fraction of production is often exported (Muller-Karger *et al.*, 2005) either by sinking, and supporting a rich benthic fauna or, alternately, resulting in anoxia (Margalef, 1978), or by horizontal advection away from the coast (Olivieri and Chavez, 2000; Pennington *et al.*, 2010). In the oligotrophic open ocean, small, photosynthetic picoplankton dominate, and the grazers are also small and have growth rates similar to their prey. This small predator–prey is characterized as a complex, low-nutrient input system that exports little of its production (e.g., non-leaky) (Azam *et al.*, 1983; Pomeroy, 1974). This oceanic food chain has low nutrient inputs, efficient internal recycling of nutrients, and need multiple trophic transfers to transform picoplankton production to living marine resources, resulting in much fewer higher-trophic-level or fisheries resources.

As previously indicated, in all these work, the phytoplankton was the base of the diet of forage fish. Indeed, even rather recent works in the NHCS has concluded that anchoveta depends mainly on phytoplankton (Alamo *et al.*, 1996a,b, 1997a,b; Alamo and Espinoza, 1998; Espinoza *et al.*, 1998a,b, 1999, 2000).

1.5. What can be the limit of the historical studies?

In theoretical sense, food-web diagrams summarising predator-prey relationships, feeding strategies, and energetic transfer are time-consuming to construct and are often subjective in their resolution and scope (Paine, 1988). They are considered as informative by linking species and ecosystem-level characteristics (e.g., Stevens *et al.*, 2003; Downing, 2005; Micheli and Halpern, 2005) but have some limitations and may be limited in their predictive power (Petchey and Gaston, 2002; Petchey *et al.*, 2004; Wright *et al.*, 2006). Indeed, many factors stem our ability to observe the relevant taxonomic, spatial, and temporal variations in trophic interactions and these constructions are subjective and potentially strongly biased (Paine, 1988; Petchey *et al.*, 2004).

Further, these diagrams typically hold all trophic links to be of equal importance, which makes them ineffectual for tracking energy or mass flow through ecological communities (Paine, 1988; Hairston and Hairston, 1993; Polis and Strong, 1996; Persson, 1999; Vander Zanden and Rasmussen, 1999). Many trophic interactions cannot be visually observed, and gut analysis is misleading if the gut contents are not assimilated and we should not underestimate the importance of subtle differences among species that manifest only under altered conditions or over long time periods (Duffy, 2002)

In the NHCS, the methods employed to study trophic functioning were not uniform. The diet of the main species (anchoveta and sardine) were based on frequency of occurrence, volume and semi-quantitative methods which have inherent biases and are considered inadequate and subjective to study trophic relationships of planktivorous fishes (James, 1987). For example, methods based on frequency of occurrence, overemphasize small prey over big ones, due to great differences of size range between phytoplankton and zooplankton (10-6-10-5 mm for diatoms to 10 mm for zooplankton). Furthermore, the diet of their fish predators (e.g. hake *Merluccius gayi peruanus* or jack mackerel *Trachurus murphyi*) were based on frequency of occurrence or prey weight (Konchina, 1983), limiting the possibility to compare the diet between groups.

The difficulties afore mentioned plead for a methodology allowing to clarify trophic relationships and distinguish actual trophic links from those potentially possible. The most classic method to study the trophic ecology is the stomach content analysis since it provides high details on ingested prey. However, this technique is time consuming and not suitable if fast results are needed (Olson *et al.*, 2010). Furthermore, it only represents a snapshot of the diet (Estrada *et al.*, 2005) even if it is still particularly suitable in long-term studies to detect changes in the ecosystem and the only technique if information is needed at the species level.

To overcome some limitation, stomach-based analyses can be combined with carbon and nitrogen stable isotope measurements (DeNiro and Epstein, 1978; Kling *et al.*, 1992). The strength of stable-isotope analyses is that they measure actual assimilation integrated over the time scale of tissue turnover in the organism. The use of stable isotopes analysis (SIA) to study trophic dynamics is attractive because it is relatively inexpensive, stable isotopes are easy to measure, and their use allows the quantification of ecological concepts (e.g. food chain length), which can then be tested statistically or experimentally (Post, 2002).

1.6. What are stable isotopes?

Most elements exist in two or more forms, known as isotopes. Isotopes have the same number of protons but differ in their number of neutrons, resulting in different masses. The lighter form is generally the more common one (Hobson and Wassenaar, 2008). This variation in the relative abundance of stable isotopes results from tiny mass differences that cause the isotopes to act differently in chemical reactions and physical processes. The lighter isotope generally forms weaker bonds than the heavier one and tends to react faster. The change in isotopic abundance is called fractionation (Karasov and Martínez del Rio, 2007). Different environments are often characterized by predictable isotopic signatures (West *et al.*, 2006).

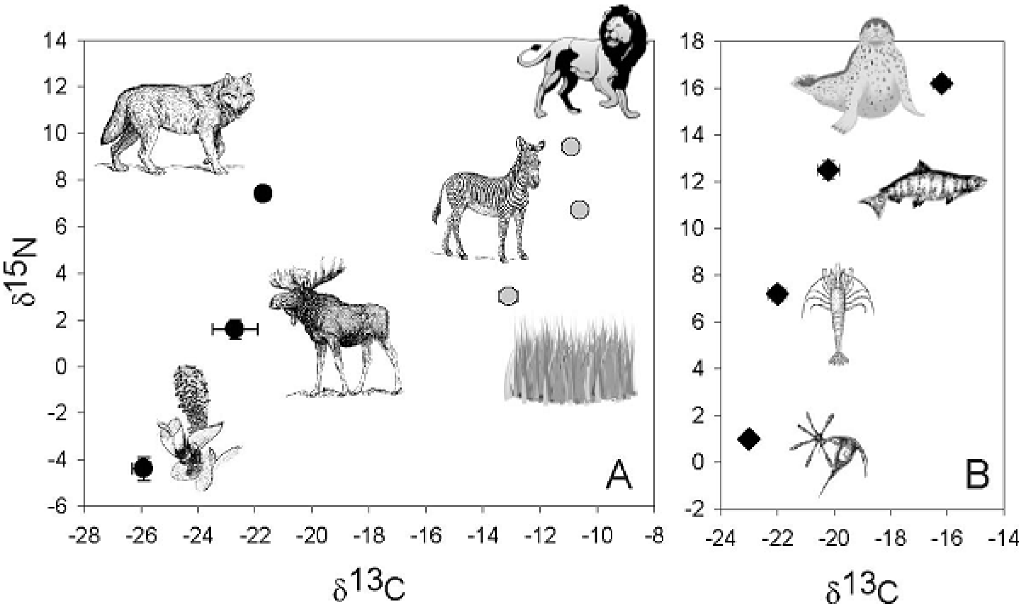

Figure 1.11: Illustration of trophic enrichment in $\delta^{13}C$ and $\delta^{15}N$ from primary producers (plants and diatoms), to herbivores, to predators for A) terrestrial ecosystems and B) marine ecosystems. Panel A also shows differences in $\delta^{13}C$ between food webs based on C_3 (black symbols) and C_4 plants (gray symbols). Values (mean ± SE) were adapted from the literature. Source: Ben-David and Flaherty (2012).

Stable isotopes are measured as isotopic deviations from international standards and are expressed as delta (δ) values as parts per thousand (Werner and Brand, 2001). These values are calculated as follows:

$$\delta X = [(Rsample/Rstandard) - 1] \times 1000$$

where X is the element (such as ^{13}C or ^{15}N), and R is the corresponding isotope ratio ($^{13}C/^{12}C$ or $^{15}N/^{14}N$). The quotient of the ratios in the sample relative to the standard is the δ value. Therefore, an increase in the δ values denotes an increase in the amount of the heavier isotope component; while a decrease in the values denotes a decrease in the heavy isotope content (Peterson and Fry, 1987).

The SIA has been accepted broadly as an important tool to examine animal migration and movement (Hobson, 1999; Rubenstein and Hobson, 2004); resource partitioning (Young *et al.*, 2010); ecophysiological processes (Gannes *et al.*, 1998); and ecosystem fluxes of carbon and nitrogen (Peterson and Fry, 1987). When used in trophic ecology studies, it serves to reconstruct diets (Tieszen *et al.* 1983), to assign species to trophic positions in food webs (Minagawa and Wada, 1984; Fry, 1991; Post, 2002), to elucidate patterns of resource acquisition and allocation (Cherel *et al.*, 2005), and to characterize niche properties (Bearhop *et al.*, 2004, Newsome *et al.*, 2007). The central observation of SIA in trophic ecology is “You are what you eat...plus a few per mille" (DeNiro and Epstein, 1978) (Fig. 1.11).

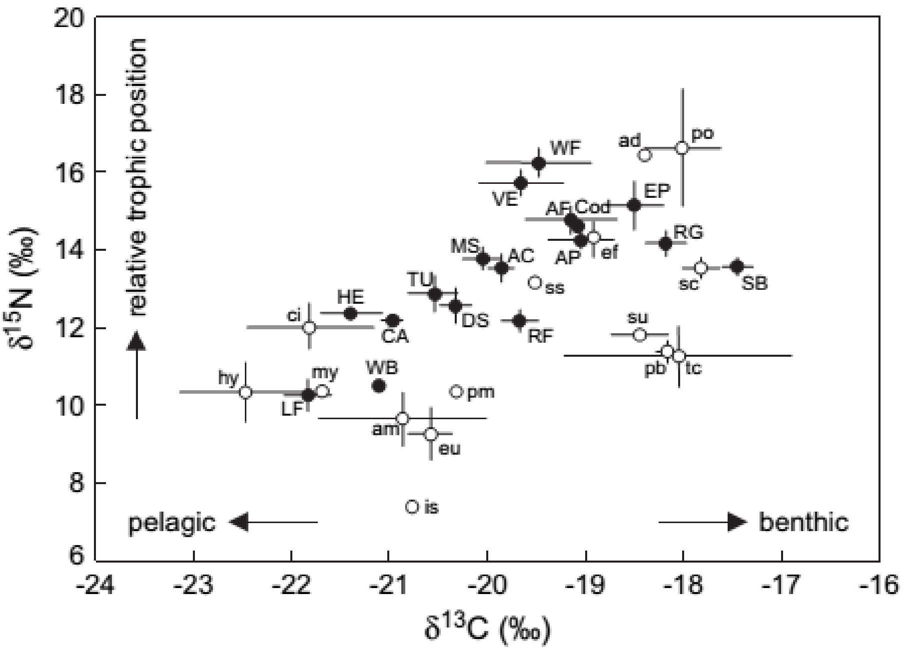

Figure 1.12 Mean (±1 SE) $\delta^{13}C$ versus mean (±1 SE) $\delta^{15}N$ for various fish (solid symbols) and invertebrates (open symbols) of the Newfoundland and Labrador continental shelf food web. The abscissa represents a continuum of feeding types ranging from highly pelagic (more negative, or depleted in ^{13}C) to highly benthic (more positive, or enriched in ^{13}C). The ordinate should represent a continuum of trophic positions. Source: Sherwood and Rose (2005).

The stable isotope ratios of carbon ($^{13}C/^{12}C$, $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$, $\delta^{15}N$) have been used extensively to trace pathways of organic matter among organisms, because the stable isotopic signature of a consumer reflects that of its diet (McCutchan *et al.* 2003). Consumer tissues are stepwise-enriched in ^{15}N relative to their food and consequently $\delta^{15}N$ measurements serve as indicators of a consumer's trophic position (McCutchan *et al.*, 2003; Vanderklift and Ponsard, 2003). In contrast, $\delta^{13}C$ values vary little (no or slight increase) along the food chain and are mainly used to determine primary sources in a trophic network (McCutchan *et al.*, 2003) (Fig. 1.12). However, the carbon and nitrogen isotopic composition of organisms does not only depend on what they eat but also where they eat, because the isotopic composition at the base of the food web (isotopic baseline, i.e., phytoplankton) can greatly vary and has been shown to propagate up to the food web (see below).

1.7. SIA present a series of advantages...

- They have the potential to provide estimates of long-term average trophic position and feeding habits and can therefore detect changes in the trophic functioning of the ecosystem.
- They are cheapest and timeless consuming compared to stomach content analyses.
- They are particularly fruitful to study spatial and ontogenetic changes in the diet of organisms.
- They can provide a continuous measure of trophic position that integrates the assimilation of energy or mass flow through all the different trophic pathways leading to an organism. Stable isotopes have the potential to simultaneously capture complex interactions, including trophic omnivory, and to track energy or mass flow through ecological communities (Peterson and Fry, 1987; Kling *et al.*, 1992, Cabana and Rasmussen, 1996).

1.8. ... but also limitations

- They do not allow the level of precision in prey item identification as the stomach content analysis.
- The SIA depends of the turnover rate i.e. how quickly the isotope signature in a body tissue changes following a dietary change (Buchheister and Latour, 2010). Other process linked to turnover rates is the replacement or conversion of existing tissue using material synthesized from recent diet (i.e., metabolism) (Hesslein *et al.*, 1993). Hence, the blood which is more metabolically active tends to respond more quickly to dietary changes (Tieszen *et al.* 1983; Hobson and Clark, 1992), whereas other tissues such as muscle can require over one year to equilibrate to a constant diet (Hesslein *et al.*, 1993; MacAvoy *et al.*, 2001).
- When comparing among ecosystems, the $\delta^{15}N$ and $\delta^{13}C$ of an organism alone provides little information about its absolute trophic position or ultimate source of carbon, because there is substantial variation among ecosystems in the $\delta^{15}N$ and $\delta^{13}C$ at the base of the food web from which organisms draw their nitrogen and carbon (δ^{15}Nbase, $\delta^{13}C_{base}$; baseline, e.g. Rounick and Winterbourn, 1986; Zohary *et al.*, 1994; Cabana and Rasmussen, 1996; MacLeod and Barton, 1998; Kitchell *et al.*, 1999; Vander Zanden and Rasmussen, 1999). Without suitable estimates of the baseline in each system, there is no way to determine if variation in the baseline of an organism reflects changes in food web structure and carbon flow, or just a variation in the baseline isotopic values. Information on the isotopic baseline is thus required to estimate an organism's trophic position (see paragraph below). These isotopic baselines can be estimated from primary producers such as particulate organic matter (POM) or primary consumers (trophic position TP ~ 2) such as zooplankton (e.g., copepods, Olson *et al.* 2010).

1.9. What is driving the baseline isotopic variations?

A number of studies have suggested that variations in carbon isotope composition among marine animals may be explained, in part, by differences in the isotope composition of marine plants between nearshore and offshore ecosystems (Michener and Schell 1994; Hobson *et al.* 1997). Factors contributing to nearshore-offshore differences in the isotopic composition of organic carbon at the base of marine food webs include differences in (1) the isotopic composition and concentration of dissolved CO_2 (Rau *et al.* 1992; Goericke and Fry 1994; Hinga *et al.* 1994), (2) the species composition and rate of growth of phytoplankton (Fry and Wainright 1991; Pancost *et al.* 1997), and (3) the input of carbon from benthic macrophytes, which are significantly enriched in ^{13}C relative to phytoplankton (Michener and Schell 1994; France1995). In areas of coastal upwelling, these factors lead to the production of relatively ^{13}C enriched organic carbon at the base of the food web. In offshore regions, where nutrients are more limited, phytoplankton growth rates are lower, and macrophytes are absent, organic carbon at the base of the food web is more enriched in ^{12}C. If nearshore-offshore carbon isotope gradients are generated by the effects of differential growth rates of phytoplankton, then differences of 2-3‰ would be expected. Isotopic gradients supported by high nearshore production of benthic macrophytes could be much larger, perhaps 5-6‰ (France 1995).

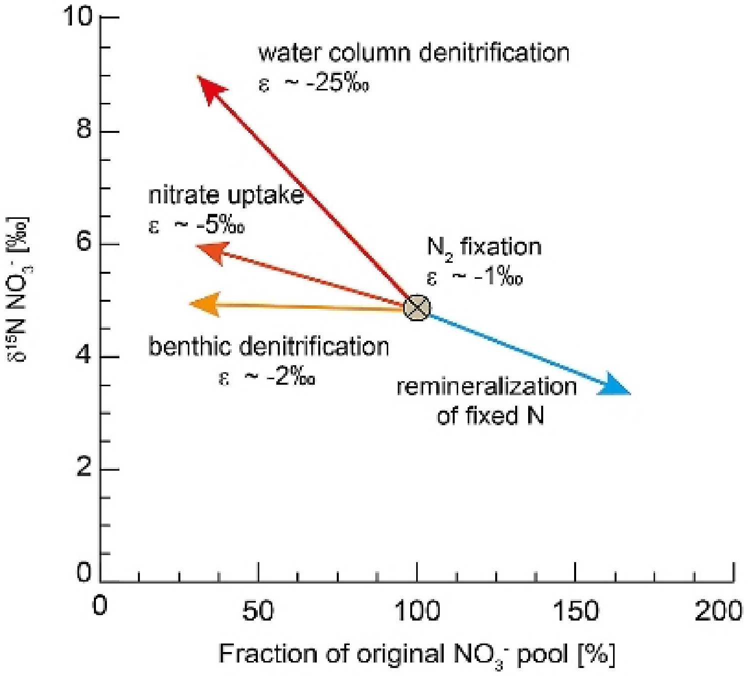

Figure 1.13: Isotopic changes during nitrate turnover in the open ocean. Source: Gruber (2004).

Systematic spatial variations in $\delta^{15}N$ values at the base of marine food webs can also occur in the oceans due to variations in the dominant dissolved N species present, demand for those nitrogenous nutrients by primary producers and N biogeochemical cycling including N inputs from N_2 fixation and atmospheric deposition and N losses due to denitrification and annamox (e.g., Dugdale and Goering 1967, Altabet 2001; Sigman *et al.* 2005). Nitrate, the predominant form of dissolved nitrogen in the open ocean, has an average stable isotope value of approximately 5‰ (e.g., Sigman *et al.*, 2000) (Fig. 1.13). This average value is determined by the interplay of nitrogen fixation on the one and denitrification (here referring to the microbial respiration of nitrate via N_2O to N_2) and anammox (bacterial comproportionation of nitrite and ammonium to N_2) on the other side. Most biological turnover processes discriminate the heavier versus the lighter isotope, leading to a slightly faster turnover of light ^{14}N in comparison to ^{15}N. Dinitrogen fixation has a small isotope effect (Delwiche and Steyn, 1970), and forms light organic matter with an isotope value of ~ −2 to +2‰, which, upon complete remineralization and oxidation, lowers the average $\delta^{15}N_{NO3}$ value in the open ocean (e.g., Montoya *et al.*, 2002; Emeis *et al.*, 2010). On the other hand, denitrification in anoxic water bodies has a large isotope effect of ~−25 ‰ (e.g., Brandes *et al.*, 1998; Voss *et al.* 2001). To date, little is known about the isotope fractionation of anammox in the water column, but it is generally assumed that anammox, just like denitrification, coincides with considerable, possibly similar, isotope fractionation (Naqvi *et al.*, 2006). The most important implication is locally that denitrification and supposingly anammox, can produce NO_3 and organic matter strongly enriched in ^{15}N (up to 20‰). These ^{15}N enrichment in NO_3^- are clearly associated with O_2 minimum zone (OMZ). As expected in regions with significant volumes of suboxic water such as the Eastern Tropical S. Pacific and the Arabian Sea, elevated $\delta^{15}N$ are found (Schäfer and Ittekkot, 1993).

These geographical variations in primary producer stable isotope values, or nitrogen (N) and carbon (C) isoscapes, have been shown to propagate up the food web and to be reflected in the isotope value of predators (Cherel and Hobson 2007; Popp *et al.* 2007; Olson *et al.* 2010; Graham *et al.* 2010; Dale *et al.* 2011). Marine isoscapes can therefore be used to delineate foraging habitats and to infer movements of marine consumers, and have been increasingly applied for this purpose across diverse predator groups, including seabirds, cephalopods, pinnipeds, rays and tunas (e.g., Lee *et al.* 2005; Newsome *et al.* 2007; Ménard *et al.* 2007; Olson *et al.* 2010; Dale *et al.* 2011; Navarro *et al.* 2013).

In addition to incorporating the primary producer $\delta^{15}N$ baseline across their foraging range, predator $\delta^{15}N$ values are also influenced by their diet and foraging ecology as $\delta^{15}N$ values increase with each trophic level (Post 2002; Vanderklift and Ponsard 2003). The complexity of regional food webs, which also influences food chain length, can differ and in turn, affect the relative trophic position of the same predator between regions, i.e., the average trophic level, relative to primary producers, at which that organism feeds (Vander Zanden and Fetzer 2007; Jenning *et al.* 2008). Accurate and reliable assessment of isotopic baselines is therefore critical to estimating a consumer's trophic position and concomitantly food chain length.

The most direct approach to dissecting the effects of foraging location (e.g., nearshore vs offshore, latitude) and trophic level on the isotopic composition of studied organisms would then be to compare isotope compositions of the organism to those from a proxy of the baseline (i.e., phytoplankton).

1.10. Trophic position estimations

Trophic position of a consumer can be calculated using the following equation from Post (2002):

$$TP_{consumer} = (\delta^{15}N_{consumer} - \delta^{15}N_{base}) / TEF + TP_{base}$$

Where TPconsumer is the trophic position of the consumer; $\delta^{15}N_{consumer}$ is the stable nitrogen signature of the consumer; $\delta^{15}N_{base}$ is the stable nitrogen signature of the dietary baseline; TEF is the trophic enrichment factor between a consumer and its prey; and, $TP_{baseline}$ is the trophic position of the baseline. Isotopic baseline is generally assessed through isotopic composition of a primary producer (TP = 1 such as POM) or a primary consumer (e.g., mussels or zooplankton, TP = 2). POM does not only reprensent primary producers and can be a mixture of several organisms, a TP of 1.5 is then often assumed instead of 1. Accordingly, mussels or zooplankton are not always strict primary consumers as they can be omnivorous. TP for these organisms vary in publications between 2 and 2.5. The most commonly TEF value used is 3.4 (Minagawa and Wada 1984), but there is substantial variations around this value and other studies for example suggested the use a TEF of 2.4 for marine fish (Vanderklift and Ponsard 2003; Olson et al 2010).

Figure 1.14 illustrates that even if the $\delta^{15}N$ isotopic values of two consumers are identical (the two stars), they can have very different trophic position (TP) when adjusted to the corresponding isotopic baseline values.

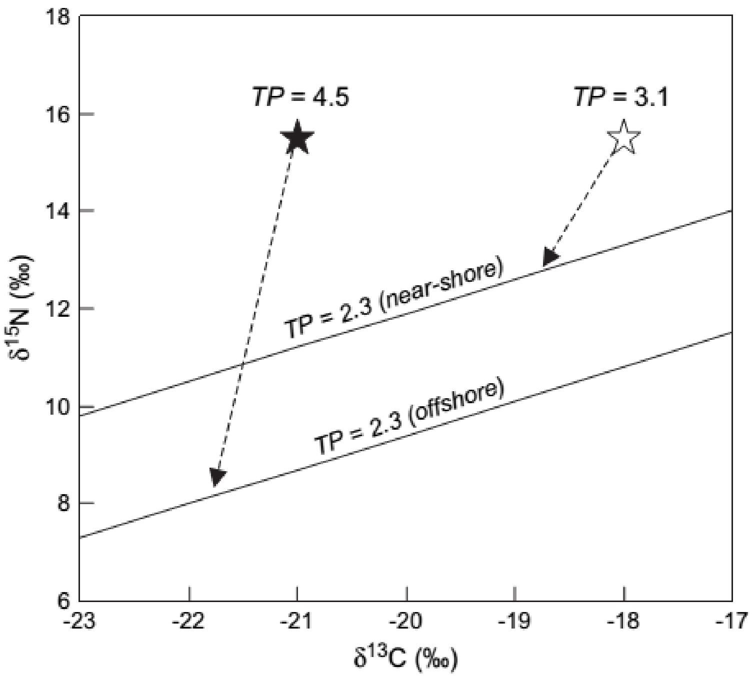

Figure 1.14: Conceptual representation of the calculation used to estimate trophic position of consumers (relative to assumed trophic position 2.3 for benthic or pelagic invertebrates) from the Newfoundland and Labrador continental shelf food web. The two stars have the same $\delta^{15}N$ signature (i.e. 15.5‰), but very different trophic positions; the white star represents a near-shore, benthic consumer that is much closer to the baseline than the black star (an offshore, pelagic consumer). Calculation assumes classical trophic fractionation factors of 3.4‰ for $\delta^{15}N$ and 0.8‰ for $\delta^{13}C$. Hence, consumers are offset to the right of their appropriate baseline $\delta^{13}C$ signature, which is actually the $\delta^{13}C$ signature of their prey (i.e. we assumed trophic fractionation of $\delta^{13}C$ only between consumers and their prey). Source: Sherwood and Rose (2005).

1.11. Specific case of oxygen minimum zones such as in the Humboldt ecosystem

As explained earlier, the Humboldt ecosystem off Peru is characterised by permanent or seasonal upwellings and by a strong OMZ that changes in intensity and depth of occurrence with latitude. Under such conditions, strong denitrification is supposed to occur, leading to high baseline $\delta^{15}N$ values. For decades, oceanic N-loss has been attributed entirely to heterotrophic denitrification. However, recent studied showed that anammox is the main N-loss process in the Peruvian OMZs (Lam *et al.* 2009; Kalvelage *et al.* 2013). The nitrogen fractionation of anammox, is still being investigated but is supposed to be the same as denitrification.

Hence baseline $\delta^{15}N$ in this region may reflect both, water-column N-loss (denitrification and anammox) increasing the $\delta^{15}N$ of upwelled NO_3^- , as well as its subsequent partial utilization in surface waters causing $\delta^{15}N$ in organic matter to be lower than upwelled $\delta^{15}N_{NO3^-}$ values (Mollier-Vogel *et al.* 2012). Organic matter $\delta^{15}N$ is then expected to vary spatially and temporally with a) subsurface OMZ intensity and b) surface gradients in the relative nitrate utilization, respectively.

The intensification of the oxygen deficient condition to the south of Peru south of 8°S (Fuenzalida *et al.*, 2009) would then contribute to latitudinal gradients in the $\delta^{15}N$ baseline values, with highest denitrification and therefore highest $\delta^{15}N$ values in the south. Indeed, a North to South gradient of $\delta^{15}N$ values has been observed along the Peruvian margin (Mollier-Vogel *et al.* 2012). The surface sediment $\delta^{15}N$ data along the margin can be separated into a northern (1°N to 8°S) and southern (8°S to 18°S) group (Fig. 3a). In the north, sediment $\delta^{15}N$ values are relatively low and uniform, ranging only between 4 to 5‰. In the southern part, values generally increase southward but reveal a larger range between 4.5 and 13‰.

Furthermore, variations of the size of the continental shelf over the north south gradient can lead to onshore offshore differences in both nitrogen and carbon isotopes.

Given these potential spatial variations in the stable isotopes values of the baseline off Peru, it is therefore essential to assess these variations to correctly interpret stable isotopes variations in the entire food web.

1.12. THESIS CHAPTERS

Taking into account this context, the main objective of this study is to better understand the trophic flows in the NHCS using both stomach content and stable isotope analyses. The study focuses on a variety of organisms from low trophic levels such as zooplankton to top predators, in an environment strongly influenced by persistent upwelling and OMZ. This study combines both long-term and specific studies on emblematic species such as anchoveta (Chapters 2 and 3), and sardine (Chapter 4), followed by a more inclusive approach considering the 'global' food web in the recent years (2008 – 2012) using stable isotope analysis (Chapter 5), and ends with general conclusion (Chapter 6):

CHAPTER 2

The first step to reach a comprehensive vision of the trophodynamics in the NHCS was to focus on the most important pelagic fish of the system, the anchoveta. For that purpose we analyse 21,203 anchoveta stomach contents sampled during 23 acoustic surveys over the period 1996–2003. We show that whereas phytoplankton largely dominated anchoveta diet in terms of numerical abundance and comprised >99% of ingested prey items, the carbon content of prey items indicated that zooplankton was by far the most important dietary component, with euphausiids contributing 67.5% of dietary carbon followed by copepods (26.3%). Then we use generalized additive models to examine stomach fullness variability relative to the diel cycle, the distance from the coast, sea surface temperature, and latitude. Results show that anchoveta feed mainly during daytime, although night-time feeding also made a substantial contribution to total food consumption. Stomach fullness also varied with latitude, distance from the coast, and temperature, but with substantial variability indicating a high degree of plasticity in anchoveta feeding behaviour. The results suggest an ecological role for anchoveta that challenges current understanding of its position in the foodweb, the functioning and the trophic models of the NHCS (Espinoza and Bertrand, 2008).

CHAPTER 3

To complete the study of anchovy trophodynamics and get new insight on ontogenetic and spatiotemporal variability in anchoveta diet we use available historical SC data since 1954. We show that whatever the period, anchoveta forage mainly on macrozooplankton. The importance of euphausiids in anchoveta diet appears directly related to euphausiids abundance. This bottom-up effect is also observed at smaller scale since the euphausiids fraction increases with anchoveta size and euphausiids accessibility. Selecting the largest prey, the euphausiids, provide an energetic advantage for anchoveta in its ecosystem where oxygen depletion imposes strong metabolic constrain to pelagic fish. Finally this study is another illustration of anchoveta plasticity which allows it to cope with its highly variable environment (Espinoza and Bertrand, 2014).

CHAPTER 4

After anchoveta, sardine is an important pelagic fish species of the NHCS. During the last decades, sardine *Sardinops sagax* was abundant from the mid 1970s to the late 1990s; then sardine collapsed in early 2000s. Trophodynamics and prey-size structure can be one of the factors explaining fish population variability (van der Lingen *et al.*, 2009). It is thus important to improve knowledge on sardine diet. For that purpose we describe the diet of sardinetrhough stomach contents in the NHCS, and compare our results with the diet of anchoveta Engraulis ringens off Peru and with the diets of sardines from the southern Benguela (also S. sagax) and the northern Canary (Sardina pilchardus) upwelling systems. The diet of sardine off Peru is based primarily on zooplankton, similar to that observed for anchoveta but with several important differences. Firstly, sardine feed on smaller zooplankton than do anchoveta, with sardine diet consisting of smaller copepods and fewer euphausiids than anchoveta diet. Secondly, whilst phytoplankton represents <2% of sardine dietary carbon, this fraction is dominated by dinoflagellates, whereas diatoms are the dominant phytoplankton consumed by anchoveta. Hence, trophic competition between sardine and anchovy in the northern Humboldt Current system is minimized by their partitioning of the zooplankton food resource based on prey size, as has been reported in other systems. Whereas sardine in the NHCS feed on smaller zooplankton than do anchovy in that system, sardine in the NHCS forage on larger prey and obtain a substantial portion of their dietary carbon from euphausiids compared to sardine from the northern Canary and southern Benguela Current systems (Espinoza *et al.*, 2009).

CHAPTER 5

Finally to obtain a more comprehensive vision of the relative trophic position of NHCS main components, we used stable iotope analyses from zooplankton to top predators in an environment strongly influenced by persistent upwelling and OMZ. For that purpose we analyzed the $\delta^{13}C$ and $\delta^{15}N$ stable isotope values of thirteen taxonomic categories collected off Peru from 2008 - 2011, i.e., zooplankton, fish, squids and air-breathing top predators. The $\delta^{15}N$ isotope signature was strongly impacted by the species, the body length and the latitude. Along the Peruvian coast, the OMZ get more intense and shallow south of ~7.5ºS impacting the baseline nitrogen stable isotopes. Also, the sampling design was unbalanced in terms of body length and geographical position. To compare $\delta^{15}N$ values and being able to estimate the trophic position (TP) of each species we employed a linear mixed-effects modelling approach taking into account the latitudinal and body length effects. We provide a new vision of the relative trophic position of key ecosystem components. Also we confirm previous stomach content-based results on anchoveta *Engraulis ringens* TP and highlight the potential remarkable importance of an often neglected ecosystem component, the squat lobster *Pleuroncodes monodon*. Indeed, our results support the hypothesis according to which this species forage to some extent on fish eggs and larvae and can thus predate on the first life stages of exploited species. However, the $\delta^{13}C$ values of these two species suggest that anchoveta and squat lobster do not exactly share the same habitat, with anchoveta having a larger and more offshore foraging range. This would potentially reduce some direct competition and/or predation.

CHAPTER 6

The manuscript ends with 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 key next steps. To do so we will use information from studies (van der Lingen *et al.*, 2009; Ayón *et al.*, 2011; Argüelles *et al.*, 2012, Alegre *et al.,* 2013, 2014) related with this dissertation.

CHAPTER 2

Revisiting Peruvian anchovy (*Engraulis ringens*) trophodynamics provides a new vision of the Humboldt Current system

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Espinoza, P. & Bertrand, A. (2008) Revisiting Peruvian anchovy (*Engraulis ringens*) trophodynamics provides a new vision of the Humboldt Current system. *Progress in Oceanography,* 79, 215-227.

Abstract:

The Peruvian anchovy or anchoveta (*Engraulis ringens*) forages on plankton and is a main prey for marine mammals, seabirds, fish, and fishers, and is therefore a key element of the food web in the Humboldt Current system (HCS). Here, we present results from the analysis of 21,203 anchoveta stomach contents sampled during 23 acoustic surveys over the period 1996–2003. Prey items were identified to the genus level, and the relative dietary importance of different prey was assessed by determination of their carbon content. Variability in stomach fullness was examined relative to the diel cycle, the distance from the coast, sea surface temperature, and latitude, using generalized additive models (GAMs). Whereas phytoplankton largely dominated anchoveta diets in terms of numerical abundance and comprised >99% of ingested prey items, the carbon content of prey items indicated that zooplankton was by far the most important dietary component, with euphausiids contributing 67.5% of dietary carbon followed by copepods (26.3%). Stomach fullness data showed that anchoveta feed mainly during daytime between 07h00 and 18h00, although night-time feeding also made a substantial contribution to total food consumption. Stomach fullness also varied with latitude, distance from the coast, and temperature, but with substantial variability indicating a high degree of plasticity in anchoveta feeding behaviour. The results suggest an ecological role for anchoveta that challenges current understanding of its position in the foodweb, the functioning of the HCS, and trophic models of the HCS.

Key words: Anchoveta *Engraulis ringens*, Carbon content, Diel feeding behaviour, Trophodynamics, Peru Humboldt Current system, Plankton

2.1. Introduction

The Peruvian anchovy or anchoveta *Engraulis ringens*, is ecologically and economically the most important pelagic fish species in the Humboldt Current system (HCS). Anchoveta is the major prey of the principal top predators including marine mammals, seabirds, fish and fishers, and more than 250 million tons of anchoveta have been harvested by the purse seine fishery since the 1950s. Anchoveta forage on plankton and is a key element of the marine food web in the HCS and have been the subject of many studies (e.g. the books edited by Pauly and Tsukayama, 1987; Pauly *et al.*, 1989a).

The first trophodynamic studies on anchoveta in Peru concluded that anchoveta subsisted mainly on phytoplankton (Rojas, 1953; Rojas de Mendiola, 1969), and the ability of clupeoids like anchoveta to feed at low trophic levels (directly on primary producers) was suggested as the reason such large populations, biomasses and fisheries could be sustained in upwelling systems (Ryther, 1969). Later studies suggested that in addition to filter-feeding on phytoplankton, anchoveta could also particulate feed on zooplankton (Rojas de Mendiola, 1989; Alamo, 1989), and zooplankton was sometimes considered equally important as phytoplankton in anchoveta diets (Alamo, 1989; Pauly *et al.*, 1989b; Jahncke *et al.*, 2004). With the exception of Konchina (1991), who suggested that anchoveta preferentially consume zooplankton, all other recent work in the HCS has concluded that anchoveta depends mainly on phytoplankton (Alamo *et al.*, 1996a,b, 1997a,b; Alamo and Espinoza, 1998; Espinoza *et al.*, 1998a,b, 1999, 2000). However, these studies were based on counts of anchoveta prey, a method considered to be inadequate for estimating dietary importance (James, 1987; Konchina and Pavlov, 1995). In contrast, methods based on prey weight (e.g. gravimetric) or on nutritional value (e.g. carbon content, caloric or energetic value) may be more ecologically relevant (Hyslop, 1980; Koslow, 1981; James, 1987; Konchina and Pavlov, 1995; van der Lingen *et al.* 2006, 2009). In other upwelling systems, these latter methods indicate that zooplankton, rather than phytoplankton, support clupeoid populations (e.g.Koslow, 1981; James, 1987; James and Chiappa-Carrara, 1990; Chiappa-Carrara and Gallardo-Cabello, 1993; van der Lingen *et al.*, 2006).

Konchina (1991) results highlighting the significance of zooplankton in the diet of anchoveta were based on gravimetric analysis of prey importance, but his study was based on a very small sample size (n= 65 fish). Here we revisit Peruvian anchoveta diet and feeding behaviour in Peru using a database which contains information on the stomach contents of 21,203 anchoveta sampled along the Peruvian coast (1996–2003). In particular we assess the relative importance of different prey types to anchoveta using a method which estimates the carbon content of prey items. We also describe variations in anchoveta stomach fullness in relation to the diel cycle, latitude, distance to the coast, and sea surface temperature, using generalized additive models. Our results confirm Konchina (1991) finding that Peruvian anchoveta subsist primarily on zooplankton, and suggest an ecological role for anchoveta that challenges current understanding of the functioning of the HCS.

2.2. Materials and methods

2.2.1. Sampling

Data were collected during 23 IMARPE (Instituto del Mar del Perú) acoustic surveys between 1996 and 2003 with the aim of estimating pelagic fish abundance in the Peruvian EEZ (Table

2.1). Fish were collected by pelagic trawling conducted throughout the survey area (Fig. 2.1), and a sub-sample of 10–50 anchoveta was randomly collected from each trawl. At sea, individual anchoveta were measured (total length) to the nearest 0.5 cm and weighed to the nearest 0.1 g, and the cardiac and pyloric sections of their stomachs were extracted fixed in 5% formalin. In the laboratory, stomach contents were extracted and weighed (wet weight, WW) to the nearest 0.01 g for samples collected between 1996 and the summer of 2001, and to the nearest 0.001 g thereafter. Stomach fullness was calculated by dividing individual stomach content weight by fish wet weight and was expressed as a percentage of fish wet weight (Hureau, 1970). The stomach contents of individual fish were then pooled into 2 cm size classes for each sub-sample, and pooled stomach contents were filtered through a 125 µm mesh. The filtered material was diluted to 100 mL using filtered seawater and a 0.1 mL sub-sample was examined under the compound microscope to identify and count phytoplankton prey. The material that remained on the mesh was diluted to 100 mL using filtered seawater and a 10 mL sub-sample was examined using a stereoscopic microscope to identify (to genus) and count zooplankton prey. All prey counts were then standardized to number per 100 mL, except for anchoveta eggs, for which the whole sample was examined.

Table 2.1: Survey code, start and end date, the number of trawls, and the number, length range (in cm) of anchoveta collected for stomach content analysis during this study.

Survey code	Start date	End date	Nº of trawls	Nº of stomach	Anchoveta length range (Min - Max)
960204	10 Feb. 1996	01 Apr. 1996	49	633	9 – 19
960809	11 Aug. 1996	27 Sep. 1996	70	1021	5.5 - 19.5
961112	16 Nov. 1996	19 Dec. 1996	39	639	9.5 – 19
970204	13 Feb 1997	23 Apr. 1997	45	739	8 - 19.5
970910	04 Sep. 1997	05 Oct. 1997	51	1259	6.5 – 19
980305	27 Mar. 1998	01 My. 1998	35	687	9.5 – 18
980809	23 Aug. 1998	17 Sep. 1998	36	624	4 – 16
981112	30 Nov. 1998	21 Dec. 1998	36	798	4 - 16.5
990203	14 Feb. 1999	28 Mar. 1999	75	1266	10 – 17
990809	28 Aug. 1999	17 Sep. 1999	19	336	10 – 18
991112	12 Nov. 1999	14 Dec. 1999	70	1412	8 – 18
000102	20 Jan. 2000	26 Feb. 2000	124	2277	6.5 - 18.5
000607	10 Jun. 2000	06 Jul. 2000	50	928	7.5 - 18.5
000809	28 Aug. 2000	23 Sep. 2000	38	574	7 - 18.5
001011	11 Oct. 2000	13 Nov. 2000	45	846	6.5 – 18
010204	03 Mar. 2001	10 Apr. 2001	78	1630	8.5 - 18.5
010708	05 Jul. 2001	06 Aug. 2001	83	1596	6.5 – 19
020203	21 Feb. 2002	18 Mar. 2002	83	1650	7 – 18
0208	10 Aug. 2002	31 Aug. 2002	30	281	9.5 – 17
021011	01 Oct. 2002	13 Nov. 2002	36	416	10 – 17
030203	26 Feb. 2003	31 Mar. 2003	45	524	6.5 - 17.5
030809	16 Aug. 2003	15 Sep. 2003	26	243	7.5 - 17.5
031012	24 Oct. 2003	10 Dec. 2003	36	824	4.5 - 17.5

2.2.2. Estimation of prey volume, dry weight and carbon content

Different procedures were followed to estimate the carbon content of phytoplankton and zooplankton and hence determine their relative dietary importance. We did not measure the size of any prey items but instead used information from the literature to estimate prey size; the lack of available references on size and volume for planktonic organisms off Peru led us to use a wide range of references published for other ecosystems. Phytoplankton size was converted to phytoplankton cell volume using references describing the organism's geometric shape and providing equations relating shape to volume, with the coefficients for each equation being obtained from the literature or from estimations made by IMARPE (Annex 1). To transform volume into carbon content we used equations given in Menden-Deuer and Lessard (2000) and Verity and Langdon (1984) (Table 2.3). For zooplankton, prosome or total organism length was estimated from the literature or from some direct measurements made by IMARPE on zooplankton from stomach content samples (Table 2.2). Zooplankton dry weight and carbon content were calculated using equations given by Alexandrov (2001), Deibel (1986), James (1987), van der Lingen (2002), Parsons *et al.* (1984) and Sameoto (1971) (Table 2.4). All prey carbon content values were standardized to µg C, and were expressed as a percentage of all fish examined in each cruise.

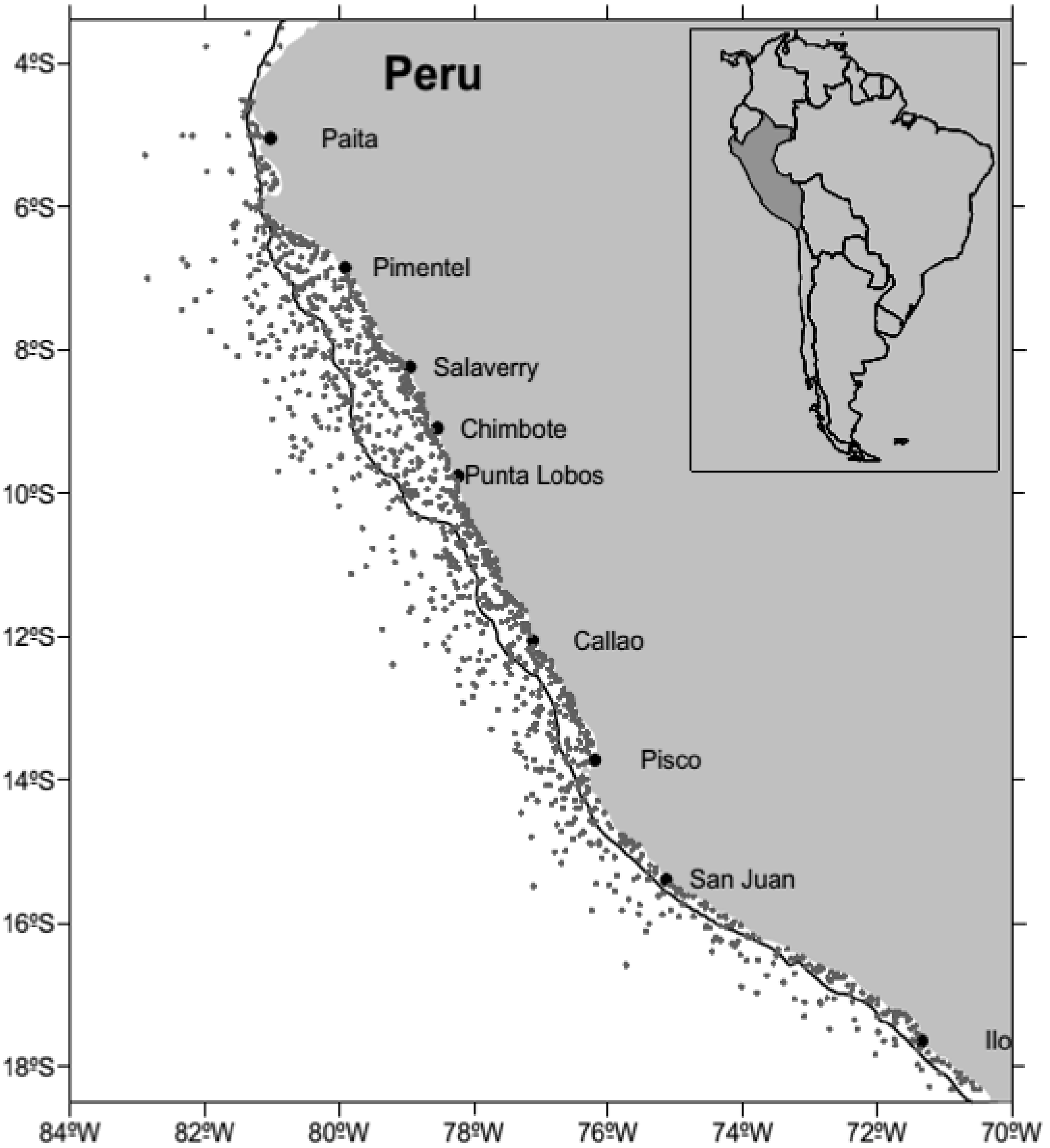

Figure 2.1: The locations of trawls (grey dots) from which anchovetas were collected for trophodynamic analysis. The black solid line indicates the 200 m isobaths

Table 2.2: Type and size of zooplankton recorded from anchoveta stomach contents; length was estimated by IMARPE except where indicated.

Name	Type	Length (mm)
Acartia	Calanoida	0.9375[a]
Aetideus	Calanoida	1.5
Calanus	Calanoida	2[b]
Calocalanus	Calanoida	1[c]
Candacia	Calanoida	1.1666[a]
Centropages	Calanoida	1.5[a]
Clausocalanus	Calanoida	0.65[b]
Clytemnestra	Harpacticoida	0.66[b]
Copilia	Poecilostomatoida	1.75[a]
Corycaeus	Cyclopoida	1[a]
Corycella	Poecilostomatoida	0.65
Euaetideus	Calanoida	0.9[b]
Eucalanus	Calanoida	4
Euchaeta	Calanoida	1.08[b]
Euchirella	Calanoida	2.5[b]
Euterpina	Harpacticoida	0.5[c]
Haloptilus	Calanoida	1.2[a]
Lubbockia	Poecilostomatoida	0.8
Lucicutia	Calanoida	1.03[a]
Macrosetella	Harpacticoida	0.7
Mecynocera	Calanoida	0.899[a]
Microsetella	Harpacticoida	0.7[c]
Nonocalanus	Calanoida	1.5
Oithona	Cyclopoida	0.5[a]
Oncaea	Poecilostomatoida	0.667[a]
Paracalanus	Calanoida	0.8[b]
Phaena	Calanoida	0.8
Pleuromamma	Calanoida	1.2[b]
Pontellina	Calanoida	1.5
Rhincalanus	Calanoida	4
Saphirina	Poecilostomatoida	2.3[b]
Scolecithrix	Calanoida	1.7[b]
Scolecithtricella	Calanoida	1.8[b]
Temora	Calanoida	1.2[b]
Harpacticoida		0.6[c]
Copepoditos		0.5[a]
Restos de copépodos		0.25
Euphausiacea		12[b]
Amphipoda		8[b]
Ostracoda		0.7
Zoea		2
Megalop		3
Cirriped larvae		0.1
Emerita sp. Larvae		5
Decapod undetermined larvae		5
Pagurus sp.		5
Pleuroncodes monodon		7
Decapoda Reptantia n/i		3
Galatheidae		7
Bivalvia		1.25
Gastropoda		1.25
Anchoveta eggs		vol: 0.27 mm^3[d]
Apendicularia		10
Echinoderm larvae		1
Chaetognata		8[b]
Squid remains		10
Polychaeta		10
Anchoa sp. Eggs		vol: 0.27 mm^3
Engraulidae eggs		vol: 0.27 mm^3
Fish eggs		vol: 0.27 mm^3
Fish larvae		15
Fish undetermined		15
Engraulidae		15
Vinciguerria sp.		15
Myctophidae		15

[a] http://earth.leeds.ac.uk/cyclops/data/ncfs-zooplank.xls

[b] Santander *et al.* (1981)

[c] Tudela and Palomera (1997)

[d] Llanos-Rivera and Castro (2004)

Table 2.3: Relationships employed to calculate dry weight and carbon content of the different categories of phytoplankton and zooplankton. Carbon contents not in µg were transformed in µg for comparison; PL: prosome length (µm); TL: total length (mm); DW: dry weight (µg); WW: wet weight (µg).

Phytoplankton	Volume (µm^3) to Carbon (pg)	
Diatoms	C=0.288 Vol$^{0.811a}$	
Dinoflagellates and other phytop.	C=0.760 Vol$^{0.819a}$	
Tintinnids, Foraminifera, Radiolaria	C=445.5 + 0.053 Vol^{b}	
Zooplankton	Length to dry weight (µg) regression	dry weight (µg) to carbon (µg)
Calanoid copepods	Ln(DW) = 2.74ln(PL) – 16.41^{c}	C=0.424 DW^{c}
Cyclopoid copepods	Ln(DW) = 1.96ln(PL) – 11.64c	C=0.424 DW^{c}
Harpacticoid copepods	Ln(DW) = 1.96ln(PL) – 11.64^{c}	C=0.424 DW^{c}
Poecilostomatoid copepods	Ln(DW) = 1.96ln(PL) – 11.64^{c}	C=0.424 DW^{c}
Euphausiacea	DW=0.0012 TL$^{3.16ci}$	C=0.424 DW^{cj}
Amphipoda, Echinoderm larvae	DW=0.005 TL$^{2.311ci}$	C=0.370 DW^{dj}
Ostracods, zoea, megalops, crustacea larvae, hermit crab and Galatheidae	DW=3.946 TL$^{2.436c}$	C=0.424 DW^{c}
Bivalvia, Gasteropod	DW=47.386 TL$^{3.663d}$	C=0.424 DW^{c}
Fish eggs	DW=0.093 Vol+0.0012^{ck}	C=0.457 DW^{c}
Apendicularia	DW=11.3TL$^{1.77e}$	C=0.387 DW^{e}
Chaetognaths	DW=0.00097 TL$^{2.2365fi}$	C=0.290 DW^{f}
Fish, squid and fish larvae	DW=0.0001 TL$^{3.582di}$	C=0.38 DW^{g}
Polychaeta	WW=0.01 TL$^{2.136h}$ DW=0.157 WW^{hi}	C=0.518 DW^{hj}

[a] Menden-Deuer and Lessard (2000)
[b] Verity and Langdon (1984)
[c] van der Lingen (2002)
[d] James (1987)
[e] Deibel (1986)
[f] Sameoto (1971)
[g] Parsons *et al.* (1984)
[h] Alexandrov (2001)
[i] DW in mg
[j] C in mg
[k] volume= 0.27 mm^3, from Llanos-Rivera and Castro (2004) as anchoveta eggs dominated fish egg fraction

2.2.3. Data analysis

For each survey from which anchoveta were collected for trophodynamic analysis we sought potential relationships between stomach fullness and the diel cycle, latitude, distance to the coast, and sea surface temperature. As the relationships are likely to be nonlinear and multivariate, a generalized additive modelling (GAM) approach was used (Hastie and Tibshirani, 1990) using S-Plus software (Insightful Corporation, Seattle, WA, USA). Cubic spline smoothers were used to estimate these nonparametric functions, and separate GAM models were performed for each survey, and also for all the surveys combined.

2.3. Results

A total of 21,203 anchoveta (*E. ringens*) ranging from 3 to 18 cm total length were analysed (Table 2.1). In total, 132 prey taxa were identified: 38 diatoms, 16 dinoflagelates, 2 silicoflagelates, 1 phytoflagelate, 4 microflagellates, 9 tintinnids, 34 copepods, and 28 other items (Tables 2.2 and Annex 1). Mean stomach fullness was 0.68% of fish WW, and varied between 0.29% WW in February–March 1999 and 1.23% WW in August–September 1998 (Fig. 2.2).

2.3.1. Dietary composition

Numerically, phytoplankton dominated anchoveta diet and comprised 99.52% of all ingested prey; copepods represented only 0.07%, euphausiids 0.003%, and other prey items accounted for only 0.40% of the total number of prey (Fig. 2.2). This view of anchoveta diet changes dramatically when prey carbon content is considered (Fig. 2.2); zooplankton was by far the most important component and contributed 98.0% of dietary carbon, whilst phytoplankton contributed only 2.0%. Among zooplankters, euphausiids dominated (contributing 67.5% of dietary carbon), followed by copepods (26.3%), and other zooplankton (4.2%). Other groups were much less important in terms of their carbon contribution, including Gastropoda (0.76%), Polychaeta (0.75%), lantern fish (*Vinciguerria lucetia* and myctophids) (0.45%), anchoveta eggs (0.40%), Amphipoda (0.40%), Bivalvia (0.31%), zoea (0.29%), megalopa (0.29%), and the red shrimp *Pleuroncodes monodon* (0.01%), but their presence illustrates the omnivorous feeding behaviour of anchoveta.

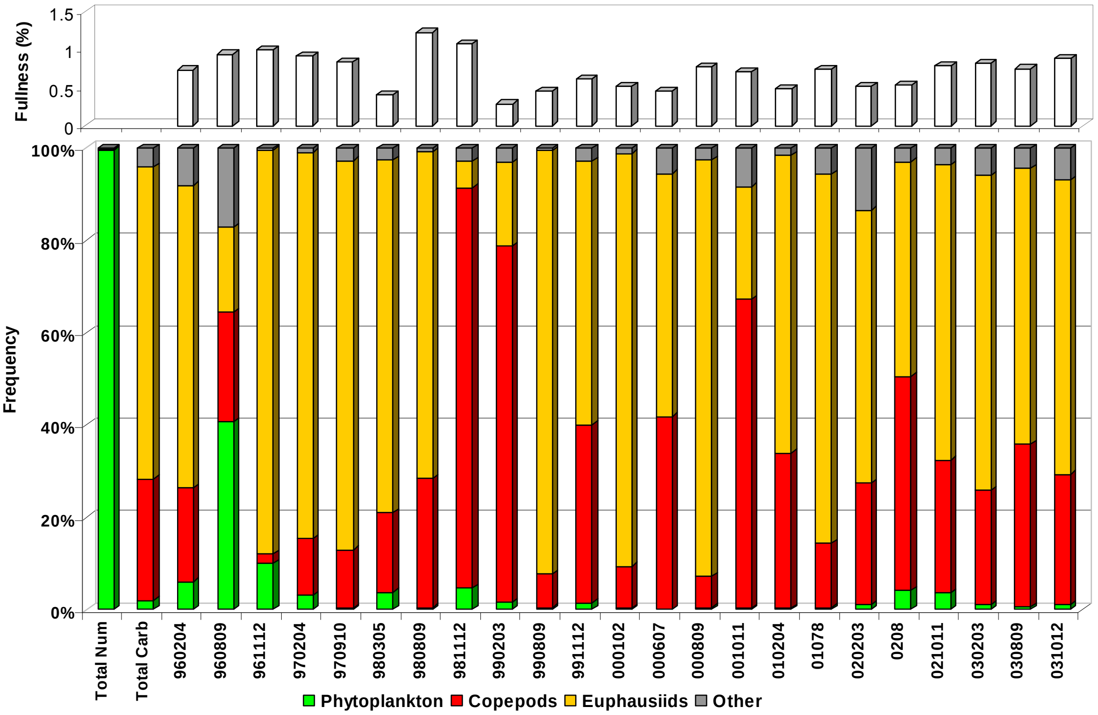

Figure 2.2: Percentage contribution of phytoplankton (green), copepods (red), euphausiids (orange) and other zooplankters (grey) by number (total num) and to dietary carbon (total carb) for the total set of 21,203 anchoveta stomach contents. Also shown are the percentage contribution to dietary carbon by prey type for each of the 23 surveys from which anchoveta stomach contents were analyzed; surveys are identified along thex-axis, with the first two numbers corresponding to the year, the following two numbers the start month of the survey, and the last two numbers the end month of the survey.

The phytoplankton carbon fraction (2%) was dominated by the diatoms *Coscinodiscus* (54.0%), *Thalassiosira* (14.6%), *Ditylum* (8.1%), and by the dinoflagellate *Protoperidinium* (6.7%). The copepod carbon fraction was dominated by the genus *Eucalanus* (69.9%), *Calanus* (12.8%) and *Centropages* (6.6%), whilst *Corycaeus* (1.3%), *Candacia* (1.2%), *Paracalanus* (1.0%) and *Scolecithrix* (1.0%) were of lesser importance.

Our results vary depending on the parameters and relationships used to estimate prey carbon content (Tables 2.2, 2.3 and Annex 1). To test the robustness of our results we re-calculated dietary carbon after increasing twofold the relative volume (and thus carbon content) of phytoplankton items and decreasing the relative size of main zooplankton items by a third. Despite these changes our results were similar to those described above; even in the most 'extreme' case where phytoplankton was increased and zooplankton decreased by the maximum amounts the contribution by phytoplankton to anchoveta dietary carbon only reached 6% of the total, which appears to confirm the robustness of our results.

Whereas the relative contribution to anchoveta dietary carbon made by different prey types varied between surveys, no seasonal trend could be identified (Fig. 2.2). Phytoplankton reached maximum levels (40.7% of total carbon content) in anchoveta diet in August–September 1996, and minimum levels (0.07%) in June–July 2000. The contribution of euphausiids was high (≥80% of total carbon content) during November–December 1996, February–April and September–October 1997, August–September 1999, January–February and August–September 2000, and July–August 2001, and the lowest value (5.8%) was recorded in November–December 1998. The maximum contribution to dietary carbon (86.7%) from copepods occurred during November–December 1998, at the end of the 1997–1998 El Niño event, and the lowest value (2.0%) was observed during November–December 1996.

2.3.2. Stomach fullness dynamics

GAM computed on the combined data from all surveys (Fig. 2.3) show that the main ingestion period for anchoveta occurred during daytime, between 07h00 and 18h00, local time, and this general pattern was observed during most of the surveys, although there were several exceptions (Fig. 2.3). For instance, during four surveys (990809, 000607, 010204, 0208) the feeding period began earlier at about 02h00 and terminated in the early afternoon, whereas during two other surveys (980305, 030809) feeding occurred mainly at night. In some instances (surveys 961112 and 970910) anchoveta showed a longer (>16 h) feeding period with no clear evacuation period.

In addition to showing a diel pattern, stomach fullness also varied with latitude (Fig. 2.3), with higher values encountered off both Northern (<6°S) and Southern (>13°S) Peru although some surveys presented very different patterns. Indeed the global trend does not seem robust and strong variability in the relationship between stomach fullness and latitude occurred during the time series; for example, high stomach fullness values were observed in the central part of Peru in 960204, 960809, 991112 and 000607 (Fig. 2.3).

Stomach fullness increased with distance from the coast and reached maximal values at distances >120 km (Fig. 2.3), but again this general trend obscures strong variability between surveys. When anchoveta were distributed close to the coast, high fullness levels could be observed close to shore, in particular during the 1997–1998 El Niño, but this was also seen in 1999, 2000 or 2001.

Anchoveta stomach fullness was related to temperature, with a minimum observed at 22°C (Fig. 2.3). However, the range of temperatures varied strongly depending on the timing of a particular survey, suggesting that this general trend is also not robust. In fact, whereas the general trend was observed for 13 surveys it was not observed in six others (960204, 970910, 990809, 020203, 010204, 010708) during which fullness increased with temperature, in two surveys (980305, 0208) where dome-shaped relationships between SST and stomach fullness were observed, in two other surveys (960809, 030203) where U-shaped patterns between SST and stomach fullness were observed, nor in one survey (980809) where a bimodal pattern was observed.

2.4. Discussion

2.4.1. Dietary composition

Our analysis of the stomach content composition of 21,203 anchoveta illustrates its omnivorous foraging character; this species feeds on both phytoplankton and zooplankton and has a large diversity of prey (132 taxa were identified at the genus level). As shown by Konchina (1991), the size range of anchoveta prey varies by several orders of magnitude, from tens of micrometers (microflagellates) to tens of millimetres (fish, e.g. *V. lucetia*).

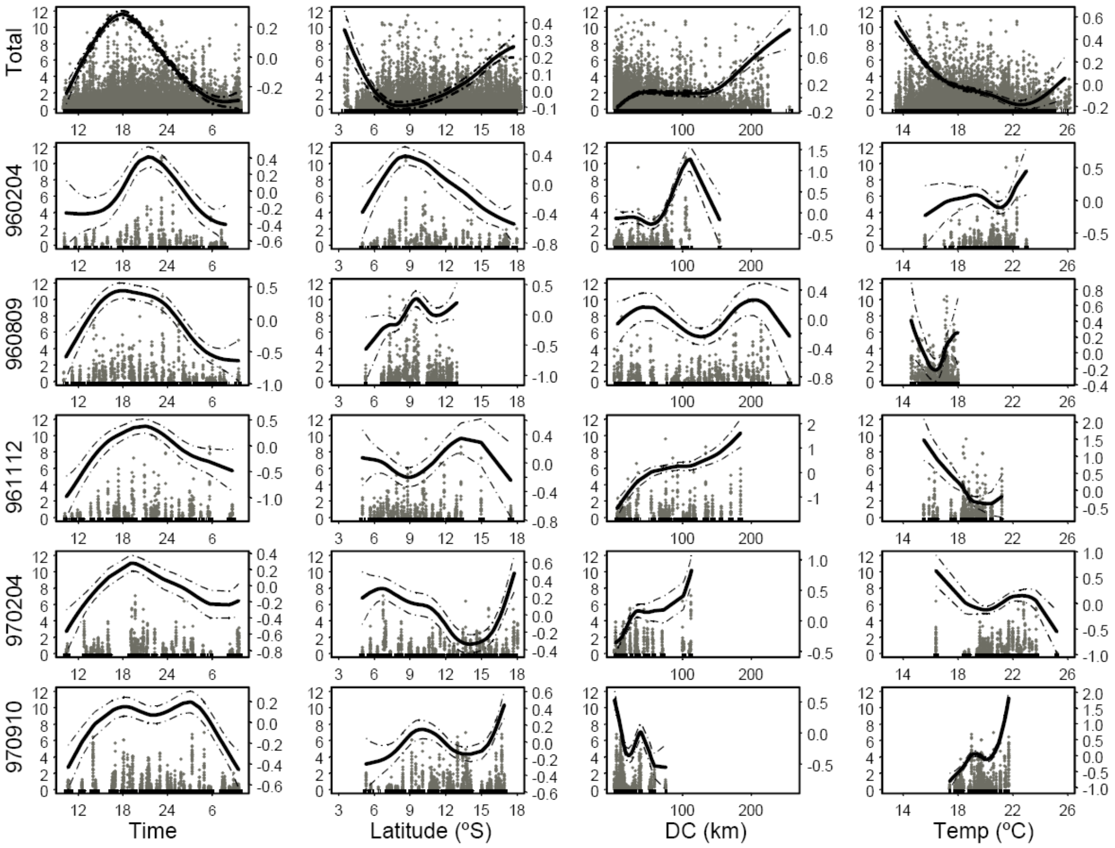

Figure 2.3: Scatter plot (grey dots) and cubic spline smoother fits (black solid lines) of GAM models (the black dashed lines show the 95% confidence limits) based on anchoveta stomach fullness according to time of day, latitude, distance from the coast (DC) and sea surface temperature (°C) for the complete set of 21,203 stomach contents (top panel) and for each of the 23 surveys from which stomach contents were analyzed (lower panels); surveys are identified along they-axis, with the first two numbers corresponding to the year, the following two numbers the start month of the survey, and the last two numbers the end month of the survey. The lefty-axis shows stomach fullness (% WW) and scaling along the righty-axes is relative and corresponds to the spline smoother that was fitted on the data such that ay-value of zero is the mean effect of the variables on the response.

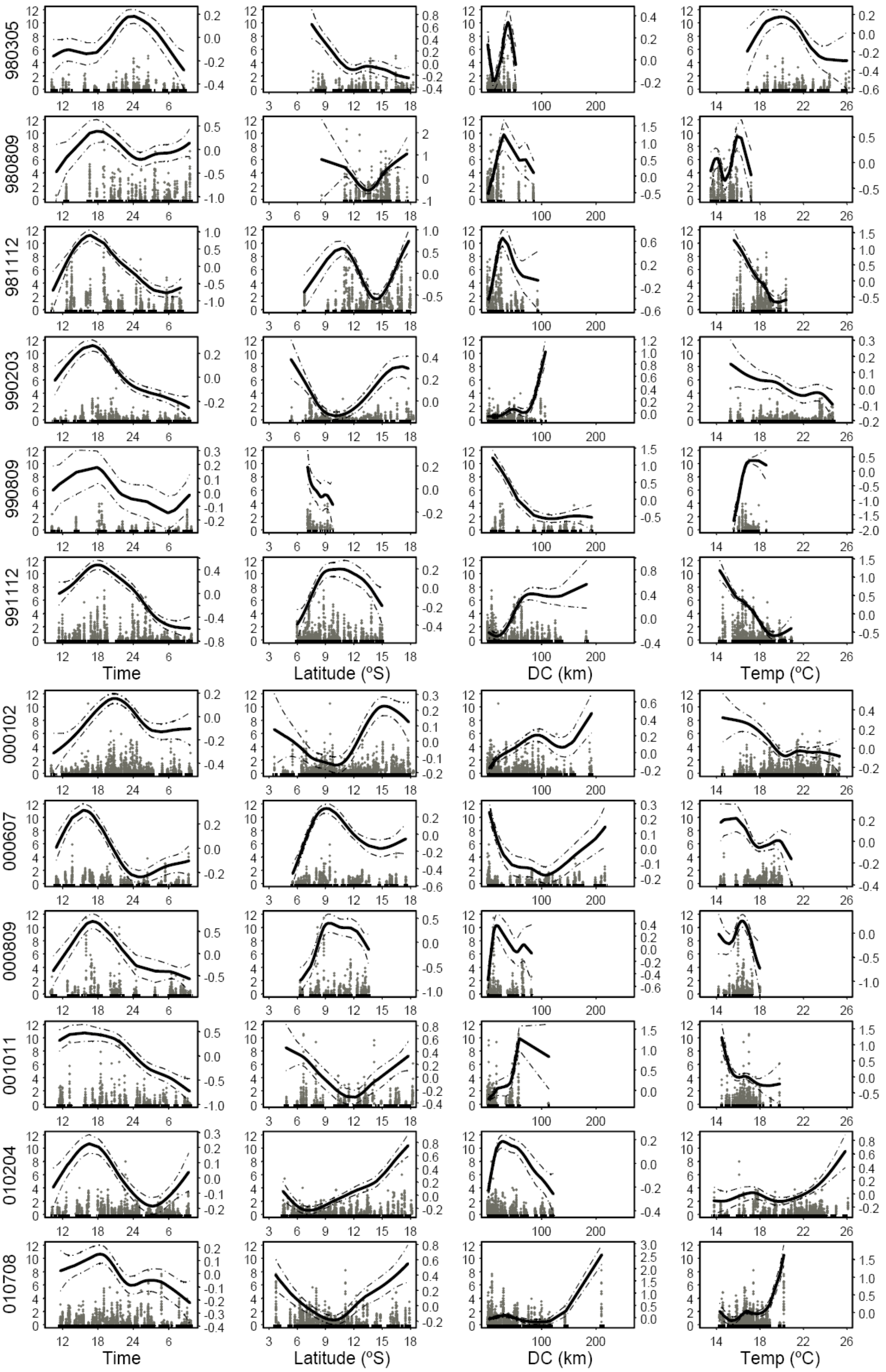

Figure 2.3 (continued)

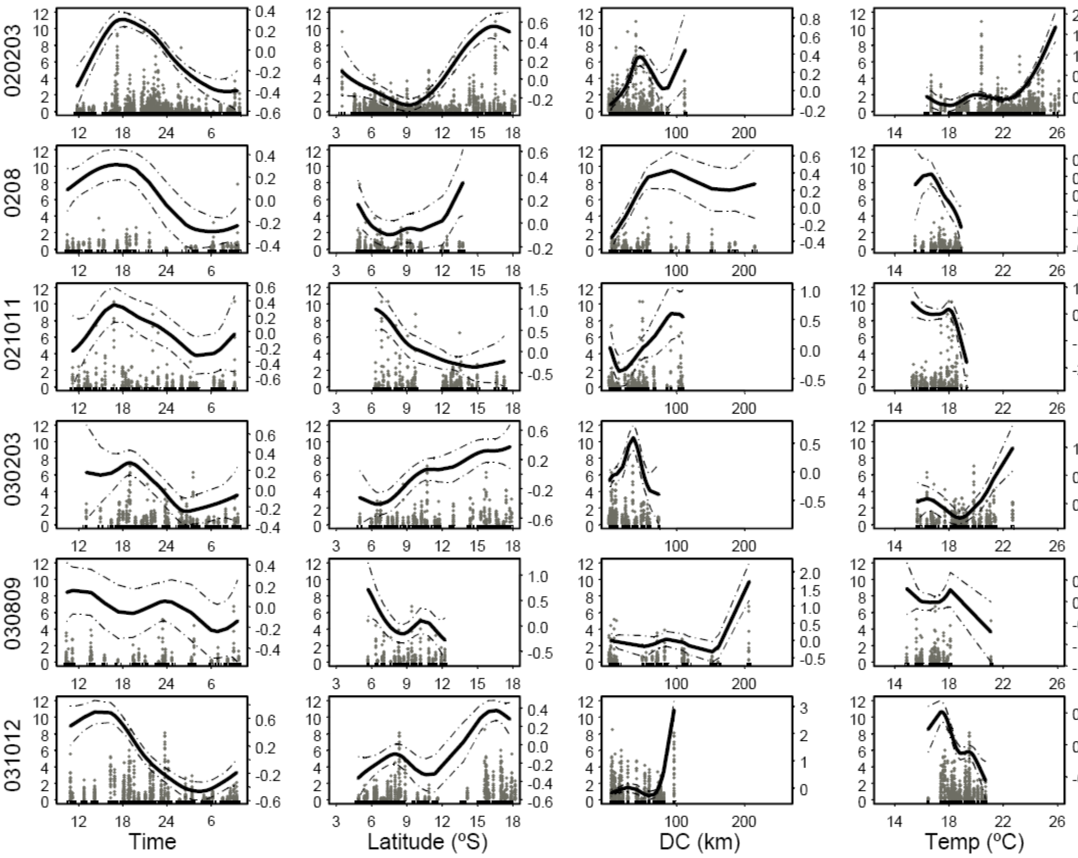

Figure 2.3 (continued)

When considering only prey numbers, anchoveta diet is dominated by phytoplankton which comprise 99.5% of all prey and the zooplankton fraction appears negligible (Fig. 2.2). However when the carbon content of prey items is considered, zooplankton becomes by far the most important component and contributes 98.0% of dietary carbon, with a strong dominance of euphausiids (67.5%) followed by copepods (26.3%). These results depend on the parameters and relationships used to estimate prey carbon content (Tables 2.2, 2.3 and Annex 1); the analysis seems robust but the exact proportion of specific taxa should be considered with caution.

The phytoplankton carbon fraction was dominated by the large solitary diatoms *Coscinodiscus* and *Ditylum*, and the chain forming *Thalassiosira*. Similar dominance has been reported for anchovy (*E. encrasicolus*; formerly *E. capensis*) in the Benguela Current system, where the most important phytoplanktonic items were the large solitary diatoms *Rhizosolenia*, *Pleurosigma* and *Coscinodiscus* (James, 1987). Previous studies performed off Peru and based on numerical or frequency of occurrence analysis also highlighted the importance of diatoms in anchoveta diet, in particular nine genera of the Coscinodiscineae: *Coscinosdiscus*, *Melosyra*, *Cyclotella*, *Skeletonema*, *Thalassiosira*, *Stephanopyxis*, *Coscinoscira*, *Planktoniella*, and *Asterolampra* (Rojas de Mendiola, 1969, 1971, 1989; Alamo, 1989; Pauly *et al.*, 1989b). Other taxa such as the diatoms *Chaetoceros* and *Asterionellopsis*, and the dinoflagellate *Protoperidinium*, were also considered important to anchoveta diet (Alamo *et al.*, 1996a,b, 1997a,b; Alamo and Espinoza, 1998; Espinoza *et al.*, 1998a,b, 1999, 2000).

Zooplankton dietary carbon was dominated by euphausiids and copepods. The most important copepods were *Eucalanus*, *Calanus* and *Centropages*, in partial agreement with Rojas de Mendiola (1971, 1989) and Pauly *et al.* (1989b) who reported that *Calanus*, *Centropages* and

Corycaeus were frequently-observed in anchoveta stomach contents. During the 1997–1998 El Niño, various studies confirmed the numerical importance of copepods and euphausiids; whereas amphipods, anchoveta eggs, *Vinciguerria* sp., and Myctophidae were of minor importance (Blaskovic' *et al.*, 1999; Espinoza *et al.*, 1998a,b, 1999, 2000).

In spite of the zooplankton dominance in anchoveta diet described above, the contribution made by different prey items varied strongly during the study period (Fig. 2.2), illustrating the anchoveta's opportunistic feeding ability. For instance, the phytoplankton fraction was high (up to 40% of carbon content) in 1996, but thereafter was never higher than 5%, irrespective of the overall environmental condition (i.e. El Niño 1997–1998 or La Niña 1999). It is difficult to relate these changes in the proportion of dietary phytoplankton to specific conditions. The proportion of anchoveta dietary carbon derived from copepods increased from November–December 1996 (2.0%) to a maximum in November–December 1998 (86.7%) and February–March 1999 (77.1%), after the 1997–1998 El Niño; the copepod fraction also reached high levels (>40%) in June–July 2000, October–November 2000 and August 2002, making the extraction of any seasonal pattern difficult.

2.4.2. The anchoveta: a predator

Our results demonstrate that anchoveta is a predator foraging at a higher trophic level than has generally been recognised (e.g. by Pauly *et al.*, 1989b; Rojas de Mendiola, 1989), with its main input of carbon coming from zooplankters such as euphausiids and large copepods. Our results differ from the conventional dogma on clupeoid feeding ecology in the HCS, in which diatoms are considered as the major food source. Such feeding low on the food chain has been invoked to explain how such large anchoveta populations can be supported in this system (Rojas de Mendiola 1971). These conclusions now appear incorrect as they are based on counts of very small (phytoplankton) prey who's caloric (carbon) contribution to anchoveta diet is often trivial (Cushing, 1978; Konchina, 1991). James (1987) demonstrated that assessing fish diet from the number of prey items is unsatisfactory due to the preponderance of minute food items and the great difference on size range between phytoplankton and zooplankton (10^{-3} mm for diatoms to 10 mm for zooplankton), which makes the use of carbon or calorie equivalents for assessing the importance of dietary components essential. The determination of prey carbon content helps in determining the true importance of a food type (James, 1988), and this method has been used to highlight the importance of zooplankton over phytoplankton for *E. mordax* off California (Koslow, 1981; Chiappa-Carrara and Gallardo-Cabello, 1993), *E. encrasicolus* and *Sardinops sagax* in the Benguela Current upwelling system (James, 1987; van der Lingen, 2002; van der Lingen *et al.*, 2006), and *Sardina pilchardus* in the north-eastern Atlantic (Garrido *et al.*, 2008); see van der Lingen *et al.* (2006, 2009), for recent reviews of clupeoid trophic ecology. In the Peruvian case, Konchina (1991) was the only scientist to conclude that anchoveta preferentially consumes zooplankton, and that most anchoveta biomass is supported by copepods and euphausiids. Finally, in Central Chile, using isotope analysis, Hückstädt *et al.* (2007) estimated the trophic level of anchoveta to 3.63, which confirm the dominance of zooplankton in anchoveta diet.

Anchoveta is therefore a 'predator' who select the largest available prey from the phytoplankton and zooplankton communities (Tables 2.2, Annexes 1 and 2). This is shown for zooplankton with the selection of euphausiids and the large copepods *Eucalanus* and *Calanus*, and for phytoplankton with the selection of the large diatom *Coscinodiscus*. Similar selectivity was observed for other anchovy species (e.g. Koslow, 1981; James, 1987; van der Lingen *et al.*, 2006).

2.4.3. Stomach fullness dynamics

As previously observed for *E. encrasicolus* (James, 1987), *E. ringens* displays an extremely high degree of opportunism in fulfilling its dietary requirements and can shift between prey types according to their availability (Fig. 2.2). This flexible feeding behavior was confirmed by the GAM models (Fig. 2.3) which illustrated the high variability between surveys when relating stomach fullness to time, latitude, distance to the coast, or SST. In the highly variable HCS anchoveta have had to evolve adaptive strategies in space and time (Bertrand *et al.*, 2004a), including its spawning behaviour (e.g. Buitrón and Perea, 2000), its mode of spatial distribution (e.g. Bertrand *et al.*, 2004b, 2008a; Gutiérrez *et al.*, 2007), or its feeding behaviour as illustrated by this study.

Such variability precludes the determination of robust patterns, and indeed results differ strongly between surveys and therefore from one dataset to another. Our study was based on more than 20,000 stomach content samples collected during an 8 year period which is, to our knowledge, the largest database on anchoveta diet, and the results we obtained from all surveys combined (Fig. 2.3) can therefore be considered as representative. However, except in the case of their diel feeding behaviour, we think that the mean signal in anchoveta stomach fullness is not a good representation of the biological reality at any one moment. Instead, we consider that the most important point arising from our stomach fullness analysis does not reside in the mean patterns but in the variability from one survey to the other (Fig. 2.3). This variability is another illustration of anchoveta plasticity.

The general trend of diel temporal variation in stomach fullness was the most consistent, and the main feeding period as determined using GAMs ranged between 07h00 and 18h00 (Fig. 2.3). This general pattern was observed for most surveys, although night-time feeding behaviour made substantial contributions to total ingestion (moon cycle could play a role). Feeding duration also varied from one survey to another, as also shown by Espinoza and Blaskovic' (2000). The primarily diurnal feeding behaviour we observed differs from results of other studies of anchoveta feeding periodicity based on a large database (5245 individuals) from samples collected over the period 1953–1982 (Pauly *et al.*, 1989b; Jarre *et al.*, 1991), which indicated that most feeding occurred between 11h00 and 24h00. This difference cannot be related to the different methods of analysis used i.e., GAM in this study and Sainsbury's method (Sainsbury, 1986) in previous studies, since applying Sainsbury's method to our data does not change the results.

So why did the main feeding period change? At least two hypotheses can be proposed to explain this difference: a shift in the ecosystem, or a problem of data collection. Anchovies in other upwelling systems are considered as daytime (e.g. northern anchovy *E. mordax*; Baxter, 1967; Loukashkin, 1970; Koslow, 1981) or night-time (e.g. Benguela anchovy *E. encrasicolus*; James 1988) foragers. At first sight the main daytime trend we found appears surprising since zooplankton perform diel migrations and a large fraction of zooplankton is generally distributed within or below the oxycline during the day, out of reach of the anchoveta (e.g. Bertrand *et al.*, 2008a; Escribano *et al.*, 2009). However our results demonstrate that anchoveta can change their feeding period and forage at night if necessary. The HCS experienced 'cold' and 'warm' years during the period (1996–2003) of our study with a dominance of the upwelling-related cold coastal water along the Peruvian coast, except during the 1997–1998 El Niño (Swartzman *et al.*, 2008). That anchoveta fed mainly during the day suggests that, even with the highly stratified conditions typical of enhanced upwelling periods, there were enough prey available during the day to sustain anchoveta. It seems therefore difficult to ascribe the difference between our results and previous studies to changes in climatic conditions. The period 1953-1982 that was previously studied included a wide range of climatic conditions: 'cold' until the beginning of the 1970s, and ‘warm’ from then until the mid 1980s. Hence we feel that it is more likely that the differences in anchoveta mean feeding periodicity between our and earlier studies was due to potential problems in the data collection (e.g. data sources varied from scientific cruises to fishing boats) for the 1953–1982 series or by the fact that the mean pattern hides important variability from one period to the other. Indeed a refined analysis of the data set used in previous studies revealed a pattern of several feeding periods per day, including some feeding during late night (Jarre-[Teichmann], 1992).

The plasticity in anchoveta foraging periodicity was even more obvious when considering the distance to the coast, latitude or SST, where mean patterns were not representative of the observations from a single survey. Inside its range of overall viable conditions anchoveta is therefore able to forage efficiently at any time, any place, or any temperature. In other words, inside its cold coastal water-related habitat (see Bertrand *et al.*, 2004a; Gutiérrez *et al.*, 2007; Bertrand *et al.*, 2008b; Swartzman *et al.*, 2008), anchoveta were probably distributed where prey were abundant and available, rather independently of other parameters (Bertrand *et al.*, 2008a).

2.4.4. A new vision of HCS functioning

If anchoveta is a predator that uses large zooplankters as the main source of dietary carbon, then our vision of HCS functioning must change. The HCS is by far the most productive eastern boundary current system in the world in terms of fish catches, but these high catches do not appear to be supported by exceptionally rates of primary production far higher than those observed in the other eastern boundary current systems (Carr, 2002; Carr and Kearns, 2003). The high fish production in the HCS could be related to a more efficient use of primary production due to, for example, a short trophic chain, and this assumption has been prevalent in the last few decades since anchoveta was considered to feed directly on primary producers and hence rely on a complete very short and efficient food chain (Ryther, 1969; Walsh, 1981). But if this is not the case, and anchoveta do not, in fact, benefit from a 2-step food chain, then the explanation for the high fish productivity in the HCS must be found elsewhere. Konchina (1991) stated that the ability of anchoveta to utilize food from several trophic levels and to choose energetically advantageous food enables it to achieve enormous biomass in a relatively short time. Yet all trophic models of the HCS developed to date, even recently, still consider that the anchoveta consumes at least as much carbon from phytoplankton as from zooplankton (e.g. Jahncke *et al.*, 2004; Neira *et al.*, 2004). Our results indicate that carbon flows in trophic models of the HCS must be re-evaluated, since the tremendous importance of anchoveta in the coastal pelagic ecosystem means that a major change in its diet should affect all the other components of that system. In particular, the fact that anchoveta forages at a higher trophic level than previously been considered implies that the primary and secondary production of the HCS may be higher than supposed (for primary production see Echevin *et al.*, 2008). No absolute estimation of zooplankton production is available (see Ayón *et al.*, 2004, 2008b for trends in zooplankton biovolume) but we hypothesize that zooplankton production could be higher in the HCS than in other upwelling systems, and 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, which were the main source of dietary carbon for anchoveta and which inhabit both near- and offshore ecosystems.

The hypothesis of higher zooplankton biomass in the HCS compared to other systems highlights the urgent need for more studies on zooplankton diversity, abundance and dynamics in the HCS, particularly for large zooplankters like euphausiids (Antezana, 2002). Studying these organisms is difficult, however, as they avoid standard samplers such as bongo nets, but new, multi-frequency acoustic measurements permit estimation of the biomass of the main zooplankton groups and facilitate the study of their distribution patterns in 2-D and 3-D (e.g. Lebourges-Dhaussy *et al.*, 2004).

Our results also bring into question current thinking on anchoveta distribution. Because of the westward drift of water masses in the HCS there is usually a spatial separation between areas of peak phytoplankton abundance and areas of peak zooplankton abundance. Hence the relationship between anchoveta distribution and chlorophyll concentration, as observed from satellite, is not necessarily direct, and it is therefore important to take into account the characteristics of the available habitat, including zooplankton abundance, to understand anchoveta distribution patterns and also changes in abundance (cf. the habitat-based hypothesis in Bertrand *et al.*, 2004a). It is not sufficient to use temperature or chlorophyll concentration as indicators of anchoveta distribution, since the plasticity of the genus *Engraulis* in general (Bakun, 1996) and *E. ringens* in particular allows it to feed successfully and distribute across a broad range of environmental variability. The dependence of anchoveta on zooplankton has previously been illustrated by Alheit and Ñiquen (2004) and Ayón *et al.* (2008b), who showed bottom-up control of anchoveta where its abundance in the HCS was linked to overall zooplankton abundance. At a smaller scale, Ayón *et al.* (2008b) also showed that this apparent bottom-up control was accompanied by a local depletion effect, as zooplankton biomass was lower in places were anchoveta was abundant.

2.4.5. Synthesis: plastic is fantastic!

Our results have demonstrated that the diet of anchoveta in Peru is based primarily on large zooplankters, but also that this species shows tremendous plasticity in its diet and feeding behaviour; anchoveta utilize food from several trophic levels, can choose energetically advantageous food types, and can fit its foraging period and duration to prey. Trophic plasticity is apparently an evolved adaptive strategy; other strategies include the ability to track and concentrate in refuge areas when conditions are adverse (Bertrand *et al.*, 2004a), change its reproductive behaviour (Buitrón and Perea, 2000), and distribute its population over a rather large temperature range (Bertrand *et al.*, 2004a; Gutiérrez *et al.*, 2008). In combination these characteristics may explain the ‘anchoveta paradox’: how a fish which (i) performs very small migrations and cannot escape adverse conditions, (ii) is mainly distributed in dense surface aggregations and is thus highly accessible to predators (fish, cephalopods, birds, mammals and fishers), and (iii) is very slow in its avoidance reactions to predators (Gerlotto *et al.*, 2006), can achieve such enormous biomass in a relatively short time.

Acknowledgments

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CHAPTER 3

Ontogenetic and spatiotemporal variability in anchoveta *Engraulis ringens* diet off Peru

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Abstract:

In this study we use available historical data since 1954 to get new insight on ontogenetic and spatiotemporal variability in Peruvian anchovy or anchoveta *Engraulis ringens* diet. Whatever the period, *E. ringens* foraged mainly on macrozooplankton and the importance of euphausiids in *E. ringens* diet appears directly related to euphausiids abundance. This bottom-up effect is also observed at smaller scale since the euphausiids fraction increased with *E. ringens* size and euphausiids accessibility. Selecting the largest prey, the euphausiids, provide an energetic advantage for *E. ringens* in its ecosystem where oxygen depletion imposes strong metabolic constrain to pelagic fish. Finally this study is another illustration of *E. ringens* plasticity which allows it to cope with its highly variable environment.

Key words: euphausiids; Humboldt Current system; oxygen; Peruvian anchovy; spatiotemporal variability; trophic ecology

3.1. Introduction

The Peruvian anchovy or anchoveta, *Engraulis ringens* Jenyns 1842, is the dominant pelagic nekton species in the coastal Northern Humboldt Current system (NHCS) off Peru. This fish has great ecological importance in channelling energy flow from primary and secondary production to higher trophic levels (Pauly *et al.*, 1989b). During decades *E. ringens* was considered to depend mainly on phytoplankton (e.g., Ryther, 1969; Rojas de Mendiola, 1989; Alamo & Espinoza, 1998). However, these studies were based on counts of *E. ringens* prey, a method considered to be inadequate for estimating dietary importance (James 1987, Konchina & Pavlov, 1995). By applying an analytical method based on the estimation of prey carbon content, Espinoza & Bertrand (2008) showed that *E. ringens* forage mainly on macrozooplankton, in particular euphausiids and large copepods. Such trophic behaviour is a general pattern for *Engraulis* spp. (van der Lingen *et al.*, 2009).

However some doubts subsisted about a potential temporal shift in *Engraulis ringens* diet towards more or less zooplankton. Indeed, *E. ringens* population was assumed to be dominated by individuals with higher affinity for zooplankton (shorter guts and less gillrakers) during the 1950s and 1960s than after the *E. ringens* collapse in 1972 (Palomares *et al.*, 1987; Hutchings, 1992). An opposite change could have occurred in the last decades explaining the strong dominance of zooplankton in *E. ringens* diet observed by Espinoza & Bertrand (2008). To check for this we revisited available historical trophic diet data since 1954.

Then, to complete previous works, we describe the feeding behaviour of *E. ringens* according to fish size (ontogenetic), spatial (latitudinal and cross-shore), and diel patterns during 1996-2003, period with available fully spatialised data. We show that in this ecosystem characterised by a strong productivity but oxygen paucity, *E. ringens* diet seems mainly driven by the availability of large prey, in particular euphausiids.

3.2. Material and methods

3.2.1. Data

The study area covers the Peruvian coastal waters from the coastline to approximately 200 km offshore. In Peru, trophic data acquisition and sample analyses were strongly modified along time. In order to study both long term changes and spatial variability we had to use available data bases according to their characteristics.

The oldest data covering the period 1954-1969 were collected at different seasons in several factory plants for *Engraulis ringens*: (i) Chimbote (9ºS) in August to December 1954 (69 stomachs) and in January to December 1955 (333 stomachs); (ii) San Juan (15ºS) in April and June 1969 (64 stomachs); Mollendo (17ºS) in March 1954 (26 stomachs), January and April 1963 (24 stomachs) and March and June 1969 (27 stomachs); and Ilo (17.5ºS) in April 1954 (11 stomachs) (Rojas de Mendiola, 1971). Individuals of *E. ringens* were randomly sampled and fixed in 10% formalin. Stomach contents items were identified and counted, taking as a unit for zooplankton at least the head and the whole cell for phytoplankton. We converted prey data count from Rojas de Mendiola (1971) into carbon content by applied the methodology described in Espinoza & Bertrand (2008). We then pooled prey data expressed in carbon content into the following six taxonomic categories: (i) diatoms; (ii) other phytoplankters, (iii) other copepods, (iv) calanoid copepods, (v) euphausiids, and (vi) other zooplankters. Unfortunately, these data were not fully spatialised.

For the period 1974 - 1988 we retrieved data from the so-called EUREKA operations; these employ about 20 fishing boats for a quasi-synoptic observation of the Peruvian coast and contributed to fish resource monitoring. The specific determination of trophic items was coarse and did not allow for a comprehensive diet analysis. However we could estimate the frequency of occurrence of euphausiids in stomach content. The same information was obtained from samples collected during scientific surveys or in factory plants in 1985, 1988-1990, 1994, 1995 and 2004-2009 (Annex 3.1).

Data for the period 1996-2003 were collected on board research vessels of the Peruvian Sea Institute (IMARPE) during 22 acoustic surveys (Table 3.1). The samples and the methodology used for stomach content analysis and conversion to carbon were described in Espinoza & Bertrand (2008). A total of 13,430 fully georeferenced stomachs of *Engraulis ringens* were used. The prey data was pooled into the same six taxonomic categories than for the period 1954-1969. We also pooled the data according to the following factors: size class, latitude, distance to the shelf break, and diel period (Table 3.2). Seasonal variability was not considered since no significant effects were depicted (Espinoza & Bertrand, 2008).

Table 3.1. Year, start and end date, number of trawls, total number of stomachs with prey contents, and length range (cm) of Engraulis ringens during 1996-2003.

Year	Start date	End date	N of trawls	N° of stomachs (with prey)	Fish total length (Min – Max)
1996	10 Feb.	01 Apr.	49	157 (147)	11.0 – 18.5
	16 Nov.	19 Dec.	39	338 (329)	9.5 - 19.0
1997	13 Feb.	23 Apr.	45	186 (184)	10.5 - 19.5
	04 Sept.	05 Oct.	51	117 (106)	11.5 – 18.5
1998	27 Mar.	01 May.	35	148 (124)	10.0 – 17.0
	23 Aug.	17 Sept.	36	348 (308)	4.0 - 15.0
	30 Nov.	21 Dec.	36	274 (232)	4.0 - 16.0
1999	14 Feb.	28 Mar.	75	1197 (1059)	10.0 - 17.0
	28 Aug.	17 Sept.	19	279 (178)	10.0 - 18.0
	12 Nov.	14 Dec.	70	1243 (999)	8.0 - 18.0
2000	20 Jan.	26 Feb.	124	1965 (1798)	6.5 - 18.5
	10 Jun.	06 Jul.	50	928 (859)	7.5 - 18.5
	28 Aug.	23 Sept.	38	512 (486)	7.0 - 18.5
	11 Oct.	13 Nov.	45	822 (717)	6.5 - 18.0
2001	03 Mar.	10 Apr.	78	1584 (1446)	8.5 - 18.5
	05 Jul.	06 Aug.	83	1274 (1208)	6.5 - 19.0
2002	21 Feb.	18 Mar.	83	1362 (1094)	7.0 - 18.0
	10 Aug.	31 Aug.	30	269 (267)	9.5 - 17.0
	01 Oct.	13 Nov.	36	415 (365)	10.0 - 17.0
2003	26 Feb.	31 Mar.	45	524 (513)	6.5 - 17.5
	16 Aug.	15 Sept.	26	243 (237)	7.5 - 17.5
	24 Oct.	10 Dec.	36	798 (774)	4.5 - 17.5

3.2.2. Analyses

From these different data sets and taking into account their characteristics we performed three kinds of analyses. First, we compared *Engraulis ringens* diet between 1954-1969 and 1996-2003. We did not enter in interannual variability because the first data set was based on only few samples of some years while the second was already described by Espinoza & Bertrand *et al.* (2008). Second, we constructed a time series of the frequency of occurrence of euphausiids between 1954 and 2009. Third, the fully spacialised data set from 1996 to 2003 allowed studying ontogenetic and spatial variability in *E. ringens* diet. Given that ANOVA assumptions for the data were not met (lack of normality), the non-parametric Kruskal-Wallis (KW) test (Scherrer, 1984) was used to identify statistical differences in the carbon content-based contribution of different prey taxa according to the following factors: size-class, latitude, distance to the shelf break, and diel period. A Tukey-type test was used for a posteriori multiple comparisons (Zar, 1999). Finally, classification and regression trees (CART, Breiman *et al.*, 1984) were used to assess the relative importance of size, latitude, distance to the shelf break, and diel period on *E. ringens* diet. 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. Splits are chosen to maximize the homogeneity of the resulting two nodes. Each terminal node (or leaf) of the final tree is characterized by a predicted prey distribution (carbon proportion for the 6 taxonomic groups), given the explanatory variables. For pruning the tree and validating the robustness of the CART results we used the recursive partitioning method (rpart; De'ath & Fabricius, 2000).

Table 3.2. Factors used to pool the data.

Factors	**Classes**
Engraulis ringens size class (cm)	By 2 cm size-class: [4-6>, [6-8>, [8-10>, [10-12>, [12-14>, [14-16>, [16-18>, [18-20>
Latitude (ºS)	By degree of latitude from 03º30'S to 18ºS
Distance to the shelf break (km)	Negative inshore, positive offshore: <-30, -30 to 0, 0 to 30, >30
Diel period	(i) 07:00≤day<17:00; (ii) 17:00≤dusk<19:00 (iii) 19:00≤night<05:00 (iv) 05:00≤dawn<07:00

3.3. Results

3.3.1. Temporal variation

Only two periods (1954-1969 and 1996-2003) encompassed precise description of the *Engraulis ringens* diet. During 1954-1969, the diet of *E. ringens* was dominated by zooplankton; the total contribution of phytoplankton representing only 0.8% of the diet expressed in carbon (Fig. 3.1). Euphausiids contribution was higher than 92.3% so more than during 1996-2003 when the mean euphausiids contribution was 67.5%. Copepods fraction was also lower during 1954-1969 (6.3%) than during 1996-2003 (26.3%).

The frequency of occurrence of euphausiids varied along time (Fig. 3.2). Even if the time series is incomplete, a pattern emerges with less euphausiids during the mid 1970s-1980s (available data: 1974-1979, 1985, 1988, 1989) and maybe during the 1950s. In this last case the number of data (available data: 1954-1955) is insufficient to provide robust results. On the opposite euphausiids were more frequent during the late 1960s-early 1970 and the late 1990s - early 2000s. This pattern is rather similar to what was observed by Ayón *et al.* (2011) who studied the temporal changes in zooplankton dominant size group (between small, medium and large zooplankton, and euphausiids) in net samples. Indeed, euphausiids dominance in zooplankton from Ayón *et al.* (2011) matches the frequency of occurrence of euphausiids in *E. ringens* diet (Fig. 3.2), except during the mid 2000s when euphausiids dominance increases while the frequency of occurrence in stomach decreased.

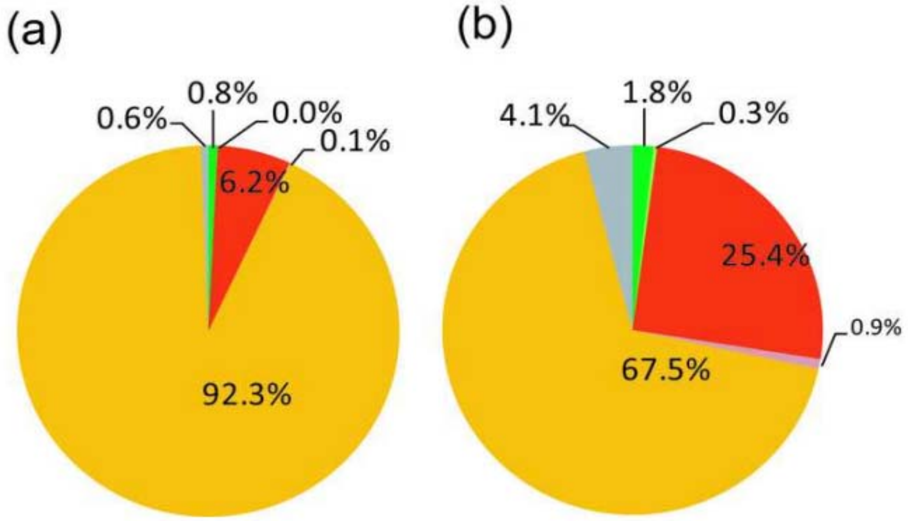

Figure 3.1 Per cent composition of prey groups (■ diatoms, ■ other phytoplankters, ■ calanoid copepods, ■ other copepods, ■ euphausiids and, ■ other zooplankters) to Engraulis ringens dietary carbon for the periods: (a) 1954–1969 (Rojas de Mendiola, 1971) and (b) 1996–2003 (Espinoza & Bertrand, 2008).

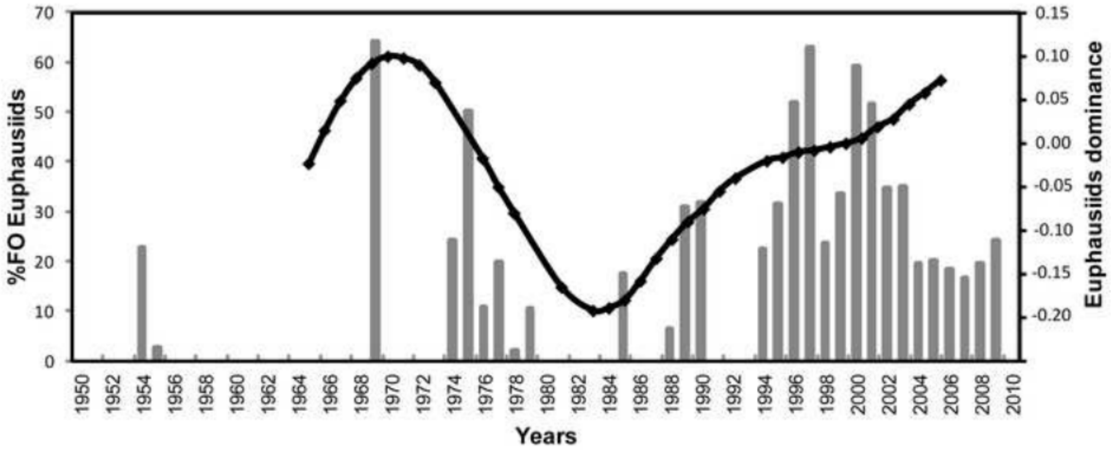

Figure 3.2 Frequency of occurrence (grey bars - left y-axis) of euphausiids in Engraulis ringens stomachs, and euphausiids dominance from Ayón et al. (2011) in zooplankton net samples (additive model results; black line - right y-axis). No bar indicates absence of data.

3.3.2 Ontogenetic variation

Across all size classes the contribution of zooplankton to *Engraulis ringens* diet in terms of carbon content was greater or equal to 95 % (Fig. 3.3a). For all size-classes the most important prey groups were euphausiids and calanoid copepods, but their relative importance varied significantly with *E. ringens* size (KW test, p<0.001; Table 3.3, Annexes 3.2, 3.3, 3.4). The most noticeable pattern was the steady increase in euphausiids contribution with *E. ringens* size (Fig. 3.3a). Euphausiids represented 23.3% of the diet of the smallest studied *E. ringens* (4-6 cm) but reached 84.9% for the largest (18-20 cm). At the same time the proportional contribution of calanoid copepods markedly decreased from 68% in the smallest size class of *E. ringens* to 11.5% in the largest. The proportion of other zooplankters also diminished with increasing size, but not as regularly, from 8.8% in the smallest to 2% in the largest *E. ringens*. The contribution of other phytoplankters remained below 0.6%, and other copepods under 2.5% without clear trend at each size class. For diatoms, its contribution increased from 0.1% in the smallest size-class to 4.4% for the 10-12 cm size-class, then diminished to <1% in the larger size-classes.

Table 3.3 Results of non-parametric ANOVA (Kruskal-Wallis test); n=1938 (the 13,430 stomachs pooled by size class).

Items	Size-class d.f.=7	Latitude d.f.=15	Distance to the shelf break d.f.=3	Diel period d.f.=3
Diatoms	H=60.5, p<0.001	H=47.7, p<0.001	H=73.0, p<0.001	H=16.7, p=0.001
Other phytoplankters	H=53.1, p<0.001	H=51.3, p<0.001	H=22.6, p<0.001	H=14.2, p=0.003
Calanoid copepods	H=24.2, p=0.001	H=44.4, p<0.001	H=10.1, p=0.018	H=80.5, p<0.001
Other copepods	H=35.8, p<0.001	H=49.5, p<0.001	H=11.0, p=0.012	H=64.2, p<0.001
Euphausiids	H=94.7, p<0.001	H=84.1, p<0.001	H=115.6, p<0.001	H=72.5, p<0.001
Other zooplankters	H=31.0, p<0.001	H=111.8, p<0.001	H=36.8, p<0.001	H=20.1, p<0.001

3.3.3 Latitudinal variation

The contribution of zooplankton to *Engraulis ringens* diet was greater or equal to 95% irrespective of latitude (Fig. 3.3b). Euphausiids and calanoid copepods, varied significantly with latitude (KW test, p<0.001, Table 3.3, Annexes 3.5, 3.6, 3.7) but no steady latitudinal trend was observed. Euphausiids were the main taxa with the exception of around latitudes 7ºS and 15ºS where the most important prey were calanoid copepods which represented 52.3 and 47.5%, respectively. The higher contributions of other zooplankters were observed close to Chicama (7ºS) and south of San Juan (16ºS) with 7.3 and 8.7%, respectively. The contribution of diatoms fluctuated between 0.04 % in the extreme north to a maximum of 4.4% at 06ºS with no apparent latitudinal trend (Fig. 3.3b).

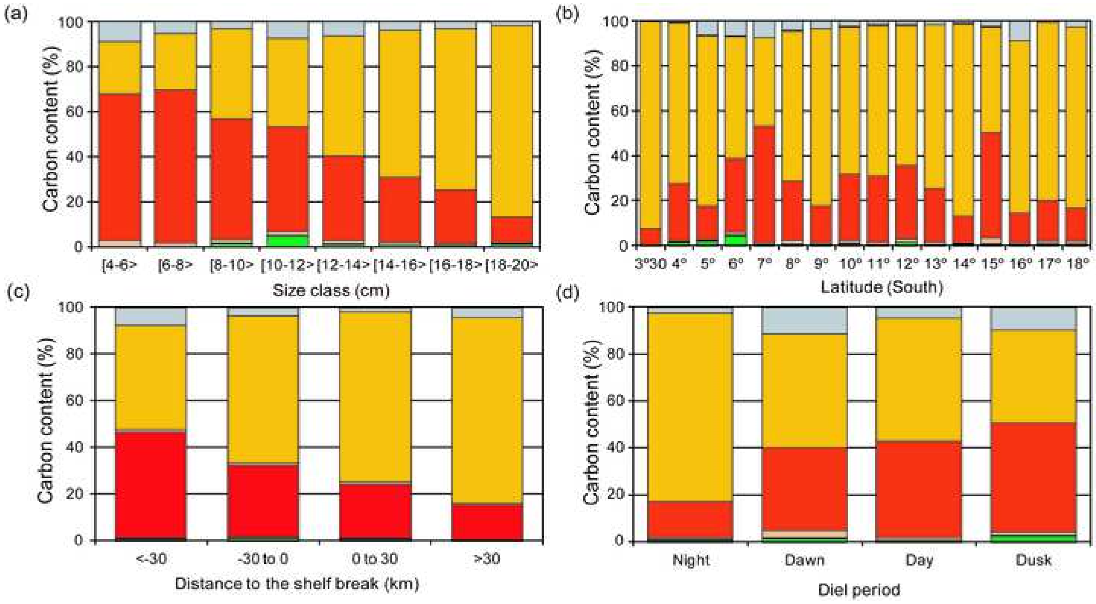

Figure 3.3 Percent contribution of prey groups (diatoms, other phytoplankters, calanoid copepods, other copepods, euphausiids, other zooplankters) to dietary carbon of Engraulis ringens by size-class (a), degree of latitude (b), distance to the shelf break (in km, zero corresponds to the shelf break, values are negative inshore and positive offshore) (c) and diel period (d) from years 1996-2003.

3.3.4 Cross-shore variation

Euphausiids contribution varied significantly according to distance to the shelf break (Fig. 3.3c, KW test, p<0.001, Table 3.3, Annexes 3.8, 3.9, 3.10). It steadily increased from 45% in the more inshore samples to reach 80% at more than 30 km from the shelf break. Contribution by calanoid copepods followed an opposite trend with a highest contribution (46%) in the more inshore samples then a decrease to 15% at more than 30 km from the shelf break. The contribution of other zooplankters was highest in the more inshore areas (7.6%) and varied between 2.0 and 4.1 further offshore. Finally, the collective contribution of diatoms, other copepods, and other phytoplankters were marginal with <1.3% of carbon content in all cases.

3.3.5 Diel variation

Engraulis ringens diet (Fig. 3.3d) showed significant differences with the diel period (KW test, $p<0.001$, Table 3.3, Annexes 3.11, 3.12, 3.13). During the night, the diet was dominated by euphausiids (80.2%). This proportion decreased to 48.8% at dawn and 52.7% during the day, and reached a minimum of 39.8% at dusk. Calanoid copepods followed an opposite trend with 15.7% during the night, 35.3% at dawn, 40.9% during the day and 46.5% at dusk.

3.3.6 CART analysis

Results of the CART (Fig. 3.4) confirmed the above described but permitted to rank the effects this way: distance to the shelf break > diel period > latitude > Size > Year. When looking at the tree (Fig. 3.4) the first cut is due the distance to the shelf break with more copepods very close to the coast. Further to the coast, the second cut was related to fish size with more euphausiids in fish larger than 14 cm. For fish less than 14 cm, copepods were more important at specific latitude (4ºS, 6ºS, 7ºS, 8ºS, 10ºS, 11ºS, 12ºS and 15ºS), in particular during all diel periods but the night.

3.4 Discussion

3.4.1 Temporal variation

The quality of available data strongly varied with time. However the use of different data sources allows for a better vision of the temporal changes in *Engraulis ringens* diet. Results complete the one from Espinoza & Bertrand (2008) and show that the diet of *E. ringens* in Peru is based primarily on large zooplankters whatever the period (Fig. 3.1). Euphausiids contribution was even higher during the 1950-1960s (92.6%) than during the late 1990-early 2000s (67.5%) while copepods presented an opposite trend (6.3% and 26.3%). Euphausiids frequency of occurrence time series shows (Fig. 3.2) that euphausiids incidence decreased during the mid 1970-1980s. This trend is in agreement with the study of temporal changes in zooplankton size-group dominance by Ayón *et al.* (2011) who showed that euphausiids were strongly dominant during the late 1960 early 1970 (the 1950s were not included in their analysis) and since the 1990s.

3.4.2 Ontogenetic changes

Both, juvenile and adult *Engraulis ringens* were largely zooplanktivorous and foraged predominantly on euphausiids and calanoid copepods, while contribution of phytoplankton to dietary carbon was ≤4.4% irrespective of size-class. This is in contrast to that of Rojas de Mendiola (1969) and Rojas de Mendiola *et al.* (1969), who applied the numerical method and proposed that *E. ringens* become more phytoplanktivorous from juvenile to adult. However, prey-size range changed ontogenetically with a steady increase in euphausiids contribution from >25% in the smallest *E. ringens* (4-6 cm) to >80% in the largest size class (18-20 cm). For Engraulis spp., filter-feeding has a high metabolic cost relative to particulate feeding (James & Probyn, 1989; van der Lingen *et al.*, 2006) and *E. ringens* select the largest available prey (Espinoza & Bertrand, 2008). Energetically oxygen does matter. Indeed, fish need sufficient amounts of both food and oxygen, but the latter might be more difficult to obtain than the former (Pauly, 2010). This is particularly the case in the NHCS which encompasses an intense and shallow oxygen minimum zone and where, close to the coast, even surface waters are undersaturated in oxygen (Bertrand *et al.*, 2011). In this system oxygen appears as an important driving factor of small pelagic fish populations and the availability of large prey such as euphausiids provides an energetic advantage to *E ringens* compared with sardine *Sardinop sagax* Jenyns, 1842 (Bertrand *et al.*, 2011). Our study supports this contention because *E. ringens* appear to select the largest available prey they can capture. Indeed, the progressive change in diet composition with fish size can be attributed to the predator's ability to capture and handle the prey, which is reflected by the size-range of prey it can capture (Crowder, 1985; Christensen, 1996; Lundvall *et al.*, 1999). The upper size limit of prey is set by physical constraints of the predator, in particular mouth gape (Hart & Hamrin, 1988), swimming capacity (Christensen, 1996; Lundvall *et al.*, 1999), and its visual acuity and reaction distance to prey which also increases with increasing predator size (Breck & Gitter, 1983). During ontogenetic shifts in size, *E. ringens* have thus greater access to larger and more energetic prey such as euphausiids.

Such ontogenetic changes in diet were observed in the other species of anchovies: *Engraulis mordax* Girard 1854 in California (Leong & O'Connell 1969; O'Connell 1972), *Engraulis encrasicolus* L. 1758 in South Africa (James & Findlay, 1989), the Northwest Mediterranean Sea (Tudela & Palomera, 1997; Plounevez & Champalbert, 2000) and the Bay of Biscay (Plounevez & Champalbert, 1999), and *Engraulis anchoita* Hubbs & Marini 1935 in Argentine (Ciechomski, 1967; Viñas & Ramírez, 1996).

This ability to adapting at different conditions was defined like dietary flexibility (James & Findlay, 1989). The above mentioned can be expressed in the foraging theory framework like a way to optimize the prey intake which provide high energy at low energetic - oxygen - cost and in turn can be digested and avoid the intra and interspecific competition (Griffiths, 1975; Pyke, 1984; Werner & Gilliam, 1984). The calanoid copepods size ingested by *Engraulis ringens* fluctuated between ~0.65 and 4.0 mm while the mean size of the euphausiids was estimated in 12 mm (Espinoza & Bertrand, 2008). These differences in prey size imply that *E. ringens* display two feeding strategies: filtering on the smaller copepods and biting on the bigger prey. Such behaviour has been described in *Engraulis mordax* in California (Leong & O'Connell, 1969; O'Connell, 1972), *Engraulis encrasicolus* L. 1758 (formerly known as *Engraulis capensis* see Grant & Bowen 1998) off South Africa (James & Findlay, 1989), the Northwest Mediterranean Sea (Tudela & Palomera, 1997; Plounevez & Champalbert, 2000) and the Bay of Biscay (Plounevez & Champalbert, 1999). The threshold to shift from filtering to biting was estimated to 0.7 mm for *Engraulis encrasicolus* (James & Findlay, 1989) and 1.5 mm for *Engraulis mordax* (Chiappa-Carrara & Gallardo-Cabello, 1993).

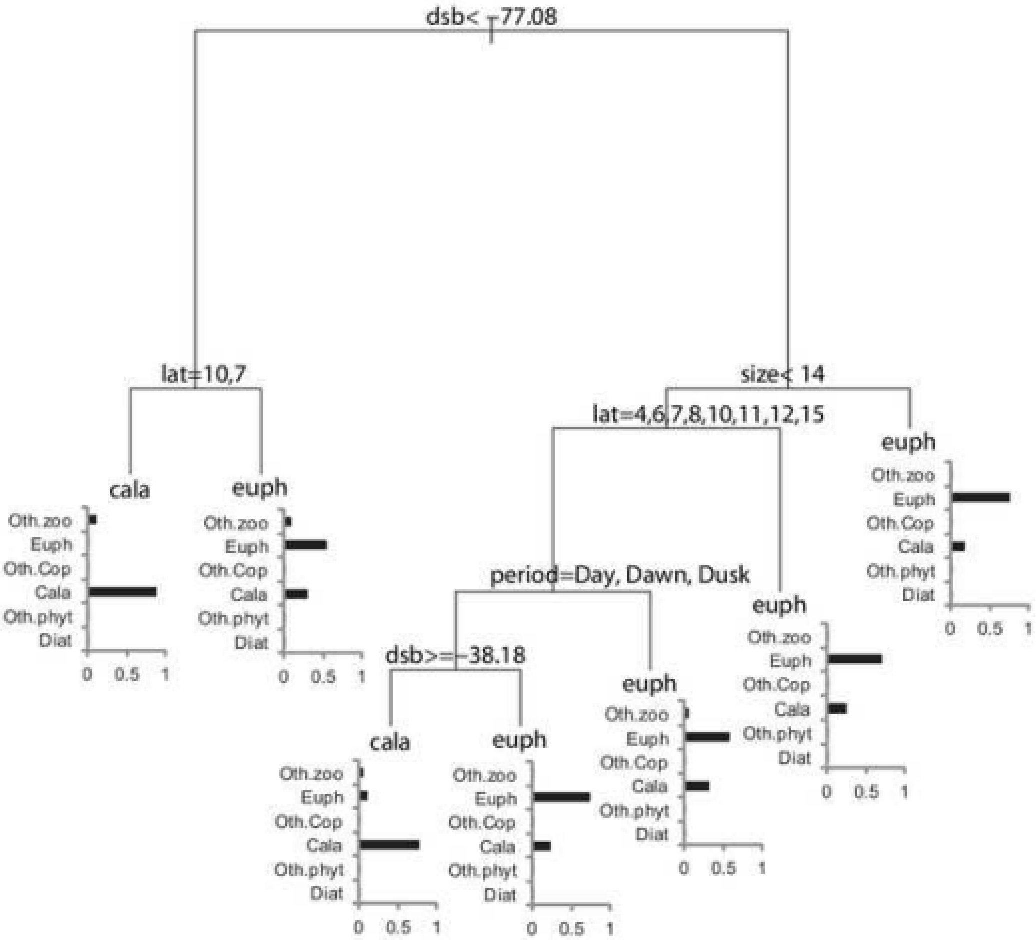

Figure 3.4 Classification and regression tree of Engraulis ringens diet according to the spatiotemporal factors from years 1996-2003: distance of the shelf break (dsb), latitude (lat), size-class (size), diel period (period). Each terminal node of the tree is characterized by a dominant prey. Below a histogram shows the predicted prey distribution (carbon proportion) for the taxonomic groups, given the explanatory variables: euphausiids (Euph), calanoid copepods (Cala), other copepods (Oth.Cop.), other zooplankton (Oth.zoo), diatoms (Diat) and other phytoplankton (Oth.phyt).

3.4.3 Spatial and diel changes

The zooplanktonic fraction dominated *Engraulis ringens* diet irrespective of latitude, refuting the contention of a latitudinal-dependent dietary shift of *E. ringens* being more zooplanktivorous in the south and phytoplanktivorous in the north of Peru previously proposed (Rojas de Mendiola, 1971; Pauly *et al.*, 1989b).

Interestingly, if euphausiids dominated *E. ringens* diet all along the coast, calanoid copepods dominated at 7ºS and 15ºS and were relatively abundant at 4ºS, 7ºS and 10-12ºS (Fig. 3.3b). At these latitudes the contribution of diatoms was also higher. In fact, by latitude, calanoid copepods were significantly correlated to diatoms (R2=0.50, p<0.001). These areas are known as active upwelling cells (Morón, 2000), with 7ºS and 15ºS corresponding to strong upwelling cells of Chicama and San Juan, respectively. In such areas the upwelled cold coastal waters are advected far from the coast and disperse coastal productivity, including zooplankton from the shelf into the offshore domain (Keister *et al.*, 2009). The abundance of diatoms and small non-vertically migrating zooplankton is usually higher within an upwelling filament than outside (Keister *et al.*, 2009).

Our results also question previous assumption according to which *Engraulis ringens* forage more on phytoplankton inshore and zooplankton more offshore (Rojas de Mendiola & Ochoa, 1973; Pauly *et* *al.*, 1989b). Indeed, the zooplankton fraction dominated *E. ringens* diet irrespective of the distance to the shelf break. Nevertheless, calanoid copepods were three time more abundant in stomachs sampled in the more inshore station than those sampled at more than 30 km from the shelf break (Fig. 3.3c), while the larger zooplankton items i.e. the euphausiids strongly dominated the diet offshore. This pattern matches the cross-shore distribution of macrozooplankton off Peru with larger and more abundant zooplankton offshore than inshore (Ballón *et al.*, 2011). Also, in our sample, *E. ringens* size increased with the distance to the coast. In particular, no *E. ringens* < 10 cm long were observed at a distance from the coast > 160 km. Both larger fish and higher availability of large prey offshore explain the observed patterns. Similar results have been observed on *Engraulis encrasicolus* and *Engraulis japonicus* Temminck & Schlegel (1846), which feed on smaller prey inshore than offshore, following the trend in anchovy size distribution (Plounevez & Champalbert, 1999; Tanaka *et al.*, 2008).

Within its coldwater coastal habitat, *Engraulis ringens* is able to forage efficiently across a range of temporal, spatial and thermal scales (Espinoza & Bertrand, 2008). However a clear diel pattern appears from our *E. ringens* diet results, with euphausiids reaching 82% during night hours while copepods accounted for ~40% during other diel periods (Fig. 3.3d). Such patterns fit with the diel vertical migration of macrozooplankton (Ballón *et al.*, 2011). Indeed *E. ringens* are restricted to the surface oxygenated water (Bertrand *et al.*, 2008a, 2010, 2011). During the day it has little access to the bulk (~79%) of the macrozooplankton community which is distributed within the oxygen minimum zone (Escribano *et al.*, 2009; Ballón *et al.*, 2011). The portion of macrozooplankton that stay in the upper layer during the day is mainly composed of small-sized subadult and juvenile euphausiids, and large copepods (Ayón *et al.*, 2008a; Ballón, 2010; Ballón *et al.*, 2011). Similar patterns were observed in *Engraulis encrasicolus* in the southern Benguela Current system (James, 1987).

In summary, *Engraulis ringens* take the bulk of its energy from zooplankton, in particular euphausiids and copepods. This is irrespective of the period, *E. ringens* size, distribution, and diel period. During the last decades the importance of euphausiids in *E. ringens* diet appears directly related to euphausiids abundance and not to physiological factors as assumed previously (e.g. Hutchings, 1992). This bottom-up effect is also observed at smaller scale since the euphausiids fraction increased with *E. ringens* size (concurrent with the capacity of *E. ringens* to capture and handle the larger prey) and euphausiids accessibility (e.g. higher offshore and/or during night). Selecting the largest prey, the euphausiids, provide an energetic advantage for *E. ringens* in its ecosystem where oxygen depletion imposes strong metabolic constrain to pelagic fish (Bertrand *et al.*, 2011). Finally this study is another illustration of *E. ringens* plasticity (see Espinoza & Bertrand, 2008) which allows it to cope with the highly variable NHCS environment.

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CHAPTER 4

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

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Abstract:

Sardines are one of the main small pelagic fish resources in eastern boundary upwelling systems (EBUS) where they play an important ecological role both as a predator of plankton and as prey of top

predators. Sardine trophodynamics have been relatively well studied in three of the EBUS (the Benguela, California and Canary upwelling systems) but not in the Humboldt Current system. In this paper we describe the diet of sardine *Sardinops sagax* in the northern Humboldt Current system (NHCS) off Peru, using an analytical method which assesses relative dietary importance in terms of estimated prey carbon content. We assessed sardine diet by examining a total of 555 stomachs collected during six surveys conducted off Peru during the period 1996–1998, and compare our results with the diet of anchoveta *Engraulis ringens* off Peru and with the diets of sardines from the southern Benguela (also *S. sagax*) and the northern Canary (*Sardina pilchardus*) upwelling systems. The diet of sardine off Peru is based primarily on zooplankton, similar to that observed for anchoveta but with several important differences. Firstly, sardine feed on smaller zooplankton than do anchoveta, with sardine diet consisting of smaller copepods and fewer euphausiids than anchoveta diet. Secondly, whilst phytoplankton represents <2% of sardine dietary carbon, this fraction is dominated by dinoflagellates, whereas diatoms are the dominant phytoplankton consumed by anchoveta. Hence, trophic competition between sardine and anchovy in the northern Humboldt Current system is minimized by their partitioning of the zooplankton food resource based on prey size, as has been reported in other systems. Whereas sardine in the NHCS feed on smaller zooplankton than do anchovy in that system, sardine in the NHCS forage on larger prey and obtain a substantial portion of their dietary carbon from euphausiids compared to sardine from the northern Canary and southern Benguela Current systems.

4.1. Introduction

Sardines (the genera *Sardinops* and *Sardina*) and anchovy (the genus *Engraulis*) are the most important commercially-exploited small pelagic fish species worldwide, and are particularly abundant in the eastern boundary current systems (EBUS; including the Benguela, California, Canary and Humboldt Current systems). These fish feed on plankton and are the dominant forage of a variety of fish, marine mammal and seabird predators, and hence are also ecologically important.

A recent synthesis on the trophic dynamics of small pelagic fish from a variety of upwelling and other systems (van der Lingen *et al.*, 2009) has shown that sardine and anchovy derive the bulk of their dietary carbon from zooplankton, a finding that contradicts many previous descriptions of exclusive or near-total phytophagy by these species. For example, Peruvian anchoveta (*Engraulis ringens*) was considered to feed directly on primary producers, which led to the belief that the large populations of anchoveta were supported by an unusually short and efficient food chain (Ryther, 1969; Walsh, 1981). This assumption was recently refuted by Espinoza and Bertrand (2008), who estimated the carbon content of prey items, as opposed to using the numerical method of stomach content analysis which is considered to be subjective (James, 1987), and showed that anchoveta forage mainly on zooplankton. Such findings improve our knowledge of the functioning of the northern Humboldt Current system (NHCS) off Peru, and illustrate the need for accurate and appropriate methods. Dietary information derived using carbon content is available for sardine and anchovy from the main EBUS (see van der Lingen *et al.*, 2009) but not for sardine (*Sardinops sagax*) in the Humboldt Current system. To date, sardine in the Humboldt Current system was generally considered as feeding mainly on phytoplankton (Rojas de Mendiola, 1966; Sanchez de Benites *et al.*, 1985; Alamo and Bouchon, 1987). This differs from recent studies on this and similar species' diet in other ecosystems, that demonstrated that sardine derive the majority of their dietary carbon from zooplankton (van der Lingen, 2002; Garrido *et al.*, 2008; van der Lingen *et al.*, 2009). A single study on sardine diet in the NHCS (Konchina, 1991) mentioned that sardine consumed mainly small copepods and tunicates, but this study has seldom been considered.

In this paper we describe the diet of sardine in the NHCS based on a method which assesses relative dietary importance according to estimated prey carbon content (James, 1987; van der Lingen, 2002). We compare our results on sardine diet and prey-size spectrum with those of the anchoveta in the NHCS. We also compare the diet of sardine from the NHCS with data on the diet of sardines in other systems, including *Sardinops sagax* from the southern Benguela (SBCS) off South Africa, *Sardina pilchardus* from the northern Canary system off Portugal (NCCS), and with published work describing clupeid diets in the California Current system (CalCS). We discuss how new insights into the functioning of these systems may be extracted from such a comparative approach. In particular, we re-examine the hypothesis (Ryther, 1969) that upwelling regions are so efficient in terms of fish production because of the direct link between phytoplankton and filter-feeding fishes.

4.2. Material and methods

4.2.1. Sardine diet in the northern Humboldt Current system (NHCS)

Sardines were collected during six acoustic surveys conducted by IMARPE research vessels between 1996 and 1998 with the aim of estimating pelagic fish abundance in the Peruvian EEZ (Table 4.1). This period encompasses the El Niño of 1997–98, one of the two strongest of the last century (Wolter and Timlin, 1998). Fish were captured using a midwater trawl net ('Engel 124/1800', 12 mm codend mesh) and a sample of 5–20 sardines was randomly collected from each trawl. Individual sardine were measured (total length; cm) and weighed (wet body mass; g) and the cardiac and pyloric sections of their stomachs were extracted onboard and immediately fixed in 5% formalin for later laboratory analysis. In the laboratory stomachs were opened and their contents extracted and weighed (wet weight, WW) to the nearest 0.01 g. The stomach contents of individual fish were then pooled according to fish length (3 cm size-classes) for each sample, and pooled stomach contents were filtered through a 125 µm mesh. The filtered material was diluted to 100 ml using filtered seawater and a 0.1-ml sub-sample was examined under the compound microscope to identify and count phytoplankton prey. The material that remained on the mesh was diluted to 100 ml using filtered seawater and a 10-mL sub-sample was examined using a stereoscopic microscope to identify (to genus) and count zooplankton prey. All prey counts were then standardized to number per 100 ml, except for anchoveta eggs, for which the whole sample was examined.

Table 4.1: Survey characteristics.

Survey code	Start date	End date	Latitudinal limits	Transect extension (nmi)	N° of trawls	N° of sardine stomachs	Sardine Length range (min. - max.)
1996/11-12	16 November 1996	19 December 1996	5°S-18°S	100	1	16	25-30
1997/02-04	13 February 1997	23 April 1997	5°S-18°S	80-90	5	67	21-30
1997/09-10	04 September 1997	05 October 1997	3º30’S-18ºS	80	6	79	10-30
1998/03-05	27 March 1998	01 May 1998	3º30’S-18ºS	50	18	287	11-29
1998/05-06	26 May 1998	24 June 1998	4ºS-18ºS	70	7	59	16-21
1998/08-09	23 August 1998	17 September 1998	5°S-18°S	80	4	47	18-22

Different procedures were followed to estimate the carbon content of phytoplankton and zooplankton and hence determine their relative dietary importance, and have been described in detail in Espinoza and Bertrand (2008). In summary, we did not measure the size of all prey items but instead estimated prey size using information from the literature and from some direct measurements, taking into account the life cycle stage (e.g. adult *Calanus* were separated from copepodite stages). The lack of available references on size and volume for planktonic organisms off Peru led us to use a wide range of references published for other ecosystems. Phytoplankton size was converted to phytoplankton cell volume using references describing the organism’s geometric shape and providing equations relating shape to volume, with the coefficients for each equation being obtained from the literature or from estimations made by IMARPE. To transform phytoplankton volume into carbon content we used equations given in Menden-Deuer and Lessard (2000) and Verity and Langdon (1984). For zooplankton, prosome or total length of various zooplankters was taken from the literature or from some direct measurements made by IMARPE on zooplankton from stomach content samples. Zooplankton dry weight and carbon content were calculated using equations given by Alexandrov (2001), Deibel (1986), James (1987), van der Lingen (2002), Parsons *et al.* (1984), and Sameoto (1971). All prey carbon content values were standardized to µg C, and the contribution to dietary carbon of a particular prey type was expressed as a percentage of the total estimated carbon content of all fish examined in each cruise. In order assess temporal (inter-survey) variability of sardine diet off Peru we pooled diet data into seven broad prey categories (dinoflagellates, diatoms, other phytoplankters, copepods, gastropods, euphausiids, and other zooplankters), and present the results for individual surveys and for all surveys pooled. All the equations and conversion factors are available in Tables 2–4 of Espinoza and Bertrand (2008).

4.2.2. Diet comparison

To compare the diet of sardine from the NHCS with that of anchoveta (*Engraulis ringens*) in the same system, and with those of sardines from the southern Benguela (SBCS) and northern Canary (NCCS) systems, we reanalysed data from published work that also examined dietary composition in terms of prey carbon content. For anchoveta we used results reported by Espinoza and Bertrand (2008), which comprised data on anchoveta stomach contents collected during individual surveys and aggregated for all surveys (as has been done for NHCS sardine in this paper). The diet of southern Benguela sardine (*Sardinops sagax*) was described by van der Lingen (2002), using samples collected from midwater trawls deployed during research surveys conducted in 1993 (number of trawls sampled = 10; stomach contents of 10 sardine per trawl were pooled for analysis) and 1994 (number of trawls sampled = 17; stomach contents of 10 sardine per trawl were pooled for analysis). The average contribution to sardine dietary carbon by prey type ($\%C_{\text{Type}}$) and by prey size ($\%C_{\text{Size}}$) was calculated for each survey, with the $\%C_{\text{Type}}$ and $\%C_{\text{Size}}$ values from each sample receiving equal weighting. For our comparison we calculated average $\%C_{\text{Type}}$ and $\%C_{\text{Size}}$ values from all 27 samples, again with equal sample weighting. Garrido *et al.* (2008) described the diet of 70 sardine (*Sardina pilchardus*) from the northern Canary Current system using samples collected fortnightly from purse-seine catches off the west and south coasts of Portugal, taken during 2002–2004, and those two datasets were also aggregated for our comparison. Further details regarding the sampling and analytical methods used for anchoveta, and sardines from the southern Benguela and northern Canary systems, are provided in Espinoza and Bertrand (2008), van der Lingen (2002), and Garrido *et al.* (2008), respectively.

In order to facilitate dietary comparisons between species and systems we first grouped diet data into the seven broad prey categories listed above, and present this information in terms of numerical dominance and relative contribution to dietary carbon. To examine the zooplankton component of sardine diet in more detail we then re-grouped the data (in terms of relative contribution to dietary carbon only) from each system/species into the following ten prey categories: (i) diatoms, (ii) dinoflagellates, (iii) other phytoplankters, (iv) calanoid copepods, (v) miscellaneous copepods (mainly cyclopoid, harpacticoid, and poecilostomatoid copepods), (vi) other copepods (including copepod nauplii), (vii) euphausiids, (viii) gastropods, (ix) fish eggs, and (x) other zooplankters (including crustacean eggs). We then compared the prey-size spectra between species and systems by examining the contribution to dietary carbon made by the following six size-classes: $0 < x < 0.5$, $0.5 \leq x$ $1.0 \leq x$ 2.0, $2.0 \leq x$ 4.0, $4.0 \leq x$ 8.0, ≥ 8.0 mm. We used the Kruskal–Wallis rank test, a non-parametric alternative to ANOVA (Scherrer, 1984), to assess whether diets between species and systems were significantly different. Because data from the SBCS are only available as percentage contribution to diet by size class and by taxonomic group, standard statistical methods (e.g. chi-square, contingency table, Kruskal–Wallis, and others) could not be used on those data. Consequently, Kruskal–Wallis tests were used to compare the diets of sardine and anchoveta from the NHCS, and of sardine from the NHCS and the NCCS, only.

4.3. Results

4.3.1. Sardine diet in the NHCS

A total of 555 sardine from the NHCS ranging from 10 to 30 cm total length were analysed (Table 4.1). Ninety-one prey taxa were identified, including 24 diatom genus, 10 dinoflagellates, 1 silicoflagellate, 1 phytoflagellate, 4 tintinnids, 1 radiolarian, 32 copepods, and 18 other genus (Annex 4).

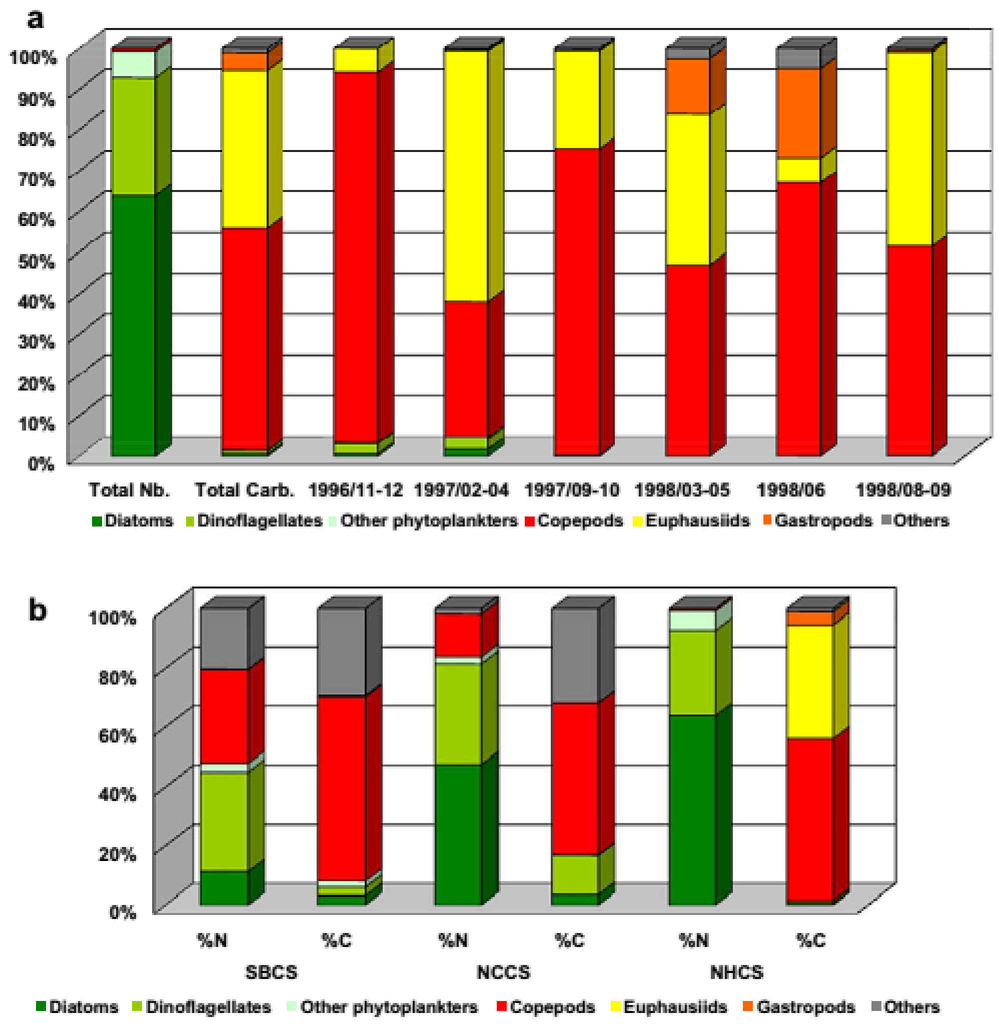

Figure 4.1: (a) Percentage contribution of diatoms, dinoflagellates, other phytoplankters, copepods, euphausiids, gastropods and other zooplankters, by number (Total Nb.) and by contribution to dietary carbon (Total Carb.) for (a) the pooled sardine stomach content data (two left histograms), and for each of the 6 surveys from which sardine stomach contents were analyzed off Peru (surveys are identified along the x-axis, with the first two numbers corresponding to the year, the following two numbers the start month of the survey, and the last two numbers the end month of the survey), and (b) by number (%N) and by contribution to dietary carbon (%C) for Sardinops sagax in the Southern Benguela current system (SBCS), Sardina pilchardus in the Northern Canary current system (NCCS), and S. sagax in the Northern Humboldt Current system (NHCS).

Numerical analysis of the diet when data from all the surveys were combined indicated that phytoplankton strongly dominated sardine diet and comprised 99.2% on average of all ingested prey, with copepods representing only 0.7%, euphausiids <0.1%, and other zooplankters <0.1% of the total number of prey (Fig. 4.1a). However, this view of sardine diet changes when prey carbon content is considered (Fig. 3.1a); zooplankton was by far the most important component and contributed 98.5% of dietary carbon, whilst phytoplankton contributed the remaining 1.5%. Among zooplankters, copepods dominated and contributed 54.5% of dietary carbon, followed by euphausiids (38.7%) and then other zooplankton (5.3%). The copepod carbon fraction was dominated by *Eucalanus* (58.4% of the total copepod contribution to dietary carbon), *Calanus* (21.5%), *Rhincalanus* (5.4%) and *Centropages* (4.5%). The phytoplankton carbon fraction was dominated by the dinoflagellates *Protoperidinium* (31.4% of the total phytoplankton contribution to dietary carbon) and *Ceratium* (16.2%), and the diatom *Coscinodiscus* (27.3%).

When the surveys are considered individually strong variability in dietary composition is seen (Fig. 4.1a). The maximum contribution to dietary carbon by copepods (90.8%) occurred during November–December 1996, whilst the minimum (33.3%) was observed during February–April 1997. The maximum contribution by euphausiids was observed in February–April 1997 (61.2%) and August–September 1998 (47.5%), whilst the minimum (5.8%) occurred in November–December 1996. The maximum contribution by other zooplankters occurred in March–May 1998 (16.2% of dietary carbon) and June 1998 (26.9%), with gastropods also having their maximum contributions during these surveys. The contribution to dietary carbon made by phytoplankton was very low (<0.3%) during the El Niño 1997–1998, whereas the highest value (4.9%) was observed in February–April 1997 just before the El Niño event.

4.3.2. Comparative trophic ecology by prey type

In all systems for which data are available the image of sardine diet is dramatically different depending on whether prey items are considered in terms of their numerical contribution or their relative contribution to dietary carbon (Fig. 4.1b). In terms of numerical dominance the phytoplankton fraction ranged between 47.8% (SBCS) and 99.2% (NHCS), whereas phytoplankton contributed between 1.5% (NHCS) and 17.0% (NCCS) of total dietary carbon. Because the numerical method is not appropriate for adequately characterizing diet, subsequent dietary comparisons will be described in terms of dietary carbon only.

Marked differences are seen between the diet of sardine and anchoveta in the NHCS, and also between sardines from the NHCS, the NCCS, and the SBCS (Fig. 4.2). Results from the Kruskal–Wallis analysis performed between systems and species (excluding the SBCS sardine) on dietary carbon by prey categories showed highly significant ($p < 0.01$) differences for all prey categories except for ‘‘Other zooplankters” ($p > 0.05$). Sardine from the NHCS had only two prey categories that accounted for more than 5% of dietary carbon, namely calanoid copepods (53.0% of dietary carbon) and euphausiids (38.7%). These two categories also dominated anchoveta diet, but in reverse order, with euphausiids (67.5%) being the most important category followed by calanoid copepods (26.3%). Sardine from the NCCS presented a very different prey spectrum and a more even spread of important prey categories, with six categories accounting for more than 8% of dietary carbon: other copepods (26.6%), fish eggs (23.8%), dinoflagellates (13.3%), miscellaneous copepods (12.3%), calanoid copepods (12.2%), and other zooplankters (8.4%). The diet of sardine in the SBCS is intermediate between sardine in the other two systems, with four prey categories accounting for more than 8% of dietary carbon: calanoid copepods (38.2%), miscellaneous copepods (18.2%), other zooplankters (17.5%), and fish eggs (14.6%).

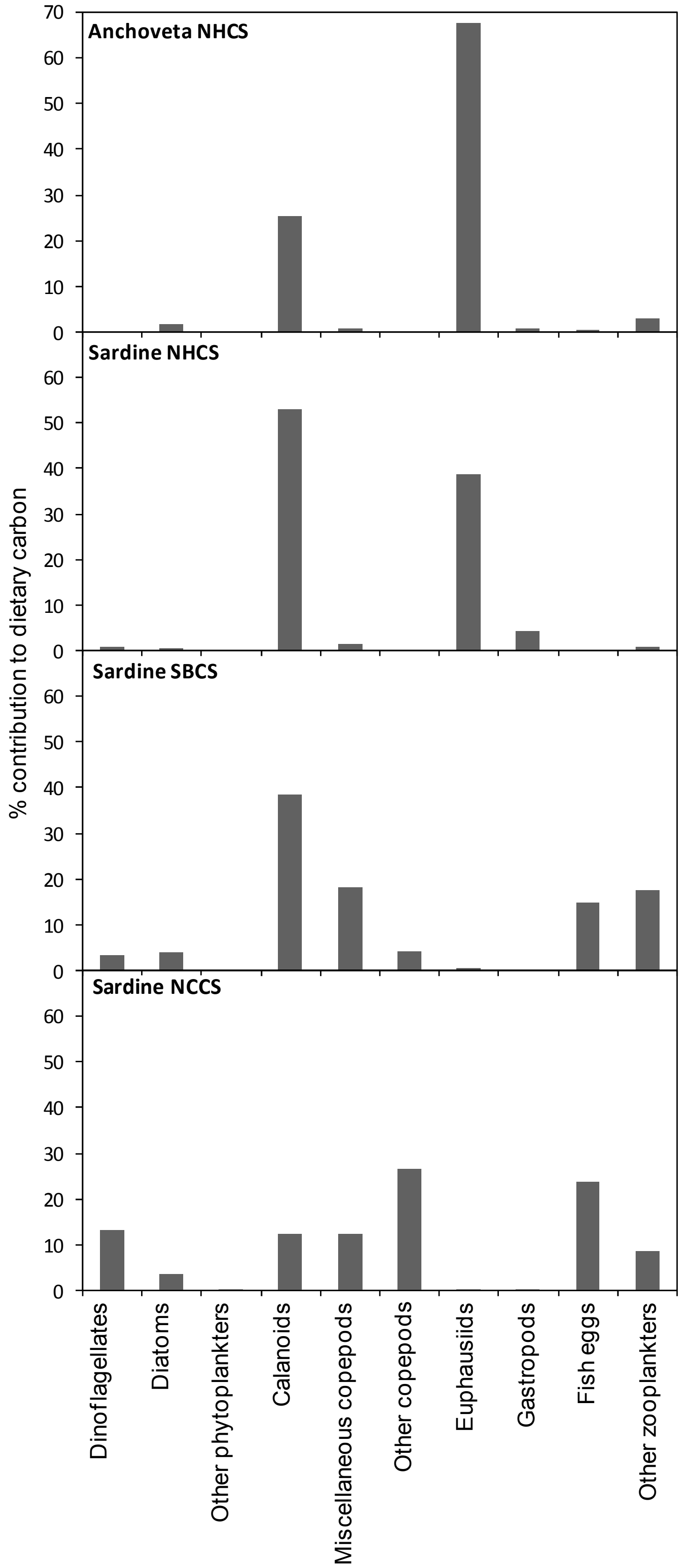

Figure 4.2: Average percentage contribution to dietary carbon (%C) by prey category for Engraulis ringens and Sardinops sagax in the Northern Humboldt Current system, S. sagax in the Southern Benguela system, and Sardina pilchardus in the Northern Canary Current system.

4.3.3. Comparative trophic ecology by prey-size class

The differences observed in the contribution to dietary carbon by prey category between fish and systems are even more clearly observed when the prey-size spectra are examined (Fig. 4.3), and results from the Kruskal–Wallis analysis performed between systems and species (excluding the SBCS sardine) on dietary carbon by prey size showed highly significant ($p < 0.01$) differences for all size classes. In the NCCS the sardine prey-size spectrum presents a decreasing trend with smaller prey contributing the majority of total dietary carbon; prey smaller than 0.5 mm contribute 49.7% of dietary carbon and this proportion decreases to zero for prey larger than 4 mm. Sardine in the SBCS also derive the majority (>90% on average) of their dietary carbon from small (<2.0 mm) zooplankton prey, and their prey-size spectra is roughly dome shaped with a mode between 1 and 2 mm. No prey larger than 4 mm were observed in sardine from that system. Finally, the prey-size spectrum of sardine in the NHCS shows an increasing trend, with prey <0.5 mm making a negligible contribution to dietary carbon and prey larger than 8 mm contributing 39.6% of dietary carbon, this size corresponding mainly to euphausiids. A similar, and even more pronounced trend is observed for anchoveta in the NHCS, for which prey larger than 8 mm contribute up to 70.9% of dietary carbon.

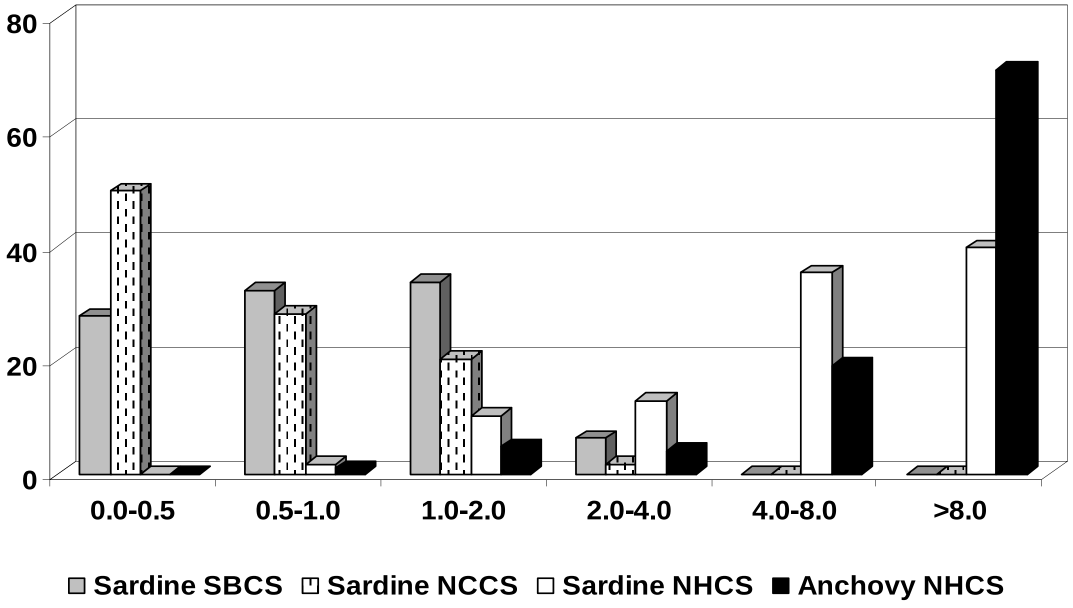

Figure 4.3: Average percentage contribution to dietary carbon (%C) by prey size class (mm) for Sardinops sagax in the Southern Benguela system, Sardina pilchardus in the Northern Canary system (Iberian coast), and S. sagax (sard) and Engraulis ringens (anch) in the Northern Humboldt system.

4.4. Discussion

4.4.1. Sardine diet in the NHCS

Our analysis of the composition of stomach contents of sardine in the NHCS illustrates its capability for foraging on a large variety of prey and over several trophic levels. When considering only prey numbers, sardine diet is dominated by phytoplankton and the zooplankton fraction is negligible (Fig. 4.1a). However, when the carbon content of prey items is considered, zooplankton becomes by far the most important component of dietary carbon. The zooplankton carbon fraction was dominated by copepods, in particular *Eucalanus* and *Calanus*, followed by euphausiids, and the importance of these taxa was previously recognised by Alamo and Bouchon (1987) and Konchina (1991). The phytoplankton carbon fraction was dominated by large dinoflagellates (mainly *Protoperidinium*, *Ceratium*, and *Coscinodiscus*), as previously observed (Alamo and Bouchon, 1987; Konchina, 1991). This very low proportion of phytoplankton could represent a limitation to sardine growth and development, since phytoplankton has more nitrogen (N) than zooplankton (i.e. the C:N ratio is higher for zooplankton than for phytoplankton). However, sardines (and anchovies) have significantly higher N absorption efficiencies from zooplankton than from phytoplankton (van der Lingen, 1998), and that sardine are better able to utilize zooplankton N (and also C and dry mass) than phytoplankton N suggests that this species derives more of its nutritional requirements from zooplankton (van der Lingen, 1998), which is supported by our results.

The contribution made by different prey categories to the diet of sardine in the NHCS strongly varied during the study period (Fig. 4.1a), illustrating the spatiotemporal opportunistic feeding behaviour of sardine which can forage on a variety of prey according to variations in plankton composition (van der Lingen, 1994; van der Lingen *et al.*, 2006). The relative contribution from phytoplankton was always low but reached a maximum in February–April 1997, prior to the El Niño, and then decreased to very low (<0.5%) levels during the El Niño of 1997–98. The proportion of sardine dietary carbon derived from copepods was highly variable and presented no clear trend (Fig. 4.1a), being highest in November–December 1996 and lowest a few months later in February–April 1997. Yet, when the contribution to dietary carbon by copepods decreased that from the euphausiids increased, and viceversa. The relative importance of copepods and euphausiids in sardine diet does not match those for anchoveta diet, described by Espinoza and Bertrand (2008) using data collected during the same surveys (Figs. 4.1a and Fig. 2.2). For instance, the highest copepod fraction observed in sardine diet in November–December 1996 corresponds to the lowest observed for anchoveta, although the very low number of sardine samples collected during this survey (Table 4.1) suggests that results should be interpreted with caution. However, this opposite trend was also observed for other surveys (in particular September–October1997andMarch–May1998) that had a larger sample size. These differences may reflect the fact that these species are ecological neighbours but not ecological analogues (Gutiérrez *et al.*, 2007), and seldom overlap spatially (Bertrand *et al.*, 2004a; Gutiérrez *et al.*, 2007; Swartzman *et al.*, 2008).

Most of the previous studies on sardine diet in the NHCS were based on qualitative methods (Rojas de Mendiola, 1966; Sanchez de Benites *et al.*, 1985; Alamo and Bouchon, 1987), and indicated that sardines depend mainly on phytoplankton with zooplankton only occasionally being important. Konchina's (1991) paper was unique in mentioning that zooplankton was by far the most important dietary component for sardine and anchoveta off Peru. However, his study was based on a relatively small sample size and was not fully recognised in Peru. The present study corroborates Konchina's (1991) results, and clearly shows that in the NHCS sardine derives the bulk of its diet from zooplankton, as is the case for anchoveta (Espinoza and Bertrand, 2008). This result is in agreement with results from other studies (see review by van der Lingen *et al.*, 2009) on *S. sagax* diet in the SBCS (van der Lingen, 2002) and in the CalCS (Parr, 1930; Emmett *et al.*, 2005; McFarlane *et al.*, 2005), as well as with results for the Iberian sardine *Sardina pilchardus* off Portugal (Garrido *et al.*, 2008). Given that our sampling had limited spatial and temporal coverage, we cannot conclude that this characterization of the diet of sardine off Peru we obtained is perfectly representative of its diet during different periods, e.g. when sardine was more abundant in the system (mid 1970s to the beginning of the 1990s). Additionally, the fact that most of our data were collected during the El Niño of 1997–98 could also impact our dietary characterization, as El Niño events are known to alter the food web towards a higher dominance of pico- and nanophytoplankton (e.g. Iriarte and González, 2004). The impact of El Niño on the food web and on fish diet has been observed in other cases (e.g. Brodeur and Pearcy, 1992; Arntz and Fahrbach, 1996), although Espinoza and Bertrand (2008) did not observe differences in anchoveta diet during the El Niño of 1997–98 compared to other, non-El Niño periods. This may be due to the fact that during the El Niño of 1997–98 local upwelling cells in the NCCS were strong enough to avoid food limitation for secondary producers (Bertrand *et al.*, 2004a). Furthermore, in an analysis of a 35-year time series of zooplankton volume, Ayón *et al.* (2004) could not relate the variability in zooplankton biomass to El Niño events.

4.4.2. Diet comparison

The diets of sardine and anchoveta in the NHCS are broadly similar and in both species are dominated by copepods and euphausiids, although in different proportions (Fig. 4.2). A second difference is related to dinoflagellates, that are consumed noticeably only by sardine. The apparent similarity in the diet of sardine and anchoveta is puzzling, since these species have very different feeding capabilities and foraging behaviours, at least in the SBCS (van der Lingen *et al.*, 2006). However, when sardine diet is compared between systems, important differences appear, even if zooplankton is always by far the most important dietary component (Figs. 4.1 and 4.2). Copepods are always the dominant prey item, but whereas calanoids are by far the most important copepod in the diet of sardine in the NHCS, they represent less than 40% in sardine from the SBCS and only 12.2% in those from the NCCS (Fig. 4.2). The contribution to sardine dietary carbon made by phytoplankton appears to be negligible (<2%) in the NHCS, and ranges between 7% and 17% in the other systems. Most of the samples from the NHCS were collected during the El Niño of 1997–98, which could have biased our results toward an underestimation of the phytoplankton fraction (note that the number of samples is also rather low in the case of the other systems), although even before El Niño the phytoplankton fraction accounted for less than 5% of sardine diet (i.e. less than in other systems). Finally, fish eggs are important prey items of sardine in the NCCS and SBCS, but apparently not in the NHCS. However, sardine in the NHCS have been observed to forage on fish eggs, with Santander *et al.* (1983) reporting an average of 16 anchoveta eggs in each sardine stomach for fish collected during August–September 1981, and the differences between that and our study likely reflect sampling limitations.

The differences in prey composition observed between sardine and anchovy and also between sardine from the three systems are related to marked differences in the modal sizes of ingested prey (Fig. 4.3). Within the NHCS, sardine and anchoveta forage principally on large items. This is particularly true for anchoveta, for which prey larger or equal to 8 mm contribute 70.9% of dietary carbon. Sardine in the NHCS derive the majority of their dietary carbon from items larger than 4 mm, and it is interesting to note that euphausiids observed in sardine stomachs were smaller (~8 mm) than those typically seen in anchoveta stomach contents (~12 mm). Also interesting is the difference in modal prey size of sardine diet between systems. If we take into account our results (Fig. 4.3) and published studies from the CalCS (e.g. Emmett *et al.*, 2005; McFarlane *et al.*, 2005; Miller and Brodeur, 2007; van der Lingen *et al.*, 2009), we can rank the size of sardine prey between systems in the following order: Canary < Benguela < California and Humboldt.

In the NCCS most of the sardine dietary carbon comes from small copepods, fish eggs and phytoplankton that are <2 mm and have a mode of <0.5 mm. The main prey of sardine in the SBCS (calanoid and cyclopoid copepods and fish eggs) are also <2 mm and have a mode between 1 and 2 mm. Finally it is only in the Humboldt and California systems that large prey, in particular euphausiids, are important in sardine diet. Therefore, it seems that in the NHCS sardine are possibly not primarily non-selective filter-feeders as in the SBCS (see van der Lingen, 2002; van der Lingen *et al.*, 2006) and probably in the NCCS (Garrido *et al.*, 2007), possibly due to local adaptations to different environments. More detailed research on sardine and anchoveta feeding behaviour should be performed in the future.

The main difference in sardine prey composition between systems is related to the euphausiids, that are absent from sardine stomach contents in the eastern Atlantic (NCCS and SBCS) but are important in the eastern Pacific (NHCS, this study; and CalCS, Emmett *et al.*, 2005; McFarlane *et al.*, 2005; Miller and Brodeur, 2007). This is a crucial finding because large prey such as euphausiids have a very high energy content per individual, which may favour or accelerate pelagic fish growth. In the Atlantic, euphausiids are less available to sardines, and fish eggs may supplant euphausiids in sardine diet, at least to a degree. We assume that the importance of euphausiids for sardine diet in the eastern Pacific is due to a higher availability of these organisms, attributable to a narrower shelf compared with Canary and Benguela systems. In the NHCS for instance, the rich, cold coastal waters can extend far away from the shelf when the upwelling is strong. This allows the coastal community, including small pelagic fish, to extend their range of distribution far away from the shelf (Swartzman *et al.*, 2008) and hence have access to the offshore vertically migrating communities, in particular the euphausiids. As stated by Espinoza and Bertrand (2008), a strong connection between the coastal and the offshore pelagic ecosystems may allow sardine and anchoveta to gain access to high energy prey such as euphausiids, which is likely one of the reasons for the high fish productivity of the NHCS (see Espinoza and Bertrand, 2008) compared to other systems (see Hutchings, 1992; Chavez *et al.*, 2008).

Local and seasonal changes in food composition are high in all systems, reflecting the impact of environmental dynamics on the specific composition of prey patches (Konchina, 1991). Gregarious fish such as sardine and anchovy are sensitive to processes (in particular patchiness) occurring at a continuum of spatial scales from the individual (dm) to populations (100s km) (Fréon *et al.*, 2005; Bertrand *et al.*, 2008a). They exhibit a highly flexible feeding behaviour and can shift between filter or particulate feeding according to the available prey (van der Lingen, 2002; Garrido *et al.*, 2007), and this opportunistic foraging behaviour allows them to cope with variability in the conditions they meet.

4.4.3. Summary

Our characterization of the diet of sardine in the NHCS based on prey carbon contents has shown that the diet of sardine off Peru is based primarily on zooplankton, similar to that observed for anchoveta *Engraulis ringens* (Espinoza and Bertrand, 2008), but with several important differences. Firstly, sardine feed on smaller zooplankton (smaller copepods and fewer euphausiids) than does anchoveta. Secondly, whilst phytoplankton represents <2% of sardine dietary carbon, this fraction is dominated by dinoflagellates, whereas diatoms are the dominant phytoplankton consumed by anchoveta. Hence, trophic competition between sardine and anchovy in the NHCS is minimized by their partitioning of the zooplankton food resource based on prey size, as has been reported in other systems (van der Lingen *et al.*, 2009). Sardine in the NHCS (this study) and in the CalCS (Emmett *et al.*, 2005; McFarlane *et al.*, 2005; Miller and Brodeur, 2007) forage on larger prey and obtain a substantial portion of their dietary carbon from euphausiids, compared to those from the NCCS and SBCS. We relate this difference to the narrower shelf in the eastern Pacific compared with the eastern Atlantic that allows clupeids to distribute over the shelf break and in offshore areas where euphausiids are abundant. Euphausiids have a high energetic content, which may favour fish growth relative to when feeding on other prey types. Additionally, the high availability of euphausiids in the eastern Pacific may limit sardine predation on fish eggs, which is very high in the NCCS and the SBCS compared with the NHCS. These last two points are probably key factors explaining the secret of the fish productivity in the NHCS. Finally our results provide an opportunity to re-examine the hypothesis of Ryther (1969) who attributed the high abundance of small pelagic fish in upwelling systems to their ability to feed directly on phytoplankton and hence benefit from a very short and efficient food chain. This theory based on phytophagy was questioned decades ago in other systems (Cushing, 1978; James, 1987) but was still considered to be the case off Peru. The ‘Peruvian short food chain’ hypothesis has now been discredited (this study; Konchina, 1991; Espinoza and Bertrand, 2008; van der Lingen *et al.*, 2009). Off Peru, anchoveta and sardine not only forage mainly on zooplankton but select large, energetically-rich zooplankters. This indicates that the energy transfer from primary production to fish through zooplankton is particularly efficient, and that the zooplankton biomass is higher than supposed. Recent estimates of zooplankton biomass, based on acoustic methods, seem to confirm the presence of high biomass of macro-zooplankton off Peru (M.Ballón, IMARPE unpublished data), but more research in this field is crucial.

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CHAPTER 5

Trophic pathways in the northern Humboldt Current system: new insight from stable isotopes analysis

Abstract:

Here we aim at better understand the trophic relationships in the northern Humboldt Current system (NHCS) following the route from zooplankton to top predators in an environment strongly influenced by persistent upwelling and oxygen minimum zone (OMZ). For that purpose we analyzed the $\delta^{13}C$ and $\delta^{15}N$ stable isotope values of thirteen taxonomic categories collected off Peru from 2008 - 2011, i.e., zooplankton, fish, squids and air-breathing top predators. The $\delta^{15}N$ isotope signature was strongly impacted by the species, the body length and the latitude. Along the Peruvian coast, the OMZ get more intense and shallow south of ~7.5ºS impacting the baseline nitrogen stable isotopes. Also, the sampling design was unbalanced in terms of body length and geographical position. To compare $\delta^{15}N$ values and being able to estimate the trophic position (TP) of each species, we employed a linear mixed-effects modelling approach taking into account the latitudinal and body length effects. We provide a new vision of the relative trophic position of key ecosystem components. Also we confirm previous stomach content-based results on anchoveta *Engraulis ringens* TP and highlight the potential remarkable importance of an often neglected ecosystem component, the squat lobster *Pleuroncodes monodon*. Indeed, our results support the hypothesis according to which this species forage to some extent on fish eggs and larvae and can thus predate on the first life stages of exploited species. However, the $\delta^{13}C$ values of anchoveta and squat lobster suggest that these two species do not exactly share the same habitat, with anchoveta having a larger and more offshore foraging range. This would potentially reduce some direct competition and/or predation.

Key words: Peru, trophic ecology, oxygen minimum zone, anchoveta *Engraulis ringens*, zooplankton, top predators, trophic position, Squat lobster *Pleuroncodes monodon*, jumbo squid *Dosidicus gigas*

5.1. Introduction

The northern Humboldt Current system (NHCS) off Peru covers less than 0.1% of the World Ocean surface but sustains ~10% of the world fish catch (Chavez et al., 2008). The NHCS is subjected to bottom-up forcing at intraseasonal (Bertrand et al., 2008b) interannual (Barber and Chavez, 1983), multidecadal (Chavez et al., 2003; Alheit and Ñiquen, 2004; Ayón et al., 2008b) and centennial time scales (Gutiérrez et al., 2009; Sifeddine et al., 2008; Valdés et al., 2008; Salvatteci, 2013). If the NHCS is the “heavyweight champion of the world” in terms of fish productivity, it generates considerably less primary production than the Northern Benguela Current System (Bakun and Weeks, 2008).

Different hypotheses have been proposed to explain this paradox:

(i) the proximity to the equator, unique among the eastern boundary upwelling systems (EBUSs, allows strong upwelling with relatively weak winds so a weak turbulence (Parrish et al., 1983), which may increase the occurrence of the optimal environmental windows for fish reproduction (Cury and Roy, 1989); (ii) differences in the trophic structure within EBUSs (e.g., food chain length, Carr and Kearns 2003); (iii) the strong influence of ENSO inter-annual variability might ‘re-set’ the ecosystem and could favour fast-growing populations like small pelagic fishes in the NHCS (Bakun and Weeks 2008); (iv) in opposition with other EBUS, the main spawning periods match the season of maximal shelf retention of ichthyoplankton and food concentration in the NHCS for both anchovy and sardine (Brochier et al. 2011). These hypotheses are not sufficient to understand the NHCS paradox and more emphasis should be put to better understand trophic relationships in this system.

Espinoza and Bertrand (2008, 2014) and Espinoza et al. (2009) showed that the Peruvian anchovy or anchoveta *Engraulis ringens* forage mainly on zooplankton refuting the prevalent direct short food chain hypothesis from diatoms to forage fish (Ryther 1969). These results suggest an ecological role for forage fish that challenges current understanding of its position in the foodweb, the functioning of the NHCS, and the current trophic models of the NHCS. In upwelling ecosystems, the role of plankton-feeding pelagic fish such as anchovy has often been enhanced, resulting for instance in anchoveta-centered model of the Peruvian ecosystem (Pauly and Tsukayama, 1987; Pauly et al., 1989a,b). However, other species can have important ecological role in this ecosystem. For example, a pelagic crustacean, the squat lobster *Pleuroncodes monodon* is particularly abundant in the NCHS since the mid-1990s (acoustic estimates ranging between 0.6 and 3.4 million tonnes), being potentially an important prey for seabirds, mammals and coastal fish (Gutiérrez et al. 2008). As anchovy, it would then constitute an important prey for apex predators (Arias-Schereiber, 1996 and Jahncke et al., 1997). Since anchoveta and squat lobster partially overlap along the Peruvian coast (Gutiérrez et al. 2008), they could compete for food. However, squat lobsters have been seldom observed in anchoveta stomachs. The question of *P. monodon* potential role relative to anchovy and apex predators such as fur seals and birds is therefore still under debate, and central to understand the trophic functioning of the NHCS. Another important species in the ecosystem is the jumbo squid *Dosidicus gigas* that is exploited by an important fishery. This species has received attention in the NCSH through stomach content and stable isotope analysis to understand its life histories, habitat and resource uses (Lorrain et al., 2011; Argüelles et al., 2012; Alegre et al., 2014). However is necessary to better understand its actual role within the food web.

There is thus a need to extend to other species than anchoveta the revision of the trophic ecology in the NHCS to reach a comprehensive and revised vision of the trophic relationships in the NHCS. Still, all the previous results were based on stomach content analysis (SCA) only.

This method has limitations since it is logistically difficult to apply for a wide suite of species; it underestimates the importance of soft bodied, rapidly digested or unidentifiable food items (Tieszen et al., 1983); and only brings a snapshot of ingested prey items (Olson et al. 2010). In contrast to SCA, the stable isotope analysis (SIA) of consumer tissues integrate dietary information over an extended period and has been proved to be a powerful tool to study the trophic ecology of marine organisms at the ecosystem scale (Hobson et al. 2002, Michener and Kaufman 2007, Yasue et al. 2013). The $\delta^{13}C$ values are generally used as a tracer of the habitat or the feeding zone of organisms (Hobson, 1999; France, 1995; Cherel and Hobson, 2007) while $\delta^{15}N$ values are mainly used as an indicator of the trophic position of organisms (Hobson and Welch, 1992; Lesage et al., 2001; Le Loc'h et al., 2008; Mèndez-Fernandez et al. 2012). However, stable isotopes do not allow reaching the taxonomic precision of the SCA, and it depends of the tissue turnover rates, i.e. how quickly changes the isotope signature in a body tissue following a dietary change (Buchheister and Latour, 2010). Furthermore, the $\delta^{15}N$ and $\delta^{13}C$ at the base of the food web from which organisms draw their nitrogen and carbon can have a high spatial variability (MacLeod and Barton, 1998; Kitchell et al., 1999; Vander Zanden and Rasmussen, 1999). These geographical variations in primary producer stable isotope values, or nitrogen and carbon isotopic baselines, have been shown to propagate up the food web and are reflected in the isotope value of organisms up to top predators (Popp et al. 2007; Cherel and Hobson 2007; Olson et al. 2010; Graham et al. 2010). Accurate and reliable assessment of isotopic baselines is therefore critical to estimating a consumer's trophic position and concomitantly food chain length.

A prominent feature of the NHCS is the presence of a shallow (25-50 m) permanent oxygen minimum zone (OMZ) along the coast (e.g., Morales et al., 1996; Strub et al., 1998; Fuenzalida et al., 2009; Bertrand et al., 2010), which strongly impacts marine life (Bertrand et al. 2008a, 2011) and hence trophic interactions. In this OMZ, in particular south of ~7.5°S where the upper limit of the OMZ is shallow (Bertrand et al. 2010; Mollier-Vogel et al. 2012), both intense denitrification and anaerobic ammonium oxidation (anammox) occur (Kuypers et al. 2005; Lam et al. 2009; Lam and Kuypers 2011), which should increase the nitrogen stable isotope values of the baseline (Graham et al. 2010, Mollier-Vogel et al. 2012). To assess these baseline variations, a primary consumer such as zooplankton can be sampled. Primary consumers can integrate isotopic variation at the base of the food web and may be less prone to short term fluctuations in stable isotope values than primary producers. As an example, McMahon et al. (2013) compiled zooplankton $\delta^{15}N$ values from the literature and produced a basin-wide isoscape for the Atlantic Ocean.

In this context, the main objective of this study is to determine the trophic pathways in the NHCS, following the route from zooplankton to top predators in an environment strongly influenced by persistent upwelling and OMZ. For that purpose we analyzed the stable isotope values of 13 taxonomic categories collected off Peru from 2008 - 2011, i.e., zooplankton, fish, squids and air-breathing top predators.

5.2. Material and methods

5.2.1. Sampling

Collection samples covered the entire Peruvian coast in the northern HCS (Table 5.1, Fig. 5.1; 03°30'-18°S). Zooplankton, fish and squid samples were collected from 2008 to 2011 during routine acoustic surveys performed by the Peruvian Institute of the Sea (IMARPE) (Table 5.1). Fish and squids were measured for standard and or mantle length (mm). In large individuals, a small piece (1 x 1 cm) of the anterior dorsal muscle was collected. In small fish, the head, gut, and caudal fin were removed, and the remaining whole body was collected. Euphausiids and copepods were analyzed as a whole. For the squat lobster, the telson was dissected and the exoskeleton removed to isolate and collect the internal muscle. All samples were stored frozen and processed later in the laboratory, except for jumbo squid samples that were stored in 70% ethanol.

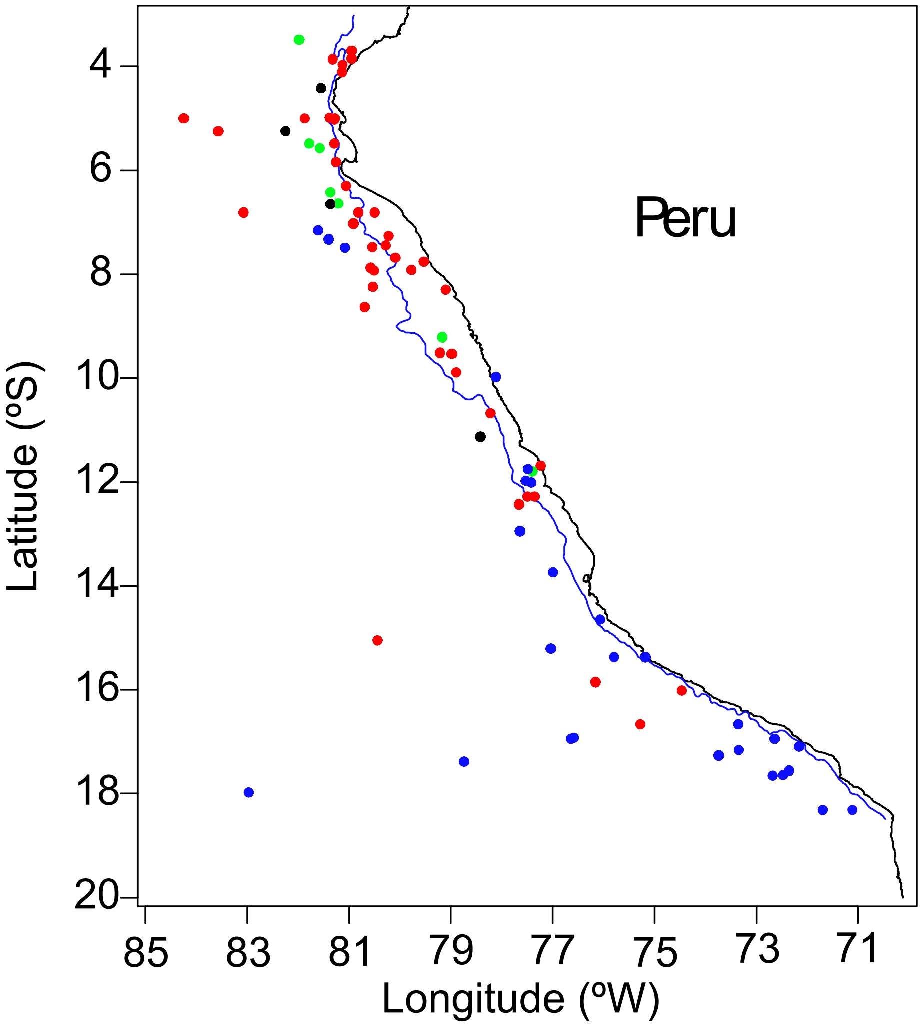

Figure 5.1. Sampling station per year, red=2008, green=2009, blue=2010, black=2011; the blue line indicate the 200 m isobath.

Seabird and fur seal blood were collected during field study in one island and a Peninsula (Table 5.1) via venipuncture, stored in 70% ethanol in the field and then stored at –20°C until analysis. Storage in 70% ethanol does not alter the bulk $\delta^{15}N$ values of blood (Hobson et al., 1997, Bugoni et al., 2008), while some studies reported a slight increase in bulk $\delta^{13}C$ values of blood.

5.2.2. Samples preparation and analysis

All samples but squid samples were dried in an oven at 60°C for 48 h and ground to a fine powder. Squid samples were first evaporated and then freeze dried for 48 h. Lipid extraction was performed on muscle samples using 20 ml of cyclohexane on powder aliquots of about 1 g.

Lipid free samples were dried at 60°C before processing. Lipids were not removed from seabird and fur seal blood samples, as it has been shown that the low lipid content of whole blood does not require lipid extraction prior to isotopic analysis (Cherel et al., 2005). Carbonates were also removed for copepods and euphausiids by soaking them in diluted HCl for 5 mn. Samples (~300µg) were analyzed using an elemental analyzer (Flash EA1112, Thermo Scientific, Milan, Italy) coupled to an isotope ratio mass spectrometer (Delta V Advantage with a Conflo IV interface, Thermo Scientific, Bremen, Germany). Results are expressed according to international standards (Vienna Pee Dee Belemnite for $\delta^{13}C$ and N_2 in air for $\delta^{15}N$) following the formula: $\delta^{13}C$ or $\delta^{15}N=[(R_{sample}/R_{standard})-1]\times10^3$ (in‰), where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Reference gas calibration was done using reference materials (USGS-24, IAEA-CH6, IAEA-600 for carbon; IAEA-N1, -N2, -N3, -600 for nitrogen). Analytical precision based on isotope values of the acetanilide (Thermo Scientific) used to estimate C and N content for each sample series was 0.1% both for carbon and nitrogen. Values are means ± SD.

5.2.3. Statistical analysis

For each species, $\delta^{13}C$ and $\delta^{15}N$ were first plotted versus body length, latitude and distance to the coast (in km). The $\delta^{15}N$ isotope signature was strongly impacted by the species, the body length and the latitude. Also, the sampling design was very unbalanced in terms of body length and geographical position. To compare $\delta^{15}N$ values and being able to estimate the trophic position (TP) of each species, a modelling approach taking into account the latitudinal and body length effects was necessary.

Linear mixed-effects (LME) models (Pinheiro and Bates 2000) are well suited for dealing with unbalanced sampling schemes and the different sources of variability affecting stable isotope data (e.g. Ménard et al. 2007, Lorrain et al. 2009, Décima et al. 2013). The LME approach takes into account the data structure and the variables of interest. Here the data were grouped by species (subclass for copepods, order for euphausiids, and family for myctophids). The species effect was treated as random variations around a population mean, while the covariates of interest, i.e. body length and latitude, were assessed as two continuous covariates. LME allowed us to combine a random-effects analysis of variance model (variability amongst species) with linear regression models. Different models were performed with latitude and body length added sequentially as fixed effects or as random effects; these models were tested using Akaike criterion and likelihood ratio tests. The assumption of normality and independence for the random effect and the residuals were graphically assessed (not shown).

In the models we only considered $\delta^{15}N$ values because it shows a stepwise enrichment between prey and consumer tissues (2-5‰) and as consequence is useful for examining trophic relationships (Minagawa and Wada, 1984, Peterson and Fry, 1987). On the other hand, carbon isotopes ratios vary little (0-1‰) with tropic levels and are mainly used to identify feeding habitats, carbon pathways and sources of primary productivity (Hobson and Welch, 1992, France and Peters, 1997).

A preliminary scrutinizing of the data showed a shift in $\delta^{15}N$ at ~7.5ºS coherent with the impact of the OMZ on the baseline nitrogen stable isotopes ($\delta^{15}N$) (Mollier-Vogel et al. 2012). Indeed, along the Peruvian coast, the OMZ get more intense and shallow south of ~7.5ºS (Fuenzalida et al., 2009; Bertrand et al., 2010, Mollier-Vogel et al. 2012). We thus split our data base and constructed different models north and south of 7.5ºS. Then we predicted the $\delta^{15}N$ at 11.7ºS for the southern zone and at 7.5ºS in the northern zone. These latitudes were selected to maximise the number of samples at one location.

Table 5.1. Data description.

Taxonomic category	Code	Year range	Storage	Sample	n	Body length range (mm)	Latitudinal range (ºS)	Longitudinal range (ºW)	$\delta^{13}C$ mean ± SD	$\delta^{15}N$ mean ± SD	C:N mean ± SD
Copepod	Copepod	2008-2010	Frozen	Full organism	33		3.85 - 14.65	76.07 - 83.57	-20.3 ± 1.3	7.6 ± 1.3	4.8 ± 0.6
Euphausiids	Euph	2008-2011	Frozen	Full organism	17	19 -24	3.85 - 14.65	76.07 - 81.87	-18.1 ± 0.9	8.8 ± 0.6	3.9 ± 0.2
Pleuroncodes monodon	SLobst	2008-2011	Frozen	Muscle tissue	43	8 - 22.9	4.42 - 12.43	77.35 - 81.55	-15.2 ± 0.4	13.3 ±1.2	3.9 ± 0.2
Dosidicus gigas	JSquid	2008-2011	Alcohol	Muscle tissue	337	20 - 988	3.48 - 18.32	71.12 - 84.25	-17.1 ± 0.9	13.4 ± 3.4	3.2 ± 0.1
Myctophidae	Myct	2008-2010	Frozen	Muscle tissue	35	35 - 100	5.25 - 7.33	81.40 - 83.57	-19.0 ± 1.0	9.0 ± 1.2	3.4 ± 0.3
Vinciguerria lucetia	Vincig	2008-2011	Frozen	Muscle tissue	23	32 - 65	5.25 - 15.05	80.25 - 83.57	-18.5 ± 0.6	10.7 ± 2.8	3.4 ± 0.1
Engraulis ringens	Anch	2008	Frozen	Muscle tissue	165	31 - 165	4.42 - 16.02	74.47 - 82.25	-16.3 ± 1.2	12.1 ± 2.3	3.3 ± 0.1
Scomber japonicus	Mackerel	2008-2011	Frozen	Muscle tissue	8	32 - 230	5.25 - 15.85	76.15 - 82.25	-17.6 ± 1.7	11.8 ± 3.3	3.2 ± 0.1
Trachurus murphyi	JM	2008-2011	Frozen	Muscle tissue	14	118 - 310	4.42 - 15.85	76.15 - 81.55	-17.2 ± 0.6	17.5 ± 2.9	3.2 ± 0.0
Merluccius gayi peruanus	Hake	2008	Frozen	Muscle tissue	84	100 - 480	3.70 - 7.47	80.28 - 81.38	-16.3 ± 0.6	11.4 ± 0.5	3.2 ± 0.1
Sula variegata	Booby	2009-2010	Alcohol	Blood	37	n.d.	11.75	77.47	-14.7 ± 0.2	14.7 ± 0.2	3.3 ± 0.0
Phalacrocorax bougainvillii	Guanay	2009-2010	Alcohol	Blood	37	n.d.	11.75	77.47	-15.0 ± 0.2	15.1 ± 0.2	3.3 ± 0.1
Arctocephalus australis	Fur seal	2010	Alcohol	Blood	16	1200 - 1490	15.37	75.18	-16.9 ± 0.3	18.3 ± 0.4	3.5 ± 0.0

Population predicted $\delta^{15}N$ values using the most parsimonious models were computed to compare the trophic positions of the different species in the range of the corresponding observed body lengths for the fixed latitudes, or in the range of the observed latitudes for a fixed body length (Table 5.2).

5.2.4. Trophic position estimation

For comparison purposes with literature data, we estimated absolute TP values based on predicted $\delta^{15}N$ values at 7.5°S and 11.7°S. The trophic position (TP) was estimated using the equation (Post, 2002):

$$TP = \gamma + (\delta^{15}N_{consumer} - \delta^{15}N_{baseline})/\Delta n$$

where $\delta^{15}N_{consumer}$ is the stable nitrogen signature of the consumer, $\delta^{15}N_{baseline}$ is the nitrogen signature of the baseline), γ is the trophic position of the organism used to establish baseline, and Δn is the is the trophic enrichment factor (TEF), i.e., the enrichment in $\delta^{15}N$ per trophic level (Vander Zanden et al. 1997; Post 2002). We used a mean TEF of 3.4‰ as the average enrichment between the muscle of marine fishes and invertebrates (e.g. Minagawa and Wada, 1984; Post, 2002). We based our food web estimates on the copepods (e.g. Miller et al., 2010). The sampled copepods were mostly large species i.e. *Eucalanus* spp. and *Centropages* spp. These species are omnivorous feeders (Boyd et al., 1980). We thus assumed a TP of 2.5 for copepods as in Olson et al. (2010). The enrichment factor can vary with prey and predator tissue types. As suggested by Cherel et al. (2010), we used 1.7‰ as the enrichment factor between prey muscle and seabirds and marine mammal blood (Hobson et al., 1996, Lesage et al., 2002, Cherel et al., 2005), and we used the following equation to estimate TP for seabirds and fur seals:

$$TP = \gamma + [(\delta^{15}N_{consumer} - 1.7 + \Delta n) - \delta^{15}N_{baseline}]/\Delta n$$

5.3. Results

5.3.1. SIA results (without modelling)

In total we estimated $\delta^{13}C$ and $\delta^{15}N$ on 831 samples from 13 taxonomic categories of the Peruvian marine food web from 2008-2011 (Fig. 5.1, Table 5.1).

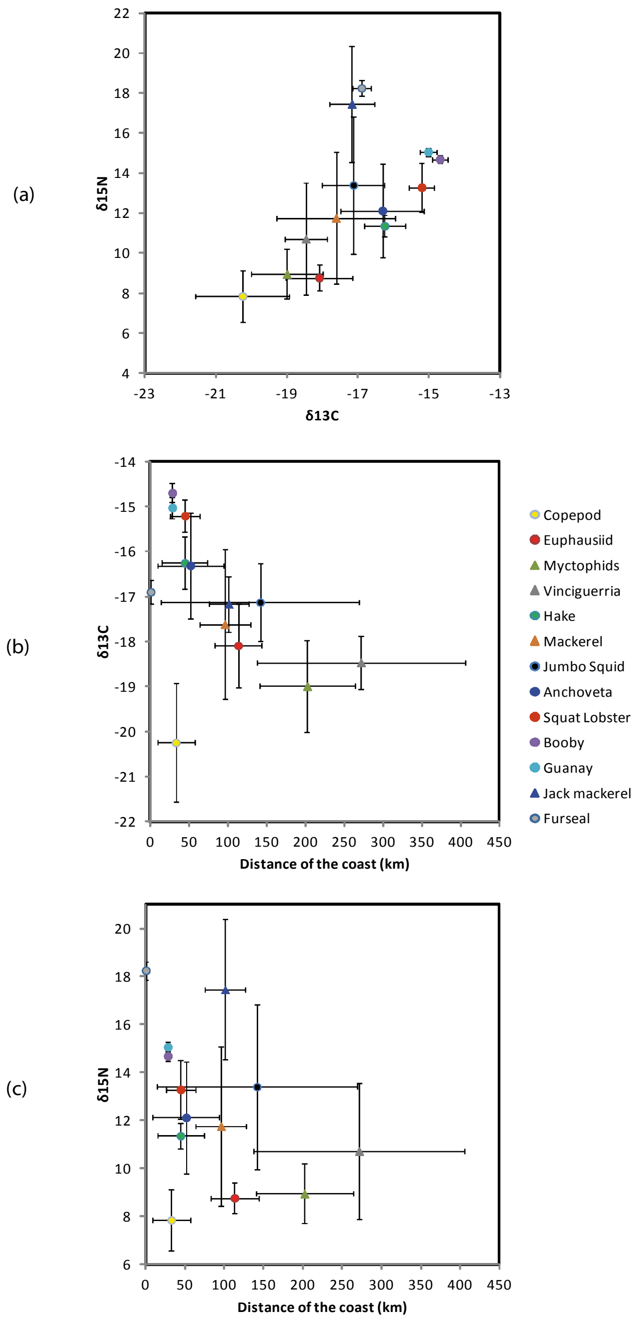

Figure 5.2: $\delta^{13}C$ vs. $\delta^{15}N$ biplot for zooplankton, nekton and top predators collected in the NHCS: (a) depicting isotopic niche space (b) $\delta^{13}C$ according to the distance from the coast (km), (c) $\delta^{15}N$ according to the distance from the coast (km). Values are x±SD (denoted in Table 1).

The $\delta^{13}C$ and $\delta^{15}N$ values showed a high variability between and within species (Fig. 5.2a). The $\delta^{15}N$ mean values varied between 18.3‰ (fur seal, *Arctocephalus australis*) and 7.9‰ (copepods) (Fig. 5.2a). Higher $\delta^{15}N$ values were found for the fur seal, the jack mackerel *Trachurus murphyi* and the seabirds (Guanay cormorant *Phalacrocorax bougainvillii* and Peruvian booby *Sula variegata*). Lowest $\delta^{15}N$ values were encountered for copepods, Euphausiids and Myctophidae (Table 5.1, Fig. 5.2a). In the case of $\delta^{13}C$, the values varied between -14.7‰ for Peruvian booby and -20.3‰ for copepods (Table 5.1, Fig. 5.2a). The C:N ratios, ranged between 3.2 and 3.9, except for copepods which C:N mean value was 4.8 (Table 5.1).

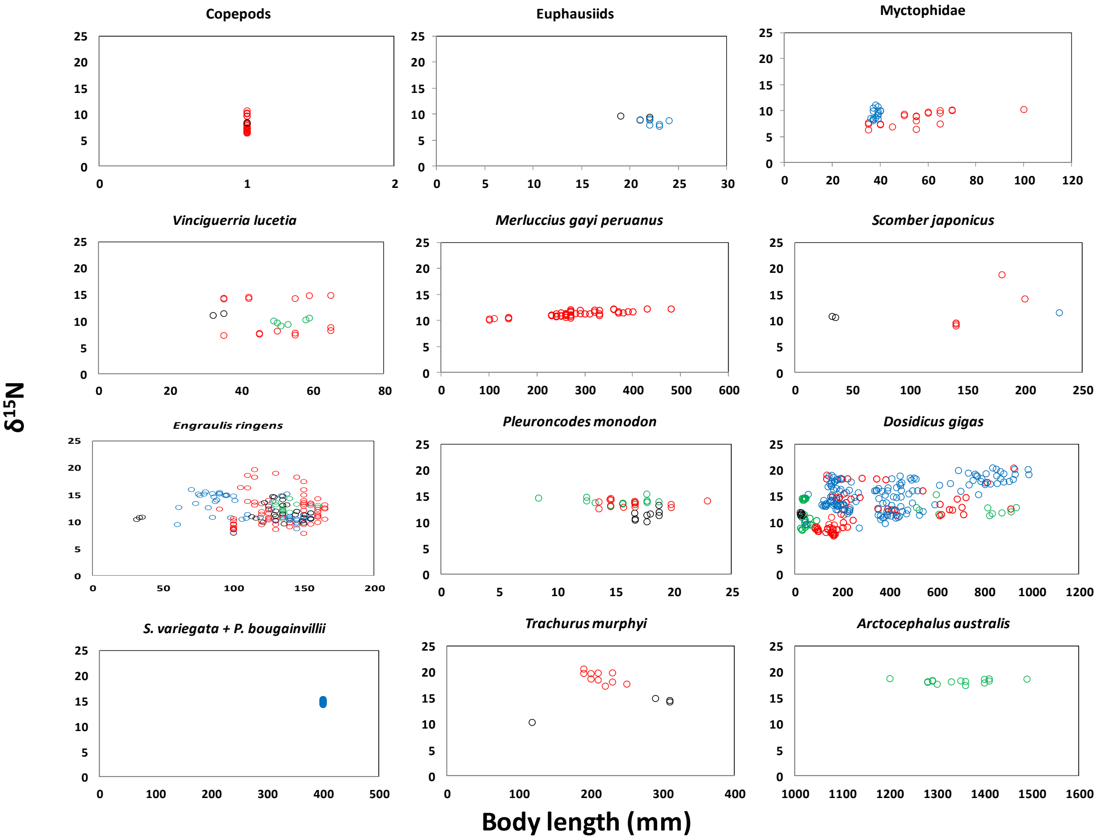

Figure 5.3 : Body length -based variability of $\delta^{15}N$ values (red=2008; green=2009; blue=2010; black=2011).

A steady decrease was observed in $\delta^{13}C$ values of the sampled species when plotted according to the distance to the coast (Fig. 5.2b). Indeed $\delta^{13}C$ values >-17‰ where only observed in the first 100 km from the coast. On the opposite, at a distance >200 km, $\delta^{13}C$ values were lower than -18‰ (mesopelagic fishes). This decreasing trend in $\delta^{13}C$ values with the distance from the coast seems species independent, i.e. appears as a general trend. Birds and squat lobster had the highest $\delta^{13}C$ values (~-15‰) with very low variability (0.1 to 0.4‰) while copepods, euphausiids and mesopelagic fish had the lowest $\delta^{13}C$ values (~-18.5‰) with high inter individual variability (0.9 to 1.3‰). Also note that fur seals showed rather low $\delta^{13}C$ values (~-17‰) when taking into account the distance to the coast of the sampling site (0 km since they were sampled in a peninsula). The negative trend in $\delta^{15}N$ values with the distance to the coast was less marked than the one observed in $\delta^{13}C$ (Fig. 5.2c).

$\delta^{15}N$ values showed a high variability for a given organisms body length (Fig. 5.3). Along-size trends in $\delta^{15}N$ can be only studied on species for which the samples encompassed a large enough range of body lengths (i.e. anchoveta, jumbo squid, hake, *Vincigerria*, squat lobster and to a lesser extent, the jack mackerel). A clear increase in δ^{15}N values with body length was observed on the jumbo squid and the hake. The other species presented no (*Vincigerria*, squat lobster, anchoveta) or a negative trend (jack mackerel). Such unexpected null or negative trends are due to interaction with latitude that was further corrected in the LME models.

Strong latitudinal variations were depicted in δ^{15}N values (Fig. 5.4). They steadily decreased from 18ºS south to ~7.5ºS and then stabilised. Such trend is particularly clear on jumbo squid for which we have more samples. On the opposite, species only sampled north of 7.5º (hake, myctophids and euphausiids) do not show clear latitudinal trend.

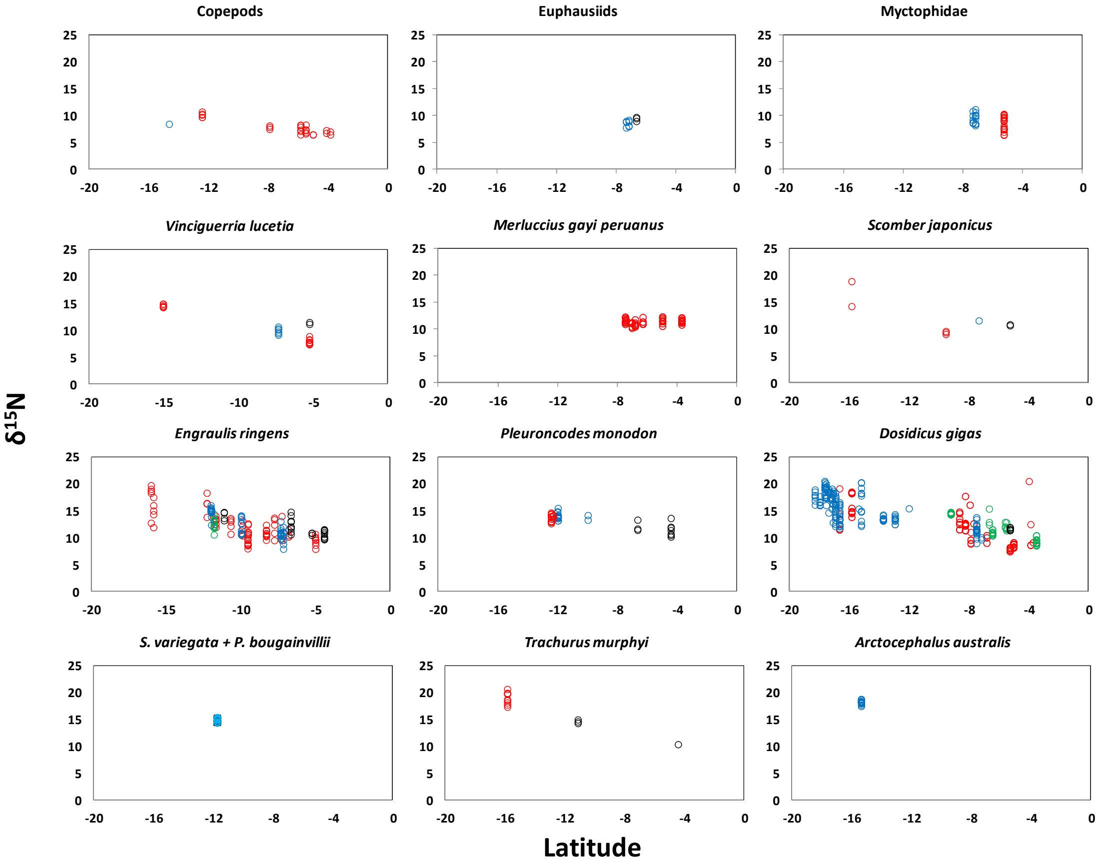

Figure 5.4: Latitudinal variability of δ^{15}N values. (red=2008; green=2009; blue=2010; black=2011).

5.3.2. LME Models

The LME models we used aimed at predicting δ^{15}N values taking into account the variability in baseline δ^{15}N values (with latitude) and the body size effect. As indicated in the Method section, two models were fitted on the data (north and south of 7.5ºS). Both models considered the species dependence but differed in their structure. The best model for the northern area had a fixed effect on both body size and latitude while the best model for the southern area had a fixed effect for body size and a random effect for latitude.

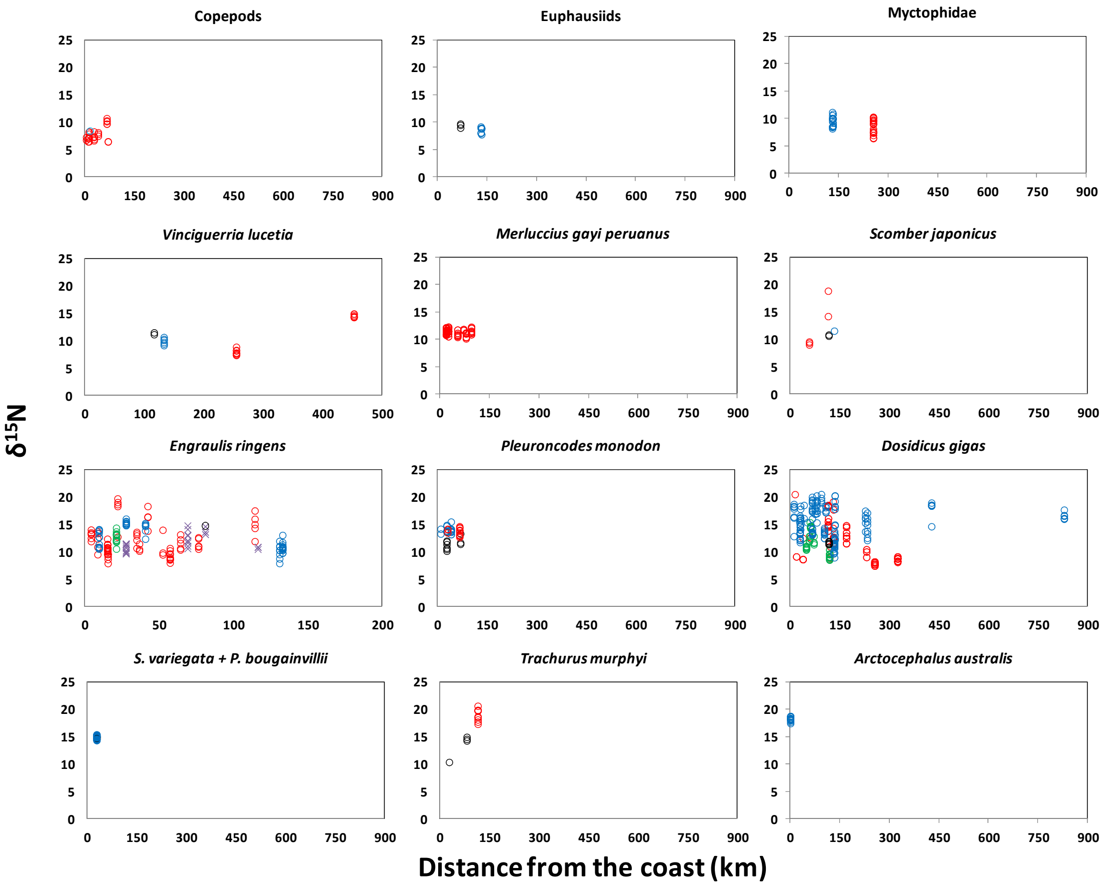

Figure 5.5: Cross shore (distance from the coast) variability of δ^{15}N values. (red=2008; green=2009; blue=2010; black=2011).

Model results for fixed body size (Fig. 5.6) illustrate the different latitudinal effect on δ^{15}N values. South of 7.5º δ15N values strongly decrease towards the north. The trends are species dependant (random latitudinal effect in the model) with higher slopes for anchoveta and jack mackerel than for jumbo squid or squat lobster. North of 7.5ºS the slopes are similar for all species (fixed latitudinal effect) and much less pronounced than further south. If we compare predicted δ^{15}N values between species in northern and southern regions, strong differences are observed. At 7.5ºS the squat lobster had the highest δ^{15}N value (12.0‰), before hake (11.7‰), mackerel (11.5‰), jumbo squid (11.1‰) and anchoveta (11.0‰). The lower δ^{15}N values were observed on copepods (7.6‰), euphausiids (8.9‰) and the mesopelagic fishes (~9.3‰). At 11.7ºS a different pattern appeared. Top predators that were not sampled in the north presented the highest δ^{15}N (fur seal: 15.9‰, jack mackerel: 15.1‰, guanay: 15.0‰, booby: 14.6‰). The following species in decreasing δ^{15}N values were the jumbo squid (14.3‰), the squat lobster (13.6‰), the anchoveta (13.5‰), the mesopelagic fish *Vinciguerria* (12.6‰), the mackerel (12.3‰) and the copepods (9.8‰).

5.3.3. Trophic position

Mean TPs were estimated with predicted δ^{15}N values for the fixed size at 11.7 and 7.5ºS (Table 5.2; Fig. 5.8). The trends are logically the same as the one previously described on predicted δ^{15}N values. At 7.5ºS the predicted TPs varied between 2.9 for Euphausiids and 3.8 for squat lobster. At 11.7 the TPs ranged between 3.2 for mackerel and 4.8 for fur seal. Curiously, as already observed in δ^{15}N values the rank between common species was different in predicted

TP values at 11.7 and 7.5ºS. The squat lobster had a higher TP (3.8) than a jumbo squid of 40 cm (3.5) at 7.5ºS but lower (3.6 vs. 3.8) at 11º7S.

Since body length is an important factor structuring trophic links within communities and ecosystems, we looked at the potential relationships between the TP and the body length for the species for which a sufficient range of size was sampled in the northern and southern regions. The predicted TP increased with body size for all species (Fig. 5.7).

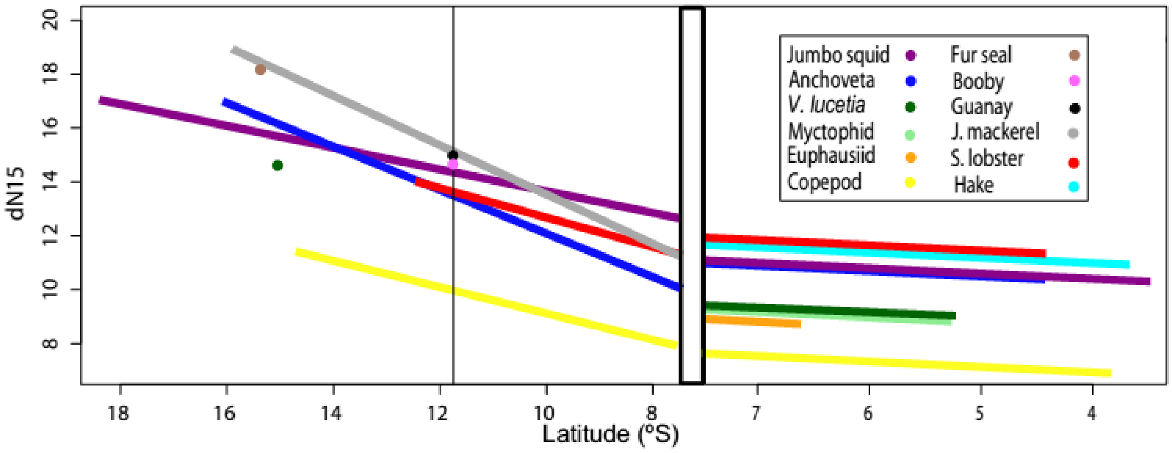

Figure 5.6: Predicted δ^{15}N values from the two LME models: north and south of 7.5ºS. For each species the latitudinal range of prediction covers the one where individuals were sampled.

5.4. Discussion

Using the stable isotope analyses, we focused on a simplified but representative (13 components) food chain in the NHCS. The δ^{15}N baseline is strongly impacted by variability in the OMZ intensity along the Peruvian coast. We thus developed a modelling approach to account for such external variability. In spite of limitations due to the unbalanced nature of our data set some patterns emerge providing new insights on trophic relationships in the system. We confirm previous stomach content-based results on anchoveta TP and suggest the potential importance of an often neglected ecosystem component, the squat lobster.

5.4.1. Pattern of variability in δ^{13}C

Our study revealed a general trend of increasing δ^{15}N and δ^{13}C values from copepods to large organisms (Fig. 5.2a). This classic pattern (e.g. Sherwood and Rose 2005, Fanelli et al. 2011, Stowasser et al. 2012) illustrate a gain in heavy isotopes up the trophic food web.

We also observed an overall decreasing trend in δ^{13}C values for multiple trophic levels with increasing distance to the coast (Fig. 5.2b). Such inshore offshore pattern is expected in many ecosystems and in upwelling systems (e.g. Sydeman et al. 1997, Miller et al., 2008). The species δ^{13}C values should decrease in the following order coastal > neritic > oceanic species, because δ^{13}C values of particulate organic matter decreases from inshore to offshore waters with the decrease of productivity (Hill et al. 2006). A decreasing cross-shore trend in productivity in the NHCS has also been estimated from Chl-a concentration (Demarcq, 2009). The species δ^{13}C values can then be interpreted in terms of inshore or offshore foraging habitat.

Interestingly, the highest $\delta^{13}C$ values were observed for birds and squat lobsters which would then indicate a much localized costal foraging area compared to mesopelagic fish and euphausiids that would forage more offshore. Tagging studies on birds indeed showed that these two species were feeding in the first tens of km of the colony very close to the coast (Weimerskirch et al., 2010, 2012). Anchoveta and squat lobster partly coincide in their $\delta^{13}C$ values showing that anchoveta can feed both onshore and offshore, and has a larger foraging range than squat lobster that would be restricted to the coast. Fur seals, while sampled at the coast, had intermediate $\delta^{13}C$ values, which can be explained by the fact that this species forage offshore at ~50-100 km from the coast (Y. Tremblay, unpublished data).

The $\delta^{13}C$ signal could also be interpreted in terms of benthic vs. pelagic influence of food items (e.g. Hobson et al. 2002). However in this study we focused only on pelagic species except for the benthopelagic hake (Lloris et al., 2003). As an example, the squat lobster *Pleuroncodes monodon* is benthic in Chile but pelagic off Peru where the intense and shallow OMZ impede it to access the sea floor (Gutiérrez et al., 2008). Yet, in upwelling systems the primary production can create substantial deposition of pelagic production to sediments, which can be re-suspended and reintegrated into both benthic and pelagic components. Such processes make difficult the precise estimation of $\delta^{13}C$-based benthic and pelagic productivities (Iitembu et al., 2012).

5.4.2. Pattern of variability in $\delta^{15}N$

Along with the increase with trophic level (Fig. 5.2a), the more noticeable pattern in $\delta^{15}N$ is related to the latitude (Fig. 5.4). We indeed observed an increasing trend of $\delta^{15}N$ values from north to south with a shift at ~7.5ºS. Such trend was already reported in previous studies (Lorrain et al., 2011; Argüelles et al., 2012) and can be related to changes in the $\delta^{15}N$ values of the baseline modulated by the OMZ intensity along the Peruvian coast (Bertrand et al., 2010; Mollier-Vogel et al., 2012). Indeed, in OMZ, strong denitrification and anammox are known to occur, and recent studied showed that anammox is the main N-loss process in the Peruvian OMZs (Lam et al., 2009; Kalvelage et al., 2013). Denitrification in anoxic water bodies has a large isotope effect of ~-25 ‰ (e.g., Brandes et al., 1998; Voss et al., 2001). To date, little is known about the isotope fractionation of anammox in the water column, but it is generally assumed that anammox has similar isotope fractionation (Naqvi et al., 2006). The most important implication is locally that denitrification and anammox can produce NO_3 and organic matter strongly enriched in ^{15}N (up to 20‰). The intensification of the oxygen deficient condition to the south of Peru south of ~8°S (Bertrand et al., 2010) would then contribute to latitudinal gradients in the $\delta^{15}N$ baseline values, with highest $\delta^{15}N$ values in the south. This North to South gradient of $\delta^{15}N$ values has been observed in sediments along the Peruvian margin (Mollier-Vogel et al., 2012). In the north (1°N to 8°S), sediment $\delta^{15}N$ values are relatively low and uniform, ranging only between 4 to 5‰ while in the southern part, values generally increase southward but reveal a larger range between 4.5 and 13‰. This is exactly what we observe in our species $\delta^{15}N$ values (Fig. 5.6).

Another factor impacting $\delta^{15}N$ values was body size. Then, the following part of the discussion will be based on modelling results correcting for both latitudinal (baseline) and body size effects.

5.4.3. Predicted $\delta^{15}N$ values and trophic positions

The modulation of the OMZ on the $\delta^{15}N$ baseline isotopic values and the shift at ~7.5ºS led us to construct two separate LME models, south and north of 7.5ºS. The unbalanced sampling scheme and the actual species distribution (e.g. hake is mostly present in the north) explain that each model comprise different species. The lack of latitudinal and body size covertures for several species also weaken the predictive power of the models we constructed. Furthermore, in the southern region, we observe different slopes between baseline and species (Fig. 5.6), indicating that these species might not be in isotopic equilibrium with their diet and that they might come from another foraging location. TP estimates in the south might therefore not be as representative as in the northern region. Finally, for consistency and comparability with other similar studies, we also made several assumptions, i.e., the TP were estimated applying a fixed TEF of 3.4‰ (Hückstädt et al. 2007, Miller et al. 2010, Iitembu et al. 2012, Chouvelon et al. 2012) and a TP of 2.5 for copepods. If all these mentioned shortcoming can blur our capability to fully describe the food webs in the NHCS, some robust patterns emerge (Fig. 5.8).

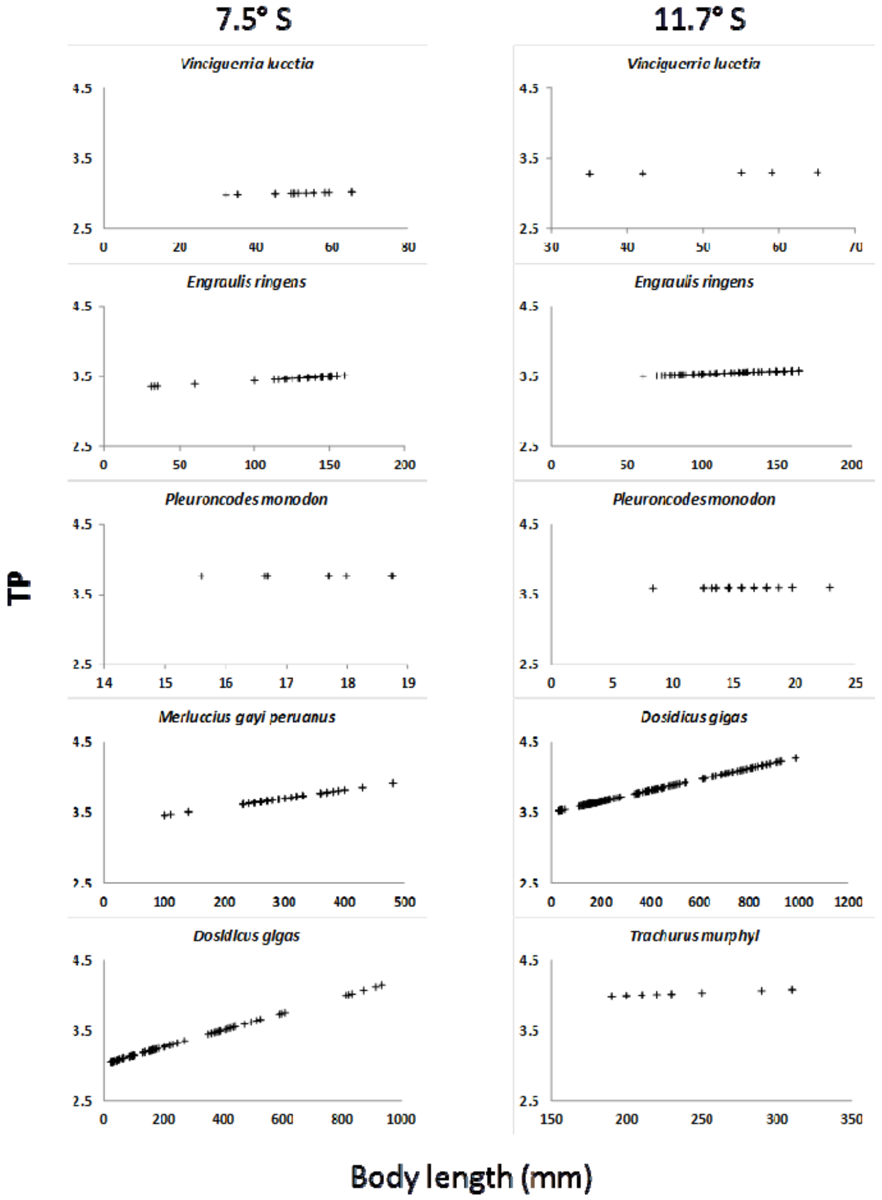

Figure 5.7 : TP variability with body length of the most important species at 7.5°S and 11.7ºS.

Euphausiids are clearly at a higher trophic level than copepods (predicted TP: 2.9). Euphausiid fraction is dominated by *Euphausia mucronata* (Ayón et al., 2008a). Our results suggest that they mainly forage over small zooplankton. Such results differ with Hückstädt et al. (2007) who proposed a TP of 2 for the krill off Chile. In the California Current system, Sydeman et al. (1997) estimated the TP of *Euphausia pacifica* to 2.5, while Miller et al. (2010) estimated the TP of *Euphausia pacifica* and *Thysanoessa spinifera* to 2.1 and 2.3, respectively. It thus seems that krill are at a higher TP in the NHCS that in the other comparables systems of the eastern Pacific. Yet krill can have a TP≥3. It is for instance the case of *Euphausia frigida* (3.0) and *Euphausia tricantha* (3.3) in Antarctica (Stowasser et al. 2012).

Above the euphausiids, mesopelagic fishes (*Vinciguerria lucetia* and myctophids) emerge as secondary consumers with a predicted TP between 3.0 and 3.2. These estimates are comparable to what have been observed in other EBUS: 3.4 in the California Current system (Choy et al., 2012) and 2.7 in the northern Benguela Current system (Iitembu et al. 2012).

Estimated TP for anchoveta (3.5-3.6) definitely refute the hypothesis of a short and efficient food chain with anchoveta foraging directly on phytoplankton (Ryther, 1969). Rather they confirm the results from Espinoza and Bertrand (2008) who showed that zooplankton was by far the most important dietary component, with euphausiids contributing 67.5% of dietary carbon followed by copepods (26.3%). The TP estimates for various *Engraulis* spp. around the world (Table 5.3.) vary between 2 and 4, most ranging between 3.0 and 3.6. Our TP estimates for anchoveta are thus in the higher range of TP estimations but similar to Hückstädt et al. (2007) who estimated the TP of *E. ringens* to 3.6. Such a rather high TP for *E. ringens* when compared with other *Engraulis* spp. is not surprising since *E. ringens* forage on larger prey than anchovies from other EBUS (Espinoza et al., 2009).

Table 5.2. Predicted $\delta^{15}N$ (‰) values and trophic position (TP) at 7.5°S and 11.7°S.

Species	Fixed body size (mm)	Predicted $\delta^{15}N$ at 7.5°S	Predicted TP at 7.5°S	Predicted $\delta^{15}N$ at 11.7°S	Predicted TP at 11.7°S
Copepod	1	7.6	2.5*	9.8	2.5*
Euphausiid	2	8.9	2.9		
Pleuroncodes monodon	20	12.0	3.8	13.6	3.6
Myctophidae	50	9.3	3.0		
Vinciguerria lucetia	50	9.4	3.0	12.6	3.2
Engraulis ringens	140	11.0	3.5	13.5	3.6
Scomber japonicus	200	11.5	3.6	12.3	3.2
Trachurus murphyi	250			15.1	4.0
Merluccius gayi peruanus	280	11.7	3.7		
Dosidicus gigas	400	11.1	3.5	14.3	3.8
Sula variegata	400			14.6	4.4
Phalacrocorax bougainvillii	400			15	4.5
Arctocephalus australis	1300			15.9	4.8

* Assumed

Patterns for organisms with TP higher than the anchovy are less clear. Indeed the squat lobster showed the highest TP (3.8) in the northern region, i.e. above the hake (3.7) or the jumbo squid (3.5). In the southern region the estimated TP of squat lobster was still high (3.6) but lower than the jumbo squid (3.8). These differences are probably a result of our unbalanced data base. However in all cases, the estimated TP for squat lobster are high and in any case higher or equal to the one of anchovy. There is a lack of squat lobster diet study in the NHCS where it has a pelagic behaviour (Gutiérrez et al., 2008). In Chile, *Pleuroncodes monodon* is benthic and forage on amphipods, zoeas, crustacean eggs, diatoms, foraminifers, bacteria, organic wastes and fish scales (Gallardo et al., 1980). In the California Current, pelagic *P. planipes* feeds on protists, zooplankton (mainly copepods, euphausiids and chaetognaths) and large diatoms; the diatom fraction being higher when diatoms are abundant (Longhurst et al., 1967). According to Gutiérrez et al. (2008) the squat lobster may also forage on eggs or larvae including those of anchoveta. Since the anchoveta and the squat lobster share a similar ecological niche, Gutiérrez et al. (2008) stated that "a potential negative competition and predation exists between these species". The high TP we obtained for the squat lobster seems to support the hypothesis according to which this species forage to some extent on fish eggs and larvae and can thus predate on the first life stages of exploited species. The δ^{13}C values of these two species however suggest that anchoveta and squat lobster do not exactly share the same habitat, with anchoveta having a larger and more offshore foraging range. This is indeed what Gutiérrez et al. (2008) observed through acoustic survey performed between 1998 and 2006 along the Peruvian coast, with the squat lobster restricted to a more coastal region when compared to anchoveta. If these hypotheses are confirmed, this would potentially reduce some direct competition for resources. Specific diet studies should be performed on the squat lobster in the NHCS to conclude.

Table 5.3: Trophic position estimates of some Engraulis spp. around the world.

Species	**Stage**	**TP**	**Method**	**Place**	**References**
Engraulis japonicus	Adults	3.3	Stable isotope δ^{15}N	Southern Japan	Takai *et al.* (2007)
	Larvae and juveniles	3.0	Stable isotope δ^{15}N	Southern Japan	Takai *et al.* (2007)
Engraulis mordax	Juveniles and adults	3.0	Stomach content	California Current	Kucas (1986) from www.fishbase.org
	Adults	3.1	Stable isotope δ^{15}N	California Current	Miller *et al.* (2010)
Engraulis encrasicolus	Larvae	3.1-3.7	Stomach content	Catalan Sea - Gulf of Lions	Tudela *et al.* (2002) from www.fishbase.org
	Juveniles and adults	3.3	Carbon content	west coast of South Africa	Armstrong *et al.* (1991) calculated here.
	Juveniles and adults	3.4	Stable isotope δ^{15}N	Atlantic coast of the Iberian Peninsula	Bode *et al.* (2007)
	Adults	2.4 - 2.9	Stable isotope δ^{15}N	Gulf of Lions (NW Mediterranean Sea)	Costalago *et al.* (2012)
	Juveniles	2.3 - 3.1	Stable isotope δ^{15}N	Gulf of Lions (NW Mediterranean Sea)	Costalago *et al.* (2012)
	Late-larvae	2.4	Stable isotope δ^{15}N	Gulf of Lions (NW Mediterranean Sea)	Costalago *et al.* (2012)
Engraulis ringens	Adults	2.1	% weight and Ecopath estimation	Central Chile	Neira and Arancibia (2004)
	n.d.	2.9	% weight and Ecopath estimation	Northern Chile	Medina *et al.* (2007)
	n.d.	3.6	Stable isotope δ^{15}N	Central Chile	Hückstädt *et al.* (2007)
	Juveniles and adults	3.5	Carbon content	Peruvian coast	Espinoza and Bertrand (2008)*
	Juveniles (14 cm)	3.4 - 3.5	Stable isotope δ^{15}N	Peruvian coast	This study
Engraulis anchoita	Juveniles and adults	2-4	Volumetric	Argentinian coast	Angelescu (1982)

* Calculated from the diet results of Espinoza and Bertrand (2008) following the method from Christensen and Pauly (1992)

The estimated TP for jumbo squid ranged between 3.5 (north) and 3.8 (south) for a jumbo squid of 40 cm. Such results are in the accordance with Hückstädt et al. (2007) who estimated jumbo squid TP to 3.8 in Chile. However such estimates seem low considering diet studies. Indeed Alegre et al. (2014) showed that *Dosidicus gigas* mainly forage on cephalopods and fish. Lower TP organisms such as euphausiids and other crustaceans and mollusks accounted to less than 18%. We could thus have expected a TP ≥ 4. The same occurs for the hake (estimated TP: 3.7) that mainly forage on fish and squids (Tam et al., 2006), crustacean accounting to only ~15%. However our estimates are similar with those for *Merlucius gayi gayi* in Chile: 3.6 (Hückstädt et al., 2007), *Merlucius productus* in California: 3.3 (Miller et al., 2010), and *Merlucius capensis* in South Africa: 3.0 - 3.6 (Iitembu et al. 2012).

The mackerel *Scomber japonicus* showed a lower trophic level (3.2-3.6) than the jack mackerel *Trachurus murphyi* (4.0) in accordance with the diet differences between these species (Alegre et al., 2013). Our estimates for *S. japonicus* are similar with those in California: 3.4 (Miller et al. (2010) and, to a lesser extent in the Bay of Biscay: 3.7 (Chouvelon et al. 2012). In the case of the jack mackerel our estimated TP are higher than those from Hückstädt et al. (2007) in Chile (3.4) and Miller et al. (2010) in California (*T. symmetricus*): 3.6.

The air breathing top predators had the highest estimated TP: 4.4 for the Peruvian booby, 4.5 for the guanay cormorant that nearly exclusively forage on anchoveta (Duffy 1983, Zavalaga and Paredes 1999) and 4.8 for the fur seal that is known to forage on small epi- or meso-pelagic fish, apparently with preference for adult anchoveta (Majluf 1989). These results are akin to the literature. Indeed, Hückstädt et al. (2007) estimated to 4.6 the TP for the sea lion *Otaria flavescens* and Cherel et al. (2010) to 4.8 the TP of Antarctic fur seal *Arctocephalus gazella*. For cormorant Sydeman et al. (1997) estimated the TP of *Phalacrocorax pelagicus* and *Phalacrocorax penicillatus* to 4.3 and 4.5, respectively.

Finally, predicted changes in TP with body size (Fig. 5.7) indicate a classic increase in TP with body size. These results are in accordance with available diet studies in the NHCS considering ontogenetic changes. Indeed Euphausiids fraction progressively increases in anchoveta diet with fish size, copepods presenting an inverse trend (Espinoza and Bertrand, 2014, Chapter 3). In hake diet, cannibalism steadily increases with size while euphausiids fraction decreases (Tam et al., 2006). The jumbo squid present a similar pattern of increase in TP with size (Argüelles et al. 2012, Alegre et al. 2014) even if at individual level large *D. gigas* can shift toward a diet dominated by euphausiids (Lorrain et al. 2011). Finally, while growing, the jack mackerel diminish its consumption of copepods but increase its predation on fish (Alegre et al., 2013).

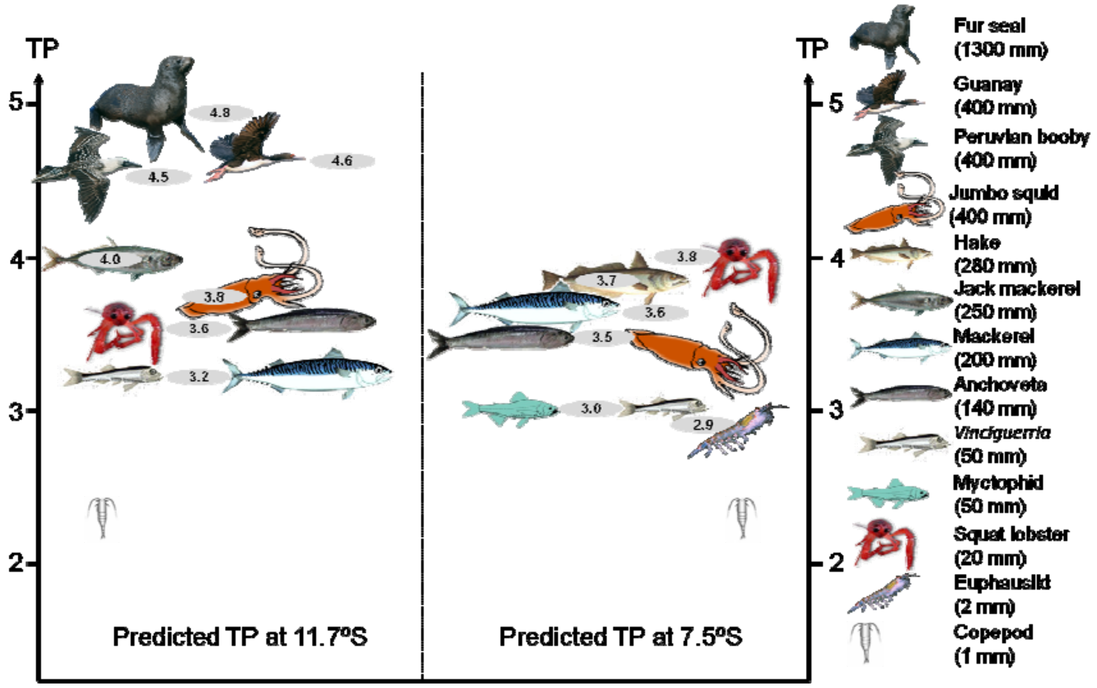

Figure 5.8. Predicted TP at 11.7ºS (Vinciguerria, mackerel, squat lobster, anchoveta, jumbo squid, jack mackerel, Peruvian booby, guanay, fur seal) and 7.5ºS (euphausiids, myctophid, Vinciguerria, anchoveta, jumbo squid, mackerel, hake and squat lobster).

5.4.4. Width of isotopic niche

Some species such as jumbo squids, mackerel and anchoveta showed large variance in their isotopic signatures (Figure 5.2), which indicates long term inter-individual differences in their foraging ecology (different habitats and/or food items). In contrast, isotopic values of other species such as birds and, to a lesser extent, fur seals suggest a very localized and specialist diet, as already discussed for birds in the previous section. This can have strong implications in terms of resilience of species face to a changing environment, with species having a wider isotopic niche being more plastic and potentially more resistant to environmental changes.

5.4.5. Conclusion

In summary, despite some limitations inherent to the stable isotope method to identify precisely the diet of species, we provide a new vision of the relative trophic position of key ecosystem components in the NHCS (Fig. 5.8). We confirm previous stomach content-based results on anchoveta *Engraulis ringens* TP and highlight the potential remarkable importance of an often neglected ecosystem component, the squat lobster *Pleuroncodes monodon*. Indeed, our results support the hypothesis according to which this species could forage to some extent on fish eggs and larvae and can thus predate on the first life stages of exploited species. Further studies on this species as fatty acids or even compound specific isotope analysis of specific fatty acids need to be undertaken, in particular as we were not able to infer its role in the diet of air-breathing top predators.

Acknowledgements

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CHAPTER 6

General conclusions and perspectives

The results presented in Chapters 2 to 5 provide significant elements to update our knowledge on the trophic relationships in the northern Humboldt Current system (NHCS). In this conclusion we discuss how these findings allows for an improved vision of the functioning of the NHCS and what are the key next steps. To do so we will use information from studies (van der Lingen *et al.*, 2009; Ayón *et al.*, 2011 and Argüelles *et al.*, 2012, Alegre *et al.,* 2014) related with this dissertation.

6.1. When the same data provide different results: on the use of SCA

In Chapters 2 to 4 we focused on the main forage fish species of the NHCS, anchoveta (*Engraulis ringens*) and sardine (*Sardinops sagax*). Their trophic ecology was studied using a classic methodology i.e., stomach content analysis. Compared with previous works, the main difference of our approach was the way we quantified the diet. Indeed most previous works based on counts of fish prey concluded that these fish consume mainly phytoplankton (e.g. Rojas de Mendiola, 1969; Alamo, 1989). Such method is known to be inadequate for estimating dietary importance since a phytoplankton cell accounts as much as a much larger and energetic prey (James, 1987; Konchina and Pavlov, 1995). Methods based on prey weight (e.g. gravimetric) or on nutritional value (e.g. carbon content, caloric or energetic value) are more ecologically relevant (Hyslop, 1980; Koslow, 1981; James, 1987). Here we estimated the carbon content of the prey and provided a very different vision of anchoveta and sardine trophic ecology. Indeed zooplankton is by far the most important dietary component for these fish. Among zooplankters, euphausiids and large copepods were the main prey whatever the period. Euphausiids contribution was even higher during the 1950-1960s (92.6%) than during the late 1990-early 2000s (67.5%), while copepods presented an opposite trend (6.3% and 26.3%). Such zooplanktonic diet is similar to what was observed for *Engraulis* spp. and *Sardinops sagax* in other ecosystems (van der Lingen et al., 2009). However, as indicated in Chapter 4, prey were larger in the NHCS compared with other eastern boundary upwelling systems (EBUS) and macrozooplankton constitute the bulk of forage fish diet even if sardine forage on smaller prey than anchoveta.

6.2. Revisiting the energetic transfer

These results constitute a major change in the understanding of trophic fluxes in the NHCS. Indeed they refute the previous hypothesis according to which the great abundance of anchoveta is based on its ability to graze on phytoplankton depicting a very short and efficient food chain (Ryther, 1969). If forage fish consume mainly macrozooplankton then the trophic chain transfer should be efficient from phytoplankton to macrozooplankton and a high biomass of macrozooplankton should occurs. Sampling macrozooplankters such as euphausiids is complicated since these organisms are known to avoid nets (Fleminger and Clutter, 1965; Brinton, 1967; Debby et al., 2004; Lawson et al., 2008) because of both visual and mechanical disturbances (Fleminger and Clutter, 1965). Robust biomass estimates are thus difficult to obtain from net sampling. To overcome such shortcoming, Ballón et al. (2011) used acoustics to estimate macrozooplankton biomass. They estimated the macrozooplankton to about 105 g m^{-2}, i.e., two to five times more than previous estimates. This direct biomass estimation of macrozooplankton is in agreement with our new findings indicating that forage fish consume mainly macrozooplankton. This high biomass also supports the hypothesis we propose according to which the NHCS high fish production is due to very efficient energetic transfer toward macrozooplankton and the fish.

6.3. Trophic ecology and population dynamics

If zooplankters are the main prey for anchoveta and sardine, does the changes in zooplankton abundance and size spectra explain the variability of these fish populations? Extensive comparisons of the morphology of sardines and anchovies and of their feeding ecology suggested that differences in gill raker morphology allow sardines to efficiently filter feed on a larger size range of zooplankton (up to 1.23 mm and down to 10 µm) than anchovies, which do not appear to be able to effectively filter feed on zooplankton >0.7 mm (van der Lingen et al., 2006). Thus, anchovies primarily feed by direct biting (particulate feeding) and show more size selective feeding, mostly taking zooplankton >1 mm, while sardines are apparently less size selective (van der Lingen et al., 2006, Espinoza et al., 2009).

Such differences led to the development of the trophic dynamics hypothesis to explain the variability between anchovy and sardine populations in other EBUS (e.g. van der Lingen et al., 2006). This hypothesis (Fig. 6.1.) argues that changes in upwelling patterns and currents lead to changes in zooplankton size, species structure and spatial distribution. Having higher upwelling (more nutrients) may lead to larger phytoplankton (e.g. diatoms), which have lower surface-to-volume ratios than smaller phytoplankton (e.g. dinoflagellates), which predominate in warmer, lower nutrient conditions due to higher potential uptake rates under nutrient limitation (Falkowski and Oliver 2007; Rykaczewski and Checkley 2008). In turn, larger zooplankton (i.e. large copepods and euphausiids, but not tunicates or gelatinous zooplankton) that may more effectively feed on large than on small phytoplankton (Peterson, 1998; Walker and Peterson, 1991), thrive under higher upwelling conditions. Under warmer conditions, smaller phytoplankton may dominate and larger zooplankton may experience food limitation (Painting et al., 1993), resulting in dominance by smaller zooplankton.

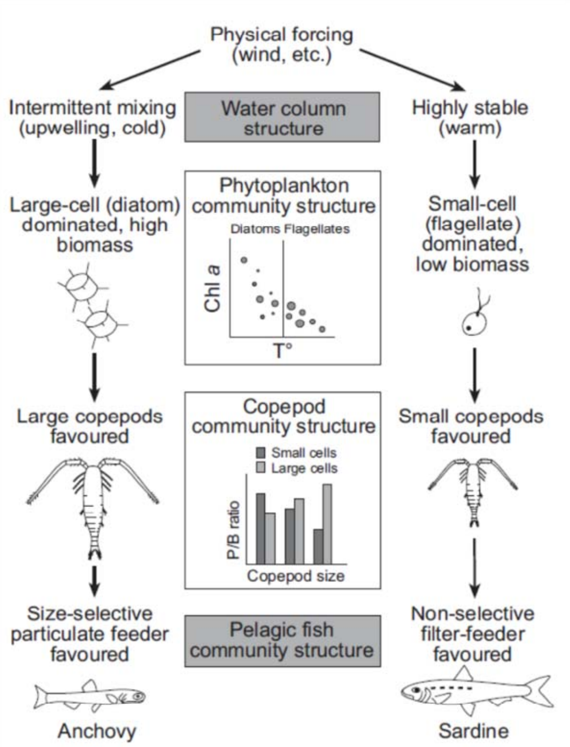

Figure 6.1. Conceptual schematic of how physical forcing may lead to environments that favour either sardine or anchovy. Source: van der Lingen et al. (2006).

Ayón et al. (2011) examined whether changes in the relative size of zooplankton in the Peruvian HCS were associated with changes in sardine and anchovy biomass as suggested by the size-selective-feeding hypothesis. To this end, zooplankton samples collected by the Peruvian Marine Research Institute (IMARPE) between 1963 and 2005 were used and the qualitatively dominance by different size classes (small, medium and large zooplankton, and euphausiids) in these samples was estimated. The temporal pattern for euphausiids dominance was highly cross-correlated (i.e. was in phase) with the time series for estimated biomass of anchovy, and small zooplankton dominance with that for estimated sardine biomass. These results support the focal hypothesis, which showed energetic advantages to sardine filter feeding on smaller zooplankton and to anchovy bite feeding on larger copepods and euphausiids. Although euphausiids predominate off the shelf break, anchovy biomass is generally highest on the shelf, suggesting a possible mismatch between anchovy feeding and euphausiids dominance. However, evidence concerning the offshore expansion of the anchovy range in cooler conditions, where both anchovy and euphausiids predominate, somewhat alleviates this apparent contradiction. A strong diel component to euphausiids and large zooplankton indicated diel migration for these zooplanktonic groups. That anchovy will preferentially eat euphausiids when they are more available (i.e. during the night and offshore) is supported by our results on anchovy diet dynamics (Chapter 3).

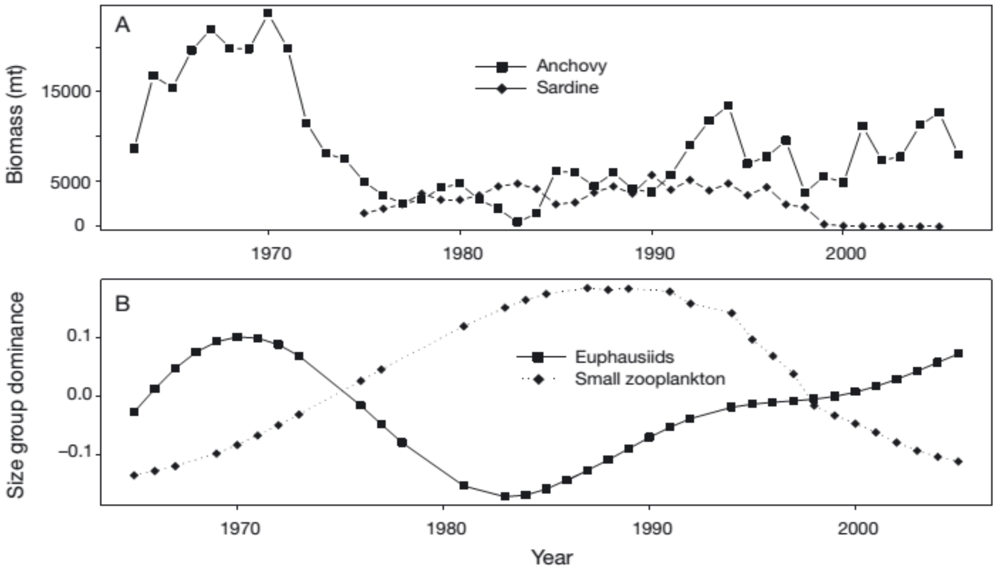

Figure 6.2: (A) Anchovy and sardine biomass estimated using virtual population analysis (VPA). Source: Ñiquen et al. (2000), R. Guevara pers. com. (B) Dominance of euphausiids and small zooplankton from generalized additive model (GAM) results. Source: Ayón et al. (2011).

Ayón et al. (2011) showed that sardine biomass was synchronous with the dominance of small zooplankton, which in turn corresponds to periods of generally warmer, lower upwelling conditions. These results support the hypothesis that sardine's capacity to efficiently filter-feed zooplankton over a large size range gives them a competitive advantage where small zooplankton is dominant (van der Lingen et al. 2006). Therefore, such results support the hypothesis that periods of low dominance of large zooplankton disfavors anchovy and gives an energetic advantage to predominately filter feeding sardines. Although sardine may have an advantage when small zooplankton dominate, Espinoza et al. (2009) showed that, at least from 1996 to 1998, sardine diets in the HCS contained surprisingly large amounts of euphausiids, comprising, on average, more than 1/3 of sardine prey carbon content. Therefore, even if filter-feeding by sardines is energetically more efficient than particulate feeding (van der Lingen, 1995), sardines in the NHCS appear to forage on large as well as small zooplankton. So why then do sardines not do better during cooler periods dominated by euphausiids? Indeed sardine could flourish whatever the zooplankton size spectra. This contradiction indicates that the conceptual hypothesis of how physical forcing may lead to environments that favour either sardine or anchovy from van der Lingen et al. (2006) (Fig. 6.1.) is not sufficient to explain sardine and anchovy dynamics in the NHCS. Other environmental factors could thus play a key role and allow us to provide a more comprehensive vision.

A fundamental environmental factor often neglected in marine ecosystem is the oxygen. Indeed fish need sufficient amounts of both food and oxygen, but the latter might be more difficult to obtain than the former (Pauly, 2010). It is particularly the case in the NHCS, which encompasses one of the most intense and shallow OMZ (Helly and Levin, 2004; Chavez et al., 2008; Fuenzalida et al., 2009; Paulmier and Ruiz-Pino, 2009). Bertrand et al. (2011) showed how the inclusion of this missing piece, the need to breath, allows the development of a comprehensive conceptual model of pelagic fish populations and change in an ocean ecosystem impacted by low oxygen.

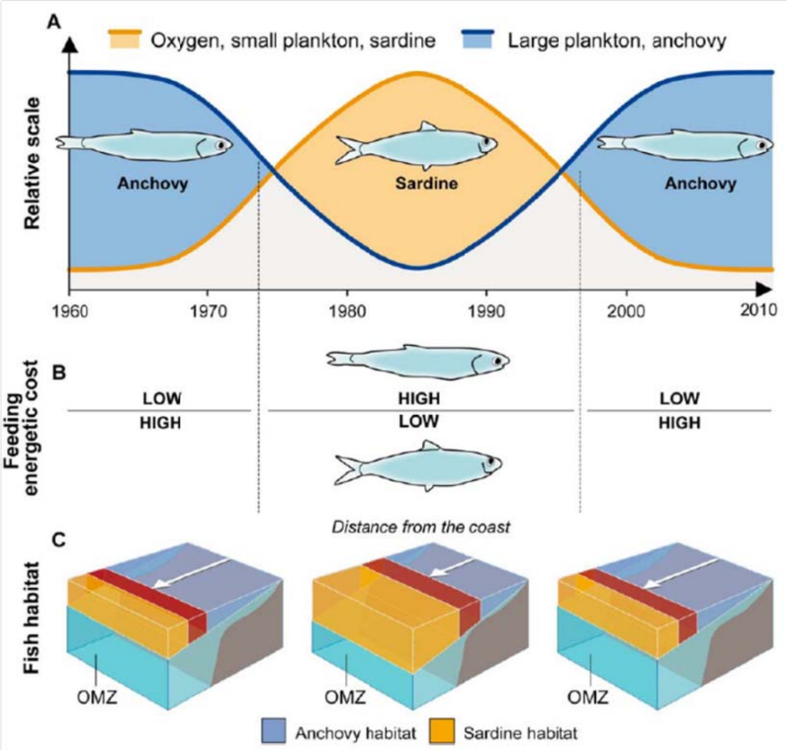

Figure 6.3. Conceptual model of decadal changes in anchovy and sardine populations in the southeastern tropical Pacific. A: Schematic of the temporal evolution of large plankton and anchovy (blue solid line), and oxygen, small plankton and sardine (red solid line) between 1960 and 2010. B: Energetic costs of feeding on dominant plankton size-spectra for anchovy and sardine according to the scenarios from A. C: Schematic of the available habitat for anchovy (blue shaded area) and sardine (red shaded area). Source: Bertrand et al. (2011).

Oxygen demand also depends on the quality and quantity of food (Pauly, 2010). The anchoveta gets most of its energy by visual selection and direct biting on macrozooplankton. Filter feeding is very expensive metabolically relative to biting for anchovies (James and Probyn, 1989; van der Lingen, 1995). In sharp contrast, filter-feeding is energetically much cheaper for sardines (van der Lingen, 1995). These results lead Bertrand et al. (2011) to suggest a conceptual model where the trophic size structure, the amount of available oxygen, and the feeding energetic cost are considered (Fig. 6.2). The last two periods of high macrozooplankton abundance (until the mid 1970s and since the late 1990s) are associated to low oxygen conditions. Sardine can shift toward a more energetically expensive direct biting on macrozooplancton but such foraging strategy became limiting if oxygen availability decrease as occurred in the late 1990s when sardine collapsed.

6.4. New insights provided by SIA

In the last two decades, the stable isotope analyses of nitrogen and carbon have been increasingly used to better understand marine food webs patterns and fluxes. In Peru so far very few studies were performed. Lorrain et al. (2011) and Arguelles et al. (2012) focused on the jumbo squid while this work is a first 'ecosystemic' contribution. Even if several shortcomings can blur our capability to fully describe the food webs (see Chapter 5) robust patterns emerged and we were able to propose a new vision of the trophic structures in the NHCS (Fig. 5.8).

6.4.1 Confirming SCA results on anchovy

Our results definitely refute the hypothesis of a short and efficient food chain with anchoveta foraging directly on phytoplankton (Ryther, 1969). Rather they confirm the results from Espinoza and Bertrand (2008) who showed that zooplankton was by far the most important dietary component, with euphausiids contributing 67.5% of dietary carbon followed by copepods (26.3%), therefore having an estimated trophic position of ~3.5.

6.4.2 The squat lobster case

The squat lobster has become abundant along the Peruvian coast since the mid-1990s with acoustic estimates ranging between 0.6 and 3.4 million tons from 1998 to 2005 (Gutiérrez et al. 2008). This species has been previously observed in stomachs of hake (*Merluccius gayi peruanus*), sharks (Paredes and Elliott, 1997), and jack mackerel (*Trachurus murphyi*) (Alegre et al., 2013). The squat lobster also constituted 75% of the diet of sea-lions and was important for sea birds in the zone of the Paracas Peninsula, 14°S (Arias-Schereiber, 1996; Jahncke et al., 1997). Last years, abundance of the squat lobster has increased and many questions have risen about its role and for example potential predation of this species by anchoveta or competition between the two species. As shown in figure 6.4, large quantities of *Pleuroncodes monodon* can be found while fishing for anchovy.

Fig. 6. 4. Anchovy and squat lobsters.

Our SIA results do not support the hypothesis that anchoveta would predate on squat lobsters as their trophic position (TP obtained from $\delta^{15}N$ values) is nearly the same, with squat lobster even having a higher TP. Still, our results support the hypothesis that squat lobsters would forage to some extent on fish eggs and larvae, thus likely predating on the first life stages of anchoveta. Competition between these two species therefore seems to occur. However, the differing $\delta^{13}C$ values of anchoveta and squat lobster suggest that these two species do not exactly share the same foraging habitat, with anchoveta having a larger and more offshore foraging range. This is in agreement with what Gutiérrez et al. (2008) found using acoustic data from surveys performed between 1998 and 2006 along the

Peruvian coast, with the squat lobster having a restricted and more coastal habitat compared to anchoveta. This would potentially reduce some direct competition and/or predation.

In any case, these results suggest the important role of the squat lobster the Humboldt Current system. More studies need to be done, in particular on its energetic content as some birds and seals have been found to forage on this species (Arias-Schereiber, 1996; Jahncke et al., 1997), which could impact their fitness. The junk-food hypothesis indeed attributes declines in productivity of marine birds and mammals to changes in the species of prey they consume and corresponding differences in nutritional quality of those prey (Romano et al. 2006).

6.4.3 The jumbo squid case

Lorrain et al. (2011) and Argüelles et al. (2012) determined the habitat and resource use of *Dosidicus gigas* in the Northern Humboldt Current System from stable isotopes analyses. The two approaches were complementary. Using $\delta^{13}C$ and $\delta^{15}N$ values of serially sampled gladius (an archival tissue) Lorrain et al. (2011) first examined high resolution variations in the trophic niche of five large (>60 cm mantle length) jumbo squids. They evidenced large inter-individual differences in jumbo squid foraging strategies with no systematic increase of trophic level with size, illustrating the high degree of plasticity of this species. Argüelles et al. (2012) then analyzed $\delta^{13}C$ and $\delta^{15}N$ values of mantle tissues of 234 jumbo squid individuals collected during 2008–2010 (note that these samples are considered within the samples used in Chapter 5). As observed globally for all species in Chapter 5, for $\delta^{13}C$ values, distance to shelf break and latitude were the main explaining factors. The $\delta^{13}C$ values followed a decreasing trend with increasing distance to the shelf break (Fig. 6.5.), which is consistent with higher $\delta^{13}C$ values corresponding to highest productivity in coastal waters than in oceanic waters (Pennington et al., 2006; Miller et al., 2008). In turn, the $\delta^{13}C$ values showed a clear bellshaped trend with lowest values north of Peru and highest values in central Peru. This variation (from north to central Peru), matched with the $\delta^{13}C$ values of zooplankton and can be related to the upwelling off Peru and reflect latitudinal changes in productivity. Indeed, this area corresponds to the richest nearshore area ranges between 7 and 15°S (Guillén and Calienes, 1981; Echevin et al. 2008). The $\delta^{13}C$ values also increased with jumbo squid mantle size, primarily reflecting increases in body mass (Hesslein et al.,1993; Herzka, 2005), or carbon differences in $\delta^{13}C$ that occur primarily at primary production, with small increases with increasing the trophic level (0.4‰, Post, 2002). These changes, suggest that jumbo squid juveniles and adults distribute over a large range of habitats, seasonally migrating to coastal waters to grow, mature, and feed, and then return to oceanic waters to spawn (Nesis, 1970, 1983; Nigmatullin et al., 2001).

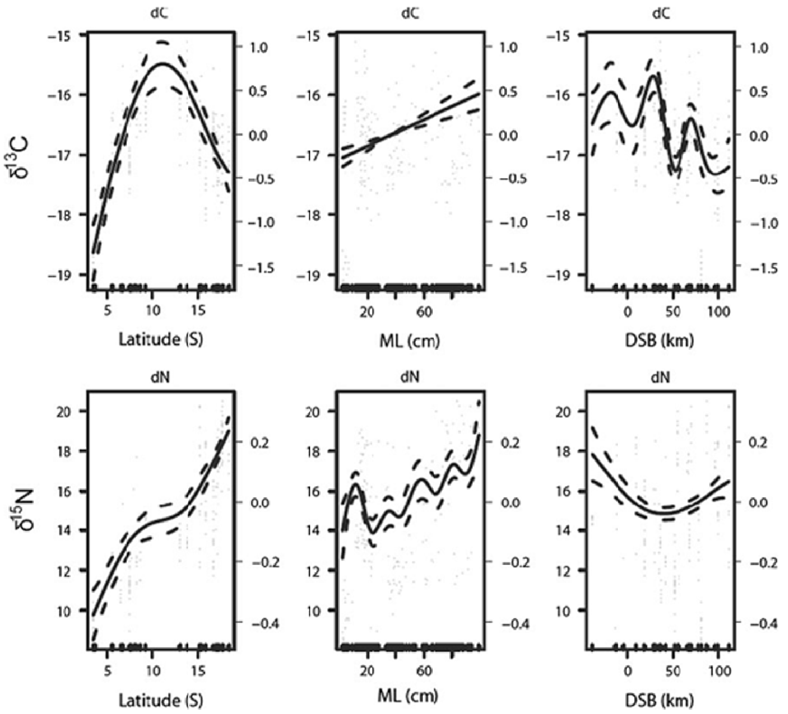

Figure 6.5: GAMs of muscle $\delta^{13}C$ and $\delta^{15}N$ values as a function of latitude, mantle length (ML) and distance to shelf break (DSB). Source: Argüelles et al. (2012).

$\delta^{15}N$ values were strongly affected by latitude (Fig. 6.5.) with increasing values from north to south were also found in zooplankton samples and were related to changes in isotope baseline values probably due to oxygen minimum zones that occur off Peru. This similar latitudinal trend in both zooplankton and *D. gigas* samples reveals that *D. gigas* is a relatively resident species at the scale of its isotopic turnover rate (i.e. a few weeks), even if this is not necessarily the case at the scale of its life. A small but significant size effect on $\delta^{13}C$ values suggests that jumbo squid perform offshore–onshore ontogenic migration, with juveniles distributed offshore. For nitrogen, the high inter-individual variability observed with mantle length indicates that *D. gigas* can prey on a high variety of resources at any stage of their life cycle. Argüelles et al. (2012) thus provided further evidence that *D. gigas* have the capability to explore a wide range of habitats and resources at any stage of their life. Such findings were complemented by the present studies and by Alegre et al. (2014) who proposed a conceptual model of jumbo squid distribution and foraging patterns along the ontogenetic cycle taking into account the presence of the oxygen minimum zone (Fig. 6.6.). They show that 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 cephalopoda. However, off Peru, contrarily to other systems, *D. gigas* does not occupy very coastal waters where a huge biomass of anchovy is present. They hypothesized 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. 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.

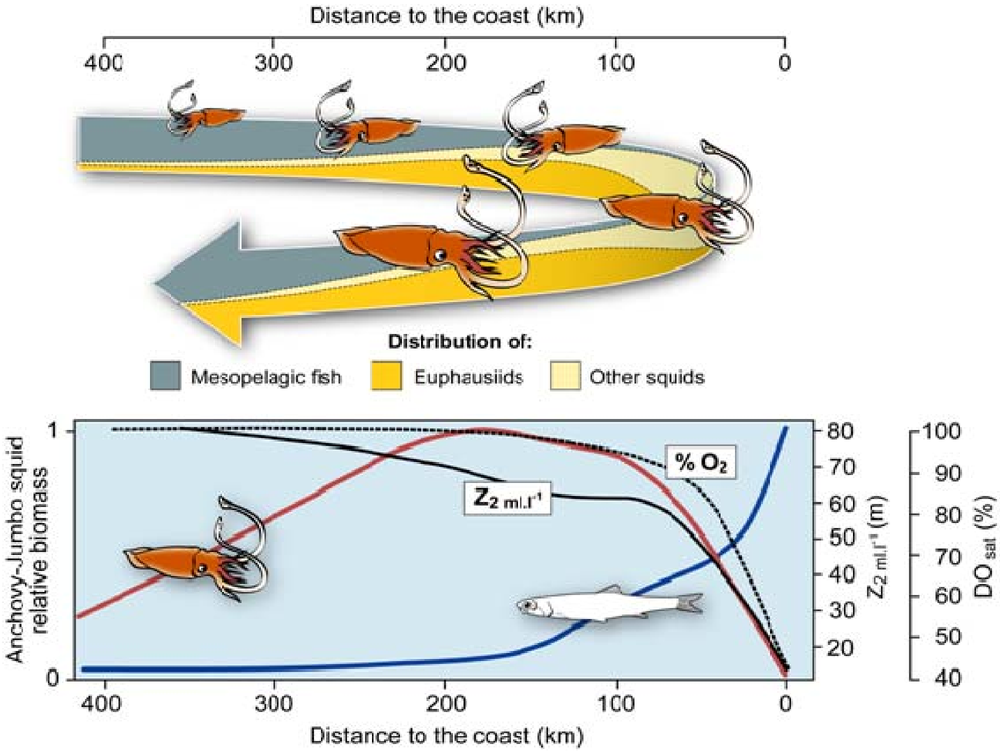

Figure 6.6: Conceptual model and cross-shore profiles of oxygen and organisms distribution. The lower panel shows the mean (spline smooth) cross-shore profiles of dissolved oxygen saturation in % (grey 639 dashed line), depth of the 2 ml.l-1 isoline in m (black solid line) and the acoustic-estimated 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. Source: Alegre et al. (2014).

This comprehensive study on jumbo squid also illustrates the potential of SIA when a large number of individuals with a good spatial and temporal resolution can be achieved. The gladius study also demonstrates the potential of archival tissues for individual life history reconstructions. This is undoubtedly two important directions to follow for future SIA in Peru (see below).

6.4.4 Perspectives for the future SIA in Peru

One main limit of this study is poor spatial and temporal resolution of sampling for most species such as squat lobster and copepods (in particular for the inshore offshore gradient). IMARPE cruises are mostly dedicated to fisheries evaluation and it was difficult to obtain time for other scientific sampling. By the way, the initial sampling protocol designed to decipher latitude, longitude and size effects, i.e., sampling the same species on the same cruise for small and large individuals at several latitudes together with onshore and offshore sampling could never be achieved. It was therefore difficult to test baseline effects properly and to assess inter annual variations and relate them to changing environmental conditions (e.g., cool vs. warm years, changes in the upper limit of the OMZ). As discussed previously in this thesis, both geographic patterns and trophic position influence the $\delta^{15}N$ values of consumers, and resolving these two components for mobile pelagic organisms requires accurate and reliable assessment of isotopic baselines. In the future, an onshore offshore sampling of the base of the food web, i.e., copepods, at two specific locations (one south, one north) and at different times of the year would help confirming some hypotheses advanced in our study.

It would also be interesting to investigate potential changes in the foraging ecology of key species of the NSCH through time, to reveal potential shifts for example in strong El Niño vs. La Niña conditions or strong upwelling's years. For example, does the foraging habitat of anchoveta extend offshore (lower $\delta^{13}C$ values and higher SD) in cooler conditions (see earlier discussion in section 6.3)? Indeed, it would be a very efficient way to monitor long term changes in foraging ecology of important species. We therefore suggest for the future to start an historical/observatory sampling in one or two specific locations at the same period in Peru of copepods, euphausiids, the squat lobster, birds, anchoveta and jumbo squids to monitor potential shifts in the trophic structure of the system. This SIA sampling has to be performed in complement with the oceanographic survey and routine SCA sampling already performed by IMARPE. A time series on SIA should help to better establish the food chain length and variability in the NSCH and to provide a database essential to understanding bioaccumulation of contaminants, climate change impacts and fisheries responses in the NSCH.

Furthermore, past changes would also be interesting to measure through archival samples, such as zooplankton stored in formaldehyde, bird feathers from collections or anchovy scales from sediment cores. Past isotopic baseline variations could be assessed through zooplankton analyses. This step is indeed a prerequisite for further relevant interpretation of stable isotope values in higher trophic level organisms. Compound-specific isotope analysis of $\delta^{15}N$ of some particular individual amino acids ($\delta^{15}N$ CSIA-AA) is a rapidly growing tool in ecological studies to assess diet and trophic position (TP) in both modern and ancient foodwebs (McClelland & Montoya, 2002; Chikaraishi et al., 2009; Germain et al., 2013). A group of amino acids, the source amino acids (e.g., phenylalanine) do not fractionate through the food web and represent the isotopic baseline, whereas a second group of amino acids, trophic amino acids (e.g., glutamic acid), do fractionate consistently with each trophic level and can provide an estimate of the consumer's trophic position (McClelland & Montoya, 2002; Popp et al., 2007; Chikaraishi et al., 2009; Lorrain et al., 2009). This method allows desiphering if variations in the bulk $\delta^{15}N$ value of the consumer are driven by fluctuations at the base of the food web or changes in their trophic position. This method necessitates tissue only from the studied organism from which the isotopic composition of several amino acids can be simultaneously done, thus resolving complications associated with high resolution spatial and temporal baseline sampling. This method has successfully been applied in several types of organisms and recently in the jumbo squid *D. gigas* to decipher its foraging and expansion range (Ruiz-Cooley et al., 2013)

6.5. Concluding remarks

This study based on the combination of stomach content and stable isotopes analyses provided a new vision of the trophic structure of the NHCS. Several paradigms were revisited (e.g. anchoveta phytophagy) and some surprises came out (e.g. the relatively high TP of the squat lobster). These findings call for a strong revision of trophic models currently used in the NHCS. Also they indicate that the use of trophic levels from international data-base or trophic models outputs can lead to strong misunderstandings. For instance the trophic position of anchoveta ranges between 2.6 and 3.1 in FishBase, it was estimated to 2.3 from trophic models (Tam et al., 2008), while our results indicates much higher values (3.5-3.6). Still, this study reveals that organism diet is highly variable in time and space. In the NHCS, marine life needs to have a high (trophic) plasticity to cope with its highly variable environment. Such variability and the role of the oxygen minimum zone on the structure and functioning of the ecosystem - as well as on the baseline nitrogen isotope values - plead for a regular trophic monitoring of the main components of the ecosystem combining stomach content and stable isotopes analyses and other new technologies such as CSIA on amino acids.

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Annex 1: Shape, size and volume of phytoplankton cells recorded from anchoveta stomach contents; cell volume was extracted from the literature (see references) or calculated from published geometric shapes and published or estimated cell sizes.

Genus	Geometric shape	Diameter (µm)	Length (µm)	Height (µm)	m[a] (µm)	Volume formula[b]	Volume values (μm^3)
DIATOMS							
Actinoptychus	Cylinder[b]					$(\pi/4).d^2.h$	16828[c]
Amphiprora	Elliptic prism[b]	10	35	10		$(\pi/4).d.l.h$	2749
Amphora	Cymbelloid[b]					$(1/6).\pi.(2b)^2.a.(\beta/360)$[d]	6187[c]
Asterionellopsis	Prism on triangle[b]		30	10[e]	10	$(½).l.m.h$	1500
Asteromphalus	Cylinder[b]	30		5		$(\pi/4).d^2.h$	3534
Bacteriastrum	Cylinder[b]	40		80		$(\pi/4).d^2.h$	100531
Cerataulina	Cylinder[b]					$(\pi/4).d^2.h$	30015[c]
Chaetoceros	Elliptic prism[b]					$(\pi/4).d.l.h$	3937[c]
Cocconeis	Elliptic prism[b]					$(\pi/4).d.l.h$	780[c]
Corethron	Cylinder + 2 half spheres[b]	20		100		$\pi.r^2.l+(4/3).\pi.r^3$[f]	35605
Coscinodiscus	Cylinder[b]					$(\pi/4).d^2.h$	994625[c]
Cylindrotheca	Prolate spheroid + 2 cylinders[b]					$(\pi/6).d^2.h+2(\pi/4).d^2.h$	158[c]
Detonula	Cylinder[b]	40		40		$(\pi/4).d^2.h$	50265
Ditylum	Prism on triangle[b]					$(½).l.m.h$	60495[c]
Eucampia	Elliptic prism[b]	24	52	30		$(\pi/4).d.l.h$	9802
Fragilariopsis	Elliptic prism[b]					$(\pi/4).d.l.h$	190[c]
Grammatophora	Elliptic prism[b]					$(\pi/4).d.l.h$	9772[c]
Guinardia	Cylinder[b]					$(\pi/4).d^2.h$	144013[c]
Gyrosigma	Prism on parallelogram[b]					$(1/2).l.b.h$[g]	63513[c]
Hemiaulus	Elliptic prism[b]	30	90	10		$(\pi/4).d.l.h$	21205.75
Lauderia	Cylinder[b]	50		90		$(\pi/4).d^2.h$	176715
Leptocylindrus	Cylinder[b]					$(\pi/4).d^2.h$	1608[c]
Licmophora	Gomphonemoid[b]					[b]	11870[c]
Lioloma	Box[b]	25	50	25		$l.l'.h$[h]	31250
Lithodesmium	Prism on triangle[b]		34	20[e]	20	$(1/2).l.m.h$	6800
Navicula	Elliptic prism[b]					$(\pi/4).d.l.h$	3013[c]
Odontella	Elliptic prism[b]					$(\pi/4).d.l.h$	13081
Planktoniella	Cylinder[b]	80		15		$(\pi/4).d^2.h$	75398
Pleurosigma	Prism on parallelogram[b]					$(1/2).l.b.h$[g]	36882
Proboscia	Cylinder[b]					$(\pi/4).d^2.h$	13641
Pseudonitzschia	Prism on parallelogram[b]					$(1/2).l.b.h$[g]	646
Pseudosolenia	Cylinder[b]	50		300		$(\pi/4).d^2.h$	589049
Rhizosolenia	Cylinder[b]					$(\pi/4).d^2.h$	108532
Skeletonema	Cylinder + 2 half spheres[b]					$(\pi).r^2.l+(4/3).\pi.r^3$[f]	459
Stephanopyxis	Cylinder + 2 half spheres[b]	40		60		$(\pi).r^2.l+(4/3).\pi.r^3$[f]	108909
Thalassionema	Box[b]					$l.l'.h$[h]	1252
Thalassiosira	Cylinder[b]					$(\pi/4).d^2.h$	14390
Tropidoneis	Prism on triangle[b]		75	18[e]	18	$(1/2).l.m.h$	12150
DINOFLAGELLATES							
Ceratium	Ellipsoid+2 cones+cylinder[b]					$(\pi/6).a.b.l + 2.(1/3).\pi . r^2.z + (\pi/4).d^2.h$[jk]	47435[i]
Dinophysis	Ellipsoid[b]					$(\pi/6).a.b.l$[j]	50000 (assumed)
Diplopelta	Ellipsoid[b]					$(\pi/6).a.b.l$[j]	50000 (assumed)
Diplopsalis	Cone + half sphere[b]					$(1/3).\pi . r^2.z + (1/2).(4/3).\pi.r^3$[fk]	50000 (assumed)
Dissodium							50000 (assumed)
Goniodoma	Sphere[b]					$(4/3).\pi.r^3$[f]	50000 (assumed)
Gonyaulax	2 cones[b]					$2.(1/3).\pi . r^2.z$[k]	50000 (assumed)
Gymnodinium	Ellipsoid[b]					$(\pi/6).a.b.l$[j]	88099[i]
Oxophysis	2 cones[b]					$2.(1/3).\pi . r^2.z$[j]	50000 (assumed)
Podolampas	Cone[b]					$(1/3).\pi . r^2.z$[k]	50000 (assumed)
Pronoctiluca	Cone + half sphere[b]					$(1/3).\pi . r^2.z + (1/2).(4/3).\pi.r^3$[fk]	50000 (assumed)
Prorocentrum	Ellipsoid[b]					$(\pi/6).a.b.l$[j]	16303[i]
Protoperidinium	2 cones[b]					$2.(1/3).\pi . r^2.z$[k]	133298[i]
Pyrocystis	Ellipsoid[b]					$(\pi/6).a.b.l$[j]	50000 (assumed)
Pyrophacus	Ellipsoid[b]					$(\pi/6).a.b.l$[j]	50000 (assumed)
Scrippsiella	Ellipsoid[b]					$(\pi/6).a.b.l$[j]	50000 (assumed)
SILICOFLAGELLATES							
Dictyocha							30000 (assumed)
Octactis							30000 (assumed)
PHYTOFLAGELLATES							
Tetraselmis	Elliptic prism[b]	10	25	5		$(\pi/4).d.l.h$	1964
MICROFLAGELLATES							
Olisthodiscus luteus	Prolate spheroid	50	110			$(\pi/6).d^2.l$	143990
TINTINNIDS							
Amphorellopsis	Cylinder[l]	30		200		$(\pi/4).d^2.h$	98175
Codonella	Cylinder[l]	30		200		$(\pi/4).d^2.h$	98175
Codonellopsis	Cylinder[l]	30		200		$(\pi/4).d^2.h$	98175
Dictyocysta	Cylinder[l]	30		200		$(\pi/4).d^2.h$	98175
Eutintinnus	Cylinder[l]	30		200		$(\pi/4).d^2.h$	98175
Favella	Cylinder[l]	30		200		$(\pi/4).d^2.h$	98175
Helicostomella	Cylinder[l]	30		200		$(\pi/4).d^2.h$	98175
Tintinnopsis	Cylinder[l]	30		200		$(\pi/4).d^2.h$	98175
Xystonella	Cylinder[l]	30		200		$(\pi/4).d^2.h$	98175
FORAMINIFERIDA	Ellipsoid[b]		200			$(\pi/6).a.b.l$[j]	523599
RADIOLARIA	Ellipsoid[b]		110			$(\pi/6).a.b.l$[j]	88698
Acanthaires	Prolate spheroid[b]	50	75			$(\pi/6).d^2.l$	98175

[a] m: height of even-sided triangle of the transapical section.

[b] Hillebrand *et al.* (1999).

[c] Snoeijs *et al.* (2002).

[d] a: length;b: height.

[e] h: base of even-sided triangle of the transapical section.

[f] r: radius.

[g] b: minor axis;l: major axis, similar to length.

[h] l’: minor base of rectangle, similar to diameter (d).

[i] Menden-Deuer and Lessard (2000).

[j] a: main axis;b: minor axis of cross section (in Foraminiferida:a= 100,b= 50; Radiolaria:a= 55,b= 28).

[k] z: height of the cone.

[l] Chiappa-Carrara and Gallardo-Cabello (1993)

Annex 2: Contribution by number and carbon content of anchoveta dietary items (data from all surveys combined).

Dietary items	Total number	Total Carbon (µg)
DIATOMS		
Actinoptychus	2249000	1733
Amphiprora	107000	19
Amphora	186000	64
Asterionellopsis	265043000	28742
Asteromphalus	719000	156
Bacteriastrum	791000	2597
Cerataulina	26000	32
Chaetoceros	206866000	49060
Cocconeis	4000	0.26
Corethron	217000	307
Coscinodiscus	60994000	1284639
Cylindrotheca	4000	0.07
Detonula	32551000	60910
Ditylum	89090000	193730
Eucampia	16313000	8107
Fragilariopsis	1487000	30
Grammatophora	3000	1
Guinardia	1831000	8045
Gyrosigma	10822000	24481
Hemiaulus	15000	14
Lauderia	7000	36
Leptocylindrus	2000	0.23
Licmophora	16000	9
Lioloma	11757000	14963
Lithodesmium	19686000	7273
Navicula	5025000	959
Odontella	1513000	950
Planktoniella	4557000	11847
Pleurosigma	2266000	3299
Proboscia	9000	6
Pseudonitzschia	33495000	1834
Pseudosolenia	27000	372
Rhizosolenia	4494000	15699
Skeletonema	972395000	40361
Stephanopyxis	572000	2004
Thalassionema	39032000	3656
Thalassiosira	513411000	348371
Tropidoneis	2000	1
DINOFLAGELLATES		
Ceratium	8046000	42746
Dinophysis	609000	3399
Diplopelta	17000	95
Diplopsalis	22000	123
Dissodium	1248000	6966
Goniodoma	1256000	7011
Gonyaulax	44000	246
Gymnodinium	2000	19
Oxophysis	53000	296
Podolampas	6000	33
Pronoctiluca	1000	6
Prorocentrum	1340000	2611
Protoperidinium	11461000	160651
Pyrocystis	704000	3930
Pyrophacus	16000	89
Scrippsiella	1002000	5593
SILICOFLAGELLATES		
Dictyocha	8469000	29262
Octactis	566000	1956
PHYTOFLAGELLATES		
Tetraselmis	6000	2
MICROFLAGELLATES		
Olisthodiscus luteus	1214000	9804
TINTINNIDS		
Amphorellopsis	10000	79
Codonella	340000	2699
Codonellopsis	83000	659
Dictyocysta	337000	2675
Eutintinnus	216000	1714
Favella	97000	770
Helicostomella	3310000	26272

Tintinnopsis	732000	5810
Xystonella	1081000	8580
FORAMINIFERIDA	1040000	29323
RADIOLARIA	1986000	10219
Acanthaires	12000	68
ZOOPLANKTON		
COPEPODA		
Acartia	40020	176227
Aetideus	16080	256667
Calanus	114300	4012932
Calocalanus	2190	11509
Candacia	47120	377775
Centropages	129440	2066103
Clausocalanus	112340	181347
Clytemnestra	6810	8543
Copilia	200	1697
Corycaeus	144420	409077
Corycella	120	146
Euaetideus	2330	9174
Eucalanus	93090	21834378
Euchaeta	34450	223544
Euchirella	280	18118
Euterpina	19930	14510
Haloptilus	10	87
Lubbockia	4910	8981
Lucicutia	18330	104803
Macrosetella	10550	14853
Mecynocera	3230	12679
Microsetella	37960	53444
Nonocalanus	360	5746
Oithona	126830	92338
Oncaea	173890	222492
Paracalanus	109280	311602
Phaena	8340	23781
Pleuromamma	400	3464
Pontellina	40	638
Rhincalanus	1070	250970
Saphirina	570	8261
Scolecithrix	13390	301165
Scolecithtricella	740	19466
Temora	3560	30832
Harpacticoida	52970	55130
Copepoditos	120290	94624
Restos de copépodos	285570	33625
Euphausiacea	61319	80233346
Amphipoda	2103	475392
Ostracoda	150	105
Zoea	38682	350220
Megalop	14205	345328
Cirriped larvae	7170	44
Emerita sp. Larvae	80	6750
Decapod undetermined larvae	1080	91125
Pagurus sp.	1	84
Pleuroncodes monodon	48	9192
Decapoda Reptantia n/i	3062	74438
Galatheidae	1	192
Bivalvia	8090	368083
Gastropoda	19910	905876
Anchoveta eggs	39611	476270
Apendicularia	180	14039
Echinoderm larvae	80	0.17
Chaetognata	2830	83314
Squid remains	5	873
Polychaeta	7992	888965
Anchoa sp. Eggs	248	2982
Engraulidae eggs	15	180
Fish eggs	1931	23218
Fish larvae	361	223898
Fish undetermined	41	25429
Engraulidae	2	1240
Vinciguerria sp.	809	501754
Myctophidae	51	31631

Annex 3.1. Year, months, source, number of trawls, total number of stomachs (with prey contents), and length range (cm) of Engraulis ringens samples used to estimate the euphausiids fraction only.

Year	Months	Source	N of trawls	N of stomachs (with prey)	Fish total length (Min – Max)
1985	Aug. - Sept.	Scientific survey	9	140 (125)	12-17.5
1988	Sept.	Scientific survey	3	30 (n.d.)	12.5-15.5
1988	Jan. - Dec.	Factory plant Chimbote	-	147 (n.d.)	9.5-20
1989	Nov. - Dec.	Scientific survey	8	84 (n.d.)	12.0-19.0
1989	Aug.	Scientific survey	4	40 (n.d.)	13.5-18.5
1989	Apr. - Dec.	Factory plant Callao	-	97 (n.d.)	10.0-18.5
1990	Nov. - Dec.	Scientific survey	5	50 (n.d.)	11.5-17.5
1990	Aug.	Scientific survey	4	42 (n.d.)	11.5-19
1990	Mar. - Apr.	Scientific survey	10	100 (n.d.)	12.5-18.5
1990	Jan. - May	Factory plant Chimbote	-	166 (n.d.)	9-18.5
1994	Aug. - Sept.	Scientific survey	31	488 (n.d.)	11.5-17.5
1994	Feb. - Mar.	Scientific survey	7	63 (n.d.)	n.d.
1994	May - Dec.	Factory plant Callao	-	320 (n.d.)	7-17.5
1995	Feb. - Mar.	Scientific survey	28	403 (n.d.)	3.5-18
2004	Feb. - Mar.	Scientific survey	77	1523 (1272)	4.5-17.5
2004	Aug. - Sept.	Scientific survey	43	749 (696)	8.5-17.0
2004	Nov. - Dec.	Scientific survey	28	309 (271)	5.0-17.5
2005	Feb. - Mar.	Scientific survey	84	1198 (1028)	6.0-17.5
2005	Aug. - Sept.	Scientific survey	33	349 (345)	9.0-18.0
2005	Nov. - Dec.	Scientific survey	65	803 (767)	7.5-17.5
2006	Feb. - Apr.	Scientific survey	54	753 (690)	4.0-17.5
2006	Aug. - Sept.	Scientific survey	12	208 (193)	8.5-16.5
2006	Nov. - Dec.	Scientific survey	97	1267 (1118)	5.0-18.0
2007	Feb. - Apr.	Scientific survey	100	1627 (1545)	5.0-18.0
2007	Aug. - Sept.	Scientific survey	67	1214 (1145)	6.5-17.5
2007	Dec.	Scientific survey	22	134 (115)	5.0-17.5
2008	Feb. - Apr.	Scientific survey	72	1079 (1000)	5.0-18.0
2008	Aug. - Sept.	Scientific survey	34	629 (574)	6.0-17.5
2008	Nov. - Dec.	Scientific survey	64	1253 (1214)	5.0-18.0
2009	Feb. - Apr.	Scientific survey	51	640 (607)	6.0-18.0
2009	Aug. - Sept.	Scientific survey	40	417 (398)	4.5-17.5
2009	Dec.	Scientific survey	44	744 (636)	5.5-18.0

Annex 3.2. Results of Tukey-type multiple comparisons post hoc analyses of diatom contribution in Engraulis ringens diet by 2 cm long size-class. In bold, significant differences (p<0.05)

	[4-6>	[6-8>	[8-10>	[10-12>	[12-14>	[14-16>	[16-18>
[4-6>							
[6-8>	0.096						
[8-10>	**0.000**	0.173					
[10-12>	**0.000**	**0.003**	0.938				
[12-14>	**0.000**	**0.000**	0.093	0.352			
[14-16>	**0.000**	**0.000**	**0.033**	0.105	0.999		
[16-18>	**0.000**	**0.000**	0.305	0.825	0.998	0.921	
[18-20>	**0.000**	**0.005**	0.769	0.997	0.998	0.966	0.999

Annex 3.3 Results of Tukey-type multiple comparisons post hoc analyses of calanoids contribution in Engraulis ringens diet by 2 cm long size-class. In bold, significant differences ($p<0.05$*).*

	[4-6>	[6-8>	[8-10>	[10-12>	[12-14>	[14-16>	[16-18>
[4-6>							
[6-8>	0.860						
[8-10>	0.998	0.268					
[10-12>	1.000	0.471	0.975				
[12-14>	0.992	0.968	0.120	0.247			
[14-16>	0.939	0.999	**0.021**	**0.027**	0.969		
[16-18>	0.999	0.916	0.332	0.690	0.998	0.757	
[18-20>	0.999	0.258	1.000	0.989	0.216	**0.035**	0.427

Annex 3.4 Results of Tukey-type multiple comparisons post hoc analyses of euphausiids contribution in Engraulis ringens diet by 2 cm long size-class. In bold, significant differences ($p<0.05$*).*

	[4-6>	[6-8>	[8-10>	[10-12>	[12-14>	[14-16>	[16-18>
[4-6>							
[6-8>	0.628						
[8-10>	**0.027**	0.956					
[10-12>	**0.004**	0.849	0.999				
[12-14>	**0.000**	0.055	0.263	0.111			
[14-16>	**0.000**	**0.000**	**0.000**	**0.000**	0.057		
[16-18>	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.795	
[18-20>	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.146	0.799

Annex 3.5 Results of Tukey-type multiple comparisons post hoc analyses of diatoms contribution in Engraulis ringens diet by 1º of latitude. In bold, significant differences ($p<0.05$*).*

	3º30'	4	5	6	7	8	9	10	11	12	13	14	15	16	17
3º30'															
4	0.999														
5	0.991	1.000													
6	1.000	0.999	0.930												
7	0.997	1.000	1.000	0.628											
8	1.000	0.999	0.993	0.999	0.891										
9	0.981	1.000	0.999	0.266	0.999	0.521									
10	0.997	1.000	1.000	0.624	1.000	0.919	0.999								
11	0.839	0.999	0.998	0.036	0.933	0.111	0.999	0.992							
12	1.000	0.999	0.440	0.999	0.053	0.954	**0.014**	0.100	**0.002**						
13	1.000	0.999	0.454	0.999	0.053	0.980	**0.013**	0.105	**0.001**	1.000					
14	0.999	1.000	0.999	0.857	1.000	0.987	0.999	1.000	0.928	0.134	0.188				
15	0.994	1.000	1.000	0.822	1.000	0.983	0.999	1.000	0.987	0.243	0.279	1.000			
16	1.000	0.999	0.997	0.999	0.984	1.000	0.793	0.976	0.300	0.997	0.999	0.998	0.995		
17	1.000	0.999	0.999	0.999	0.999	1.000	0.989	0.999	0.769	0.999	0.999	0.999	0.999	1.000	
18	0.999	1.000	0.999	0.994	0.999	0.999	0.999	0.999	0.890	0.551	0.649	1.000	0.999	0.999	0.999

Annex 3.6 Results of Tukey-type multiple comparisons post hoc analyses of calanoids contribution in Engraulis ringens diet by 1º of latitude. In bold, significant differences ($p<0.05$*).*

	3º30'	4	5	6	7	8	9	10	11	12	13	14	15	16	17
3º30'															
4	0.956														
5	0.604	0.999													
6	0.876	1.000	0.970												
7	0.916	1.000	0.856	1.000											
8	0.779	1.000	0.996	1.000	0.999										
9	0.365	0.979	0.999	0.110	**0.038**	0.268									
10	0.867	1.000	0.972	1.000	1.000	1.000	0.150								
11	0.502	0.999	1.000	0.850	0.716	0.982	0.999	0.925							
12	0.937	1.000	0.836	1.000	1.000	0.999	0.050	0.999	0.647						
13	0.803	1.000	0.999	0.999	0.999	1.000	0.520	1.000	0.996	0.999					
14	0.444	0.996	0.999	0.397	0.208	0.680	1.000	0.479	0.999	0.232	0.821				
15	0.624	1.000	0.999	0.999	0.999	1.000	0.995	0.999	1.000	0.998	0.999	0.999			
16	0.525	0.999	1.000	0.861	0.820	0.988	0.999	0.939	1.000	0.784	0.994	1.000	0.999		
17	0.214	0.932	0.996	0.175	0.124	0.402	0.999	0.262	0.963	0.135	0.478	0.999	0.947	0.997	
18	0.453	0.967	0.999	0.362	0.246	0.640	1.000	0.452	0.999	0.263	0.788	1.000	0.997	0.999	0.999

Annex 3.7. Results of Tukey-type multiple comparisons post hoc analyses of euphausiids contribution in Engraulis ringens diet by 1º of latitude. In bold, significant differences (p<0.05).

	3º30'	4	5	6	7	8	9	10	11	12	13	14	15	16	17
3º30'															
4	0.815														
5	0.603	1.000													
6	0.080	0.990	0.229												
7	0.315	1.000	0.999	0.159											
8	**0.044**	0.982	0.153	1.000	0.066										
9	0.396	1.000	1.000	0.159	1.000	0.088									
10	0.058	0.984	0.224	1.000	0.235	1.000	0.188								
11	0.107	0.999	0.826	0.999	0.921	0.999	0.872	0.999							
12	0.396	1.000	1.000	0.078	1.000	**0.035**	1.000	0.118	0.770						
13	0.498	1.000	1.000	**0.044**	0.999	**0.023**	0.999	0.053	0.505	0.999					
14	0.539	1.000	1.000	0.132	0.999	0.074	1.000	0.145	0.742	1.000	1.000				
15	0.319	1.000	0.999	0.788	1.000	0.638	1.000	0.752	0.997	1.000	0.999	0.999			
16	0.989	0.996	0.690	**0.000**	**0.044**	**0.000**	0.203	**0.000**	**0.001**	0.183	0.710	0.659	0.131		
17	0.747	1.000	0.999	**0.012**	0.951	**0.000**	0.997	**0.015**	0.176	0.997	0.999	0.999	0.954	0.982	
18	0.240	0.999	0.994	1.000	0.999	1.000	0.997	1.000	1.000	0.994	0.953	0.986	0.999	0.183	0.791

Annex 3.8 Results of Tukey-type multiple comparisons post hoc analyses of diatoms contribution in Engraulis ringens diet according to the distance to the shelf break (Negative inshore, positive offshore). In bold, significant differences (p<0.05).

	< -30	[-30 – 0>	[0-30>
< -30			
[-30 – 0>	**0.010**		
[0-30>	**0.000**	**0.000**	
>30	**0.000**	**0.000**	0.409

Annex 3.9 Results of Tukey-type multiple comparisons post hoc analyses of calanoids contribution in Engraulis ringens diet according to the distance to the shelf break (Negative inshore, positive offshore). In bold, significant differences (p<0.05).

	< -30	[-30 – 0>	[0-30>
< -30			
[-30 – 0>	0.890		
[0-30>	0.712	0.924	
>30	**0.013**	**0.031**	0.213

Annex 3.10 Results of Tukey-type multiple comparisons post hoc analyses of euphausiids contribution in Engraulis ringens diet according to the distance to the shelf break (Negative inshore, positive offshore). In bold, significant differences (p<0.05)

	< -30	[-30 – 0>	[0-30>
< -30			
[-30 – 0>	**0.000**		
[0-30>	**0.000**	**0.000**	
>30	**0.000**	**0.000**	0.086

Annex 3.11 Results of Tukey-type multiple comparisons post hoc analyses of diatoms contribution in Engraulis ringens diet by diel period (07:00≤day<17:00; 17:00≤dusk<19:00; 19:00≤night<05:00; 05:00≤dawn<07:00). In bold, significant differences (p<0.05).

	Night	Day	Dusk
Night			
Day	**0.046**		
Dusk	0.394	0.999	
Dawn	**0.001**	**0.073**	0.248

Annex 3.12 Results of Tukey-type multiple comparisons post hoc analyses of calanoids contribution in Engraulis ringens diet by diel period (07:00≤day<17:00; 17:00≤dusk<19:00; 19:00≤night<05:00; 05:00≤dawn<07:00). In bold, significant differences (p<0.05).

	Night	Day	Dusk
Night			
Day	**0.000**		
Dusk	**0.000**	**0.001**	
Dawn	0.998	**0.000**	**0.000**

Annex 3.13 Results of Tukey-type multiple comparisons post hoc analyses of euphausiids contribution in Engraulis ringens diet by diel period (07:00≤day<17:00; 17:00≤dusk<19:00; 19:00≤night<05:00; 05:00≤dawn<07:00). In bold, significant differences (p<0.05)

	Night	Day	Dusk
Night			
Day	**0.000**		
Dusk	**0.000**	**0.053**	
Dawn	**0.000**	0.690	0.809

Annex 4: Contribution by number (total) and carbon (total and by survey) of the prey in the sardine diet.

Dietary items	Number	Carbon content (µg)						
	Total	Total	1996/11-12	1997/02-04	1997/09-10	1998/03-05	1998/05-06	1998/08-09
Diatoms								
Asterionellopsis	43035	4.7	0.0	0.0	0.0	4.4	0.3	0.0
Bacteriastrum	167	3.8	0.0	3.3	0.0	0.1	0.4	0.0
Chaetoceros	47266	91.5	6.6	62.8	10.7	8.5	2.6	0.2
Coscinodiscus	4983	10036.1	610.8	8445.8	631.9	43.7	51.3	252.7
Detonula	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ditylum	126	17.7	0.0	0.0	17.4	0.1	0.2	0.0
Eucampia	92	3.5	3.5	0.0	0.0	0.0	0.0	0.0
Fragilariopsis	43	0.9	0.0	0.9	0.0	0.0	0.0	0.0
Grammatophora	16	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Guinardia	280	1.2	0.0	0.0	0.0	1.2	0.0	0.0
Gyrosigma	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hemiaulus	20	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lauderia	334	1.7	0.0	0.0	0.0	1.7	0.0	0.0
Lithodesmium	277	26.3	0.0	25.9	0.4	0.0	0.1	0.0
Navicula	374	4.5	0.0	3.8	0.6	0.0	0.1	0.0
Planktoniella	42	104.0	36.4	67.6	0.0	0.0	0.0	0.0
Pleurosigma	35	1.5	0.0	1.5	0.0	0.0	0.0	0.0
Pseudo-nitzschia	31014	26.9	0.0	25.2	0.0	1.6	0.1	0.1
Rhizosolenia	905	310.3	97.8	0.0	206.1	0.8	2.1	3.5
Skeletonema	391	5.2	0.0	5.2	0.0	0.0	0.0	0.0
Stephanopyxis	105	28.4	0.0	0.0	28.0	0.3	0.0	0.0
Thalassionema	1924	21.0	0.0	6.6	14.0	0.1	0.0	0.2
Thalassiosira	3798	2374.4	4.7	2362.0	7.5	0.1	0.1	0.0
Lioloma	36	44.5	0.0	44.5	0.0	0.0	0.0	0.0
Dinoflagellates								
Ceratium	1195	5955.9	1747.9	3942.0	239.1	0.3	0.1	26.6
Dinophysis	227	1250.4	39.1	1183.4	27.9	0.0	0.0	0.0
Dissodinium	273	860.3	0.0	809.4	44.7	0.6	0.1	5.6
Gonyaulax	85	474.5	39.1	435.4	0.0	0.0	0.0	0.0
Podolampas	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Prorocentrum	119	194.9	0.0	194.9	0.0	0.0	0.0	0.0
Protoperidinium	4023	11553.0	1107.4	9587.8	616.8	43.5	1.4	196.2
Pyrocystis	26	55.9	0.0	0.0	0.0	0.1	0.0	55.8
Scrippsiella	7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diplopsalis	14	78.1	78.1	0.0	0.0	0.0	0.0	0.0
Silicoflagellates								
Dyctiocha	753	575.6	0.0	566.6	6.9	0.8	1.2	0.0
Phytoflagellates								
Tetraselmis	4175	1.1	0.0	0.0	0.0	0.0	1.1	0.0
Tintinnids								
Eutintinnus	3	23.8	0.0	23.8	0.0	0.0	0.0	0.0
Favella	2	15.9	0.0	7.9	7.9	0.0	0.0	0.0
Helicostomella	48	381.0	222.2	158.7	0.0	0.0	0.0	0.0
Tintinnopsis	212	1682.7	0.0	1682.7	0.0	0.0	0.0	0.0
Radiolaria	115	591.7	0.0	591.7	0.0	0.0	0.0	0.0

Copepoda								
Acartia	139	1959.5	0.0	220.2	528.4	572.5	462.4	176.1
Aetideus	24	3830.8	957.7	0.0	159.6	319.2	0.0	2394.3
Calanus	1099	287891.9	8075.0	27033.8	170979.7	55120.8	10883.7	15798.9
Calocalanus	86	1681.7	0.0	262.8	210.2	630.6	315.3	262.8
Candacia	294	20323.8	1844.0	2806.1	10422.5	4890.5	360.8	0.0
Centropages	441	59617.5	16600.3	10534.8	10694.4	18515.8	1197.1	2075.0
Clausocalanus	466	4689.5	500.4	855.6	1033.1	1372.1	314.8	613.4
Clytemnestra	60	244.6	0.0	125.5	0.0	62.7	56.5	0.0
Copilia	6	509.0	0.0	254.5	0.0	254.5	0.0	0.0
Corycaeus	764	16542.1	708.1	5438.5	5863.4	1784.5	566.5	2181.1
Euaetideus	139	1752.2	0.0	0.0	1338.7	0.0	413.4	0.0
Eucalanus	374	782228.5	75056.4	147767.3	215787.2	199368.6	10554.8	133694.2
Euchaeta	374	18720.6	1946.7	1816.9	6618.7	4672.0	616.5	3049.8
Euchirella	148	17147.3	0.0	0.0	0.0	2588.3	8735.4	5823.6
Euterpina	198	851.8	0.0	138.3	611.6	36.4	65.5	0.0
Lucicutia	22	743.3	514.6	0.0	0.0	171.5	57.2	0.0
Macrosetella	20	28.2	0.0	0.0	0.0	0.0	28.2	0.0
Mecynocera	95	3729.2	0.0	0.0	0.0	3729.2	0.0	0.0
Microsetella	119	788.4	0.0	492.8	0.0	197.1	98.6	0.0
Nonocalanus	10	1596.2	0.0	0.0	1596.2	0.0	0.0	0.0
Oithona	546	2828.5	203.9	458.7	1703.6	247.5	127.4	87.4
Oncaea	1044	10939.7	371.1	3083.6	3928.1	934.0	268.7	2354.3
Paracalanus	552	10863.9	1283.1	1967.5	3763.9	2195.6	541.8	1112.1
Phaena	26	741.4	0.0	57.0	0.0	627.3	0.0	57.0
Pleuromamma	8	692.9	0.0	0.0	0.0	692.9	0.0	0.0
Rhincalanus	31	72710.9	0.0	0.0	68019.9	4691.0	0.0	0.0
Saphirina	5	724.7	0.0	0.0	144.9	579.7	0.0	0.0
Scolecithricella	14	3682.7	0.0	0.0	3682.7	0.0	0.0	0.0
Temora	81	7015.1	0.0	259.8	6062.4	0.0	0.0	692.9
Harpacticoida	177	1092.8	0.0	738.9	0.0	208.2	83.3	62.4
Copepodite	609	2737.5	0.0	715.8	1062.0	306.8	228.1	424.8
Copepods remains	1192	783.6	101.3	143.7	262.6	107.1	68.9	100.1
Other zooplankters								
Euphausiacea	2614	949766.9	6903.4	377145.4	164592.4	239440.1	3270.0	158415.6
Amphipoda	2	4521.1	0.0	0.0	0.0	4521.1	0.0	0.0
Bivalvia	4	1819.9	0.0	0.0	0.0	1819.9	0.0	0.0
Gastropoda	465	105101.6	0.0	1819.9	910.0	88722.1	11829.6	1819.9
Apendicularia	3	1122.9	0.0	0.0	0.0	1122.9	0.0	0.0
Zoea	29	2625.6	0.0	633.8	1358.1	633.8	0.0	0.0
Megalopa	8	1944.8	0.0	0.0	0.0	1944.8	0.0	0.0
Anchovy eggs	60	721.4	0.0	312.6	108.2	276.5	24.0	0.0
White anchovy eggs	16	192.4	0.0	0.0	0.0	192.4	0.0	0.0
Engraulidae eggs	80	961.9	0.0	0.0	0.0	961.9	0.0	0.0
Unidentified fish eggs	326	3919.7	0.0	396.8	709.4	2308.5	408.8	96.2
Cirriped larvae	25	1.0	0.0	0.3	0.6	0.0	0.1	0.0
Unidentified fish larvae	3	836.6	0.0	0.0	836.6	0.0	0.0	0.0
Chaetognata	75	2208.0	0.0	0.0	0.0	0.0	2208.0	0.0
Unidentified fish	1	278.9	0.0	0.0	278.9	0.0	0.0	0.0
Unidentified decapoda	16	3889.6	0.0	0.0	0.0	2431.0	0.0	1458.6
Myctophidae	2	557.8	0.0	557.8	0.0	0.0	0.0	0.0
Polychaeta	2	222.5	0.0	222.5	0.0	0.0	0.0	0.0

Annex 5

Publications and manuscripts

Article 1.
Revisiting Peruvian anchovy (*Engraulis ringens*) trophodynamics provides a new vision of the Humboldt Current system.
Espinoza P., Bertrand A. 2008. Progress in Oceanography, 79: 215-227

Article 2.
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.
Espinoza P., Bertrand A., van der Lingen C.D., Garrido S., Rojas de Mendiola B. 2009. Progress in Oceanography, 83: 242–250.

Article 3.
Trophic dynamics
van der Lingen C.D., Bertrand A., Bode A., Brodeur R., Cubillos L., Espinoza P., Friedland K., Garrido S., Irigoien X., Möllman C., Rodriguez-Sanchez R., Tanaka H. & Temming A. 2009. Climate Change and Small Pelagic Fish. Chapter 7, 112-157 Published by Cambridge University.

Article 4.
Long term changes in size distribution of zooplankton in the Humboldt Current Ecosystem off Peru: Evidence for alternating conditions favoring sardine or anchovy energetics.
Ayón P., Swartzman G., Espinoza P., Bertrand A. 2011. Marine Ecology Progress Series, 422: 211–222.

Article 5
Tracking habitat and resource use for *Dosidicus gigas*: a stable isotope analysis in the Northern Humboldt Current System.
Argüelles J., Lorrain A., Cherel Y., Graco M., Tafur R., Alegre A., Espinoza P., Taipe A., Ayón P., Bertrand A. 2012. Marine Biology, 159:2105–2116.

Article 6
Ecología trófica del jurel *Trachurus murphyi* en el Perú entre 1977 – 2011.
Alegre A., Espinoza P., Espino M. 2013. Revista Peruana de Biología, 20:75–82.

Article 7
Comprehensive model of jumbo squid Dosidicus gigas trophic ecology in the northern Humboldt Current system.
Alegre A, Ménard F, Tafur R, Espinoza P, Arguelles J, Maehara V, Simier M, Bertrand A. 2014. PLoS ONE, 9(1): e85919. doi:10.1371/journal.pone.0085919.

Article 8
Ontogenetic and spatiotemporal variability in anchoveta *Engraulis ringens* diet off Peru.
Espinoza P. & Bertrand A. Journal of Fish Biology, 84: 422 435.

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Revisiting Peruvian anchovy (*Engraulis ringens*) trophodynamics provides a new vision of the Humboldt Current system

Pepe Espinoza [a,*], Arnaud Bertrand [a,b]

[a] *Instituto del Mar del Perú, Esquina Gamarra y Gral. Valle s/n, Apartado 22, Callao, Lima, Peru*
[b] *Institut de Recherche pour le Développement (IRD), CRH, Avenue Jean Monnet, BP 171, 34203 Sète Cedex, France*

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A B S T R A C T

The Peruvian anchovy or anchoveta (*Engraulis ringens*) forages on plankton and is a main prey for marine mammals, seabirds, fish, and fishers, and is therefore a key element of the food web in the Humboldt Current system (HCS). Here, we present results from the analysis of 21,203 anchoveta stomach contents sampled during 23 acoustic surveys over the period 1996–2003. Prey items were identified to the genus level, and the relative dietary importance of different prey was assessed by determination of their carbon content. Variability in stomach fullness was examined relative to the diel cycle, the distance from the coast, sea surface temperature, and latitude, using generalized additive models (GAMs). Whereas phytoplankton largely dominated anchoveta diets in terms of numerical abundance and comprised >99% of ingested prey items, the carbon content of prey items indicated that zooplankton was by far the most important dietary component, with euphausiids contributing 67.5% of dietary carbon followed by copepods (26.3%). Stomach fullness data showed that anchoveta feed mainly during daytime between 07h00 and 18h00, although night-time feeding also made a substantial contribution to total food consumption. Stomach fullness also varied with latitude, distance from the coast, and temperature, but with substantial variability indicating a high degree of plasticity in anchoveta feeding behaviour. The results suggest an ecological role for anchoveta that challenges current understanding of its position in the foodweb, the functioning of the HCS, and trophic models of the HCS.

1. Introduction

The Peruvian anchovy or anchoveta *Engraulis ringens*, is ecologically and economically the most important pelagic fish species in the Humboldt Current system (HCS). Anchoveta is the major prey of the principal top predators including marine mammals, seabirds, fish and fishers, and more than 250 million tons of anchoveta have been harvested by the purse seine fishery since the 1950s. Anchoveta forage on plankton and is a key element of the marine food web in the HCS and have been the subject of many studies (e.g. the books edited by Pauly and Tsukayama, 1987; Pauly et al., 1989a).

The first trophodynamic studies on anchoveta in Peru concluded that anchoveta subsisted mainly on phytoplankton (Rojas, 1953; Rojas de Mendiola, 1969), and the ability of clupeoids like anchoveta to feed at low trophic levels (directly on primary producers) was suggested as the reason such large populations, biomasses and fisheries could be sustained in upwelling systems (Ryther, 1969). Later studies suggested that in addition to filter-feeding on phytoplankton, anchoveta could also particulate feed on zooplankton (Rojas de Mendiola, 1989; Alamo, 1989), and zooplankton was sometimes considered equally important as phytoplankton in anchoveta diets (Alamo, 1989; Pauly et al., 1989b; Jahncke et al., 2004). With the exception of Konchina (1991), who suggested that anchoveta preferentially consume zooplankton, all other recent work in the HCS has concluded that anchoveta depends mainly on phytoplankton (Alamo et al., 1996a,b, 1997a,b; Alamo and Espinoza, 1998; Espinoza et al., 1998a,b, 1999, 2000). However, these studies were based on counts of anchoveta prey, a method considered to be inadequate for estimating dietary importance (James, 1987; Konchina and Pavlov, 1995). In contrast, methods based on prey weight (e.g. gravimetric) or on nutritional value (e.g. carbon content, caloric or energetic value) may be more ecologically relevant (Hyslop, 1980; Koslow, 1981; James, 1987; Konchina and Pavlov, 1995; van der Lingen et al. 2006, in press). In other upwelling systems, these latter methods indicate that zooplankton, rather than phytoplankton, support clupeoid populations (e.g. Koslow, 1981; James, 1987; James and Chiappa-Carrara, 1990; Chiappa-Carrara and Gallardo-Cabello, 1993; van der Lingen et al., 2006).

Konchina (1991) results highlighting the significance of zooplankton in the diet of anchoveta were based on gravimetric analysis of prey importance, but his study was based on a very small sample size ($n = 65$ fish). Here we revisit Peruvian anchoveta diet

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* Corresponding author. Tel.: +56 1 4202000.
E-mail addresses: pespinoza@imarpe.gob.pe (P. Espinoza), Arnaud.Bertrand@ird.fr (A. Bertrand).

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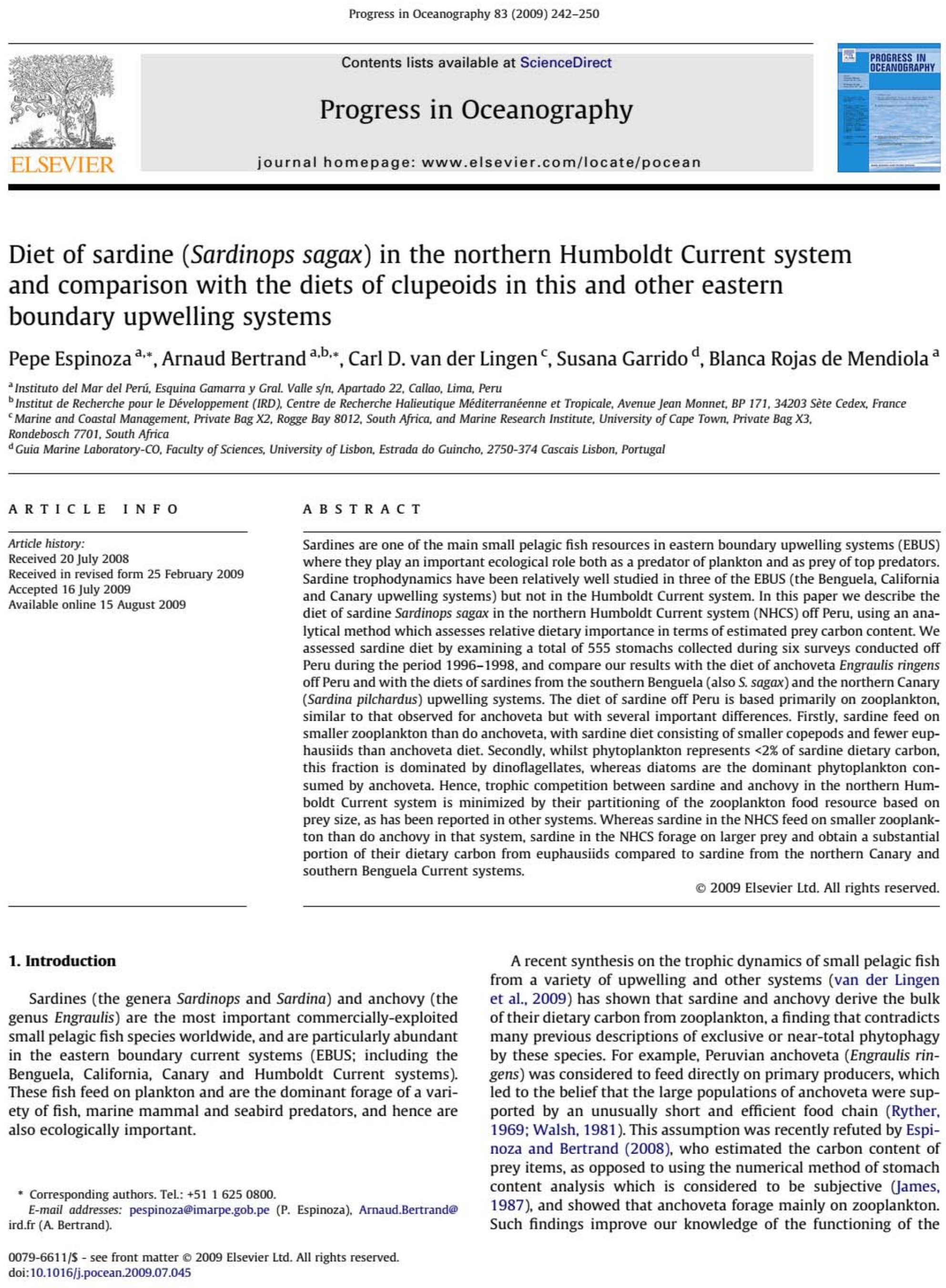

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Diet of sardine (*Sardinops sagax*) in the northern Humboldt Current system and comparison with the diets of clupeoids in this and other eastern boundary upwelling systems

Pepe Espinoza [a,*], Arnaud Bertrand [a,b,*], Carl D. van der Lingen [c], Susana Garrido [d], Blanca Rojas de Mendiola [a]

[a] *Instituto del Mar del Perú, Esquina Gamarra y Gral. Valle s/n, Apartado 22, Callao, Lima, Peru*
[b] *Institut de Recherche pour le Développement (IRD), Centre de Recherche Halieutique Méditerranéenne et Tropicale, Avenue Jean Monnet, BP 171, 34203 Sète Cedex, France*
[c] *Marine and Coastal Management, Private Bag X2, Rogge Bay 8012, South Africa, and Marine Research Institute, University of Cape Town, Private Bag X3, Rondebosch 7701, South Africa*
[d] *Guia Marine Laboratory-CO, Faculty of Sciences, University of Lisbon, Estrada do Guincho, 2750-374 Cascais Lisbon, Portugal*

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ABSTRACT

Sardines are one of the main small pelagic fish resources in eastern boundary upwelling systems (EBUS) where they play an important ecological role both as a predator of plankton and as prey of top predators. Sardine trophodynamics have been relatively well studied in three of the EBUS (the Benguela, California and Canary upwelling systems) but not in the Humboldt Current system. In this paper we describe the diet of sardine *Sardinops sagax* in the northern Humboldt Current system (NHCS) off Peru, using an analytical method which assesses relative dietary importance in terms of estimated prey carbon content. We assessed sardine diet by examining a total of 555 stomachs collected during six surveys conducted off Peru during the period 1996–1998, and compare our results with the diet of anchoveta *Engraulis ringens* off Peru and with the diets of sardines from the southern Benguela (also *S. sagax*) and the northern Canary (*Sardina pilchardus*) upwelling systems. The diet of sardine off Peru is based primarily on zooplankton, similar to that observed for anchoveta but with several important differences. Firstly, sardine feed on smaller zooplankton than do anchoveta, with sardine diet consisting of smaller copepods and fewer euphausiids than anchoveta diet. Secondly, whilst phytoplankton represents <2% of sardine dietary carbon, this fraction is dominated by dinoflagellates, whereas diatoms are the dominant phytoplankton consumed by anchoveta. Hence, trophic competition between sardine and anchovy in the northern Humboldt Current system is minimized by their partitioning of the zooplankton food resource based on prey size, as has been reported in other systems. Whereas sardine in the NHCS feed on smaller zooplankton than do anchovy in that system, sardine in the NHCS forage on larger prey and obtain a substantial portion of their dietary carbon from euphausiids compared to sardine from the northern Canary and southern Benguela Current systems.

1. Introduction

Sardines (the genera *Sardinops* and *Sardina*) and anchovy (the genus *Engraulis*) are the most important commercially-exploited small pelagic fish species worldwide, and are particularly abundant in the eastern boundary current systems (EBUS; including the Benguela, California, Canary and Humboldt Current systems). These fish feed on plankton and are the dominant forage of a variety of fish, marine mammal and seabird predators, and hence are also ecologically important.

A recent synthesis on the trophic dynamics of small pelagic fish from a variety of upwelling and other systems (van der Lingen et al., 2009) has shown that sardine and anchovy derive the bulk of their dietary carbon from zooplankton, a finding that contradicts many previous descriptions of exclusive or near-total phytophagy by these species. For example, Peruvian anchoveta (*Engraulis ringens*) was considered to feed directly on primary producers, which led to the belief that the large populations of anchoveta were supported by an unusually short and efficient food chain (Ryther, 1969; Walsh, 1981). This assumption was recently refuted by Espinoza and Bertrand (2008), who estimated the carbon content of prey items, as opposed to using the numerical method of stomach content analysis which is considered to be subjective (James, 1987), and showed that anchoveta forage mainly on zooplankton. Such findings improve our knowledge of the functioning of the

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* Corresponding authors. Tel.: +51 1 625 0800.
E-mail addresses: pespinoza@imarpe.gob.pe (P. Espinoza), Arnaud.Bertrand@ird.fr (A. Bertrand).

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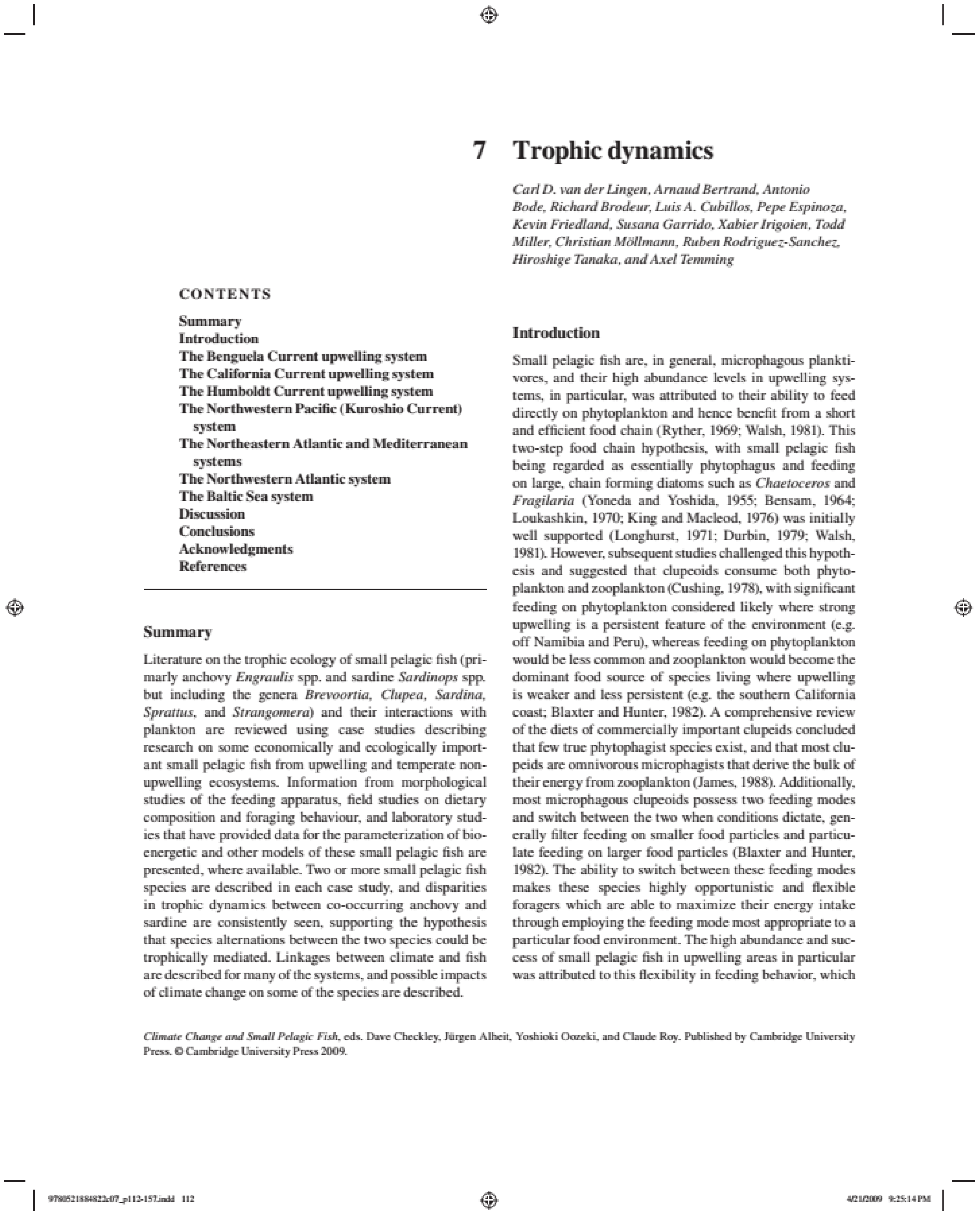

7 Trophic dynamics

Carl D. van der Lingen, Arnaud Bertrand, Antonio Bode, Richard Brodeur, Luis A. Cubillos, Pepe Espinoza, Kevin Friedland, Susana Garrido, Xabier Irigoien, Todd Miller, Christian Möllmann, Ruben Rodriguez-Sanchez, Hiroshige Tanaka, and Axel Temming

CONTENTS

Summary

Literature on the trophic ecology of small pelagic fish (primarly anchovy *Engraulis* spp. and sardine *Sardinops* spp. but including the genera *Brevoortia, Clupea, Sardina, Sprattus*, and *Strangomera*) and their interactions with plankton are reviewed using case studies describing research on some economically and ecologically important small pelagic fish from upwelling and temperate non-upwelling ecosystems. Information from morphological studies of the feeding apparatus, field studies on dietary composition and foraging behaviour, and laboratory studies that have provided data for the parameterization of bioenergetic and other models of these small pelagic fish are presented, where available. Two or more small pelagic fish species are described in each case study, and disparities in trophic dynamics between co-occurring anchovy and sardine are consistently seen, supporting the hypothesis that species alternations between the two species could be trophically mediated. Linkages between climate and fish are described for many of the systems, and possible impacts of climate change on some of the species are described.

Introduction

Small pelagic fish are, in general, microphagous planktivores, and their high abundance levels in upwelling systems, in particular, was attributed to their ability to feed directly on phytoplankton and hence benefit from a short and efficient food chain (Ryther, 1969; Walsh, 1981). This two-step food chain hypothesis, with small pelagic fish being regarded as essentially phytophagus and feeding on large, chain forming diatoms such as *Chaetoceros* and *Fragilaria* (Yoneda and Yoshida, 1955; Bensam, 1964; Loukashkin, 1970; King and Macleod, 1976) was initially well supported (Longhurst, 1971; Durbin, 1979; Walsh, 1981). However, subsequent studies challenged this hypothesis and suggested that clupeoids consume both phytoplankton and zooplankton (Cushing, 1978), with significant feeding on phytoplankton considered likely where strong upwelling is a persistent feature of the environment (e.g. off Namibia and Peru), whereas feeding on phytoplankton would be less common and zooplankton would become the dominant food source of species living where upwelling is weaker and less persistent (e.g. the southern California coast; Blaxter and Hunter, 1982). A comprehensive review of the diets of commercially important clupeids concluded that few true phytophagist species exist, and that most clupeids are omnivorous microphagists that derive the bulk of their energy from zooplankton (James, 1988). Additionally, most microphagous clupeoids possess two feeding modes and switch between the two when conditions dictate, generally filter feeding on smaller food particles and particulate feeding on larger food particles (Blaxter and Hunter, 1982). The ability to switch between these feeding modes makes these species highly opportunistic and flexible foragers which are able to maximize their energy intake through employing the feeding mode most appropriate to a particular food environment. The high abundance and success of small pelagic fish in upwelling areas in particular was attributed to this flexibility in feeding behavior, which

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Long-term changes in zooplankton size distribution in the Peruvian Humboldt Current System: conditions favouring sardine or anchovy

Patricia Ayón[1], Gordon Swartzman[2,*], Pepe Espinoza[1], Arnaud Bertrand[1,3]

[1]Instituto del Mar del Perú (IMARPE), Gamarra y General Valle s/n Chucuito, La Punta Callao, Peru
[2]School of Aquatic and Fisheries Science, University of Washington, Box 355020, Seattle, Washington 98195, USA
[3]Institut de Recherche pour le Développement (IRD), UMR 212 EME,
Centre de Recherche Halieutique Méditerranéenne et Tropicale, Avenue Jean Monnet, BP 171, 34203 Sète Cedex, France

ABSTRACT: Changes in the size distribution of zooplankton in the Humboldt Current System have been hypothesized to underlie observed changes in sardine and anchovy populations, the dominant pelagic fish species. To examine this hypothesis, the size distribution of over 15 000 zooplankton data samples collected since the 1960s was qualitatively determined. Dominance of each size group of zooplankton (small, medium and large) and of euphausiids was modelled using generalized additive models as a function of year, latitude, time of day, distance from the 200 m isobath (a surrogate for on-shelf versus off-shelf), sea surface temperature and salinity. The temporal (yr) pattern for euphausiid dominance was highly cross-correlated (i.e. was in phase) with the time series for estimated biomass of anchovy, and small zooplankton dominance with that for estimated sardine biomass. This supports the focal hypothesis based on feeding-energetic experiments, which showed energetic advantages to sardine filter feeding on smaller zooplankton and to anchovy bite feeding on larger copepods and euphausiids. Although euphausiids predominate offshore from the shelf break, anchovy biomass is generally highest on the shelf, suggesting a possible mismatch between anchovy feeding and euphausiid dominance. However, evidence concerning the offshore expansion of the anchovy range in cooler conditions, where both anchovy and euphausiids predominate, somewhat alleviates this apparent contradiction. A strong diel component to euphausiids and large zooplankton indicated diel migration for these zooplankton groups. That anchovy will preferentially eat euphausiids when they are more available (i.e. during the night and offshore) is supported by anchovy diet data.

KEY WORDS: Anchovy · Sardine · Abundance · Zooplankton size dominance · Feeding energetics · Euphausiids · Humboldt Current System

INTRODUCTION

The Humboldt Current System (HCS) off the coasts of Peru and Chile is one of the 4 major upwelling systems of the world. With <0.1% of the world ocean surface, the Peruvian landings represent 8% of the world's fish catches on average since 1970, and the landings of Peruvian anchovy *Engraulis ringens* alone reached 15% of the annual global fish catches in some years. The HCS has been dominated for long time periods by 2 pelagic clupeid fish species (Chavez et al. 2003, Alheit & Ñiquen 2004, Gutiérrez et al. 2007, Swartzman et al. 2008, Barange et al. 2009): the Peruvian anchovy and Pacific sardine *Sardinops sagax*. During the last 50 yr, both species showed high levels of biomass, but with apparent different periods of high and low biomass (Chavez et al. 2003). When looking farther in the past, paleostudies show that while anchovy scale deposition rates fluctuated over periods of 25 to 40 yr, only 2 peak periods of sardine occurred

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[*]Corresponding author. Email: gordie@apl.washington.edu

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ORIGINAL PAPER

Tracking habitat and resource use for the jumbo squid *Dosidicus gigas*: a stable isotope analysis in the Northern Humboldt Current System

Juan Argüelles · Anne Lorrain · Yves Cherel · Michelle Graco · Ricardo Tafur · Ana Alegre · Pepe Espinoza · Anatolio Taipe · Patricia Ayón · Arnaud Bertrand

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Abstract To determine the habitat and resource use of *Dosidicus gigas* in the Northern Humboldt Current System, we analysed carbon and nitrogen stable isotopes of 234 individuals collected during 2008–2010. Large variations in mantle stable isotope ratios were recorded, with values ranging from −19.1 to −15.1 ‰ (δ^{13}C) and from 7.4 to 20.5 ‰ (δ^{15}N). Most of the variation was explained by latitude, followed by distance to shelf break for carbon and by squid size for nitrogen. Latitudinal variations with increasing values from north to south were also found in zooplankton samples and were related to changes in isotope baseline values probably due to oxygen minimum zones that occur off Peru. This similar latitudinal trend in both zooplankton and *D. gigas* samples reveals that *D. gigas* is a relatively resident species at the scale of its isotopic turnover rate (i.e. a few weeks), even if this is not necessarily the case at the scale of its life. A small but significant size effect on δ^{13}C values suggests that jumbo squid perform offshore–onshore ontogenic migration, with juveniles distributed offshore. For nitrogen, the high inter-individual variability observed with mantle length indicates that *D. gigas* can prey on a high variety of resources at any stage of their life cycle. This large-scale study off the coast of Peru provides further evidence that *D. gigas* have the capability to explore a wide range of habitats and resources at any stage of their life.

Introduction

Cephalopods, and particularly squid, are a central component in marine food webs worldwide. They are a valuable prey source for fish, marine mammals and birds and are a voracious predator of a wide variety of prey, including fish, crustaceans and other squid (Clarke 1996; Croxall and Prince 1996; Klages 1996; Smale 1996). Because of their high feeding rates and generalist feeding strategy, squid can potentially exert trophodynamic control on the recruitment of the early life stages of fish (Dawe 1988; Rodhouse and Nigmatullin 1996; Hunsicker and Essington 2008). Determining and quantifying their trophic relationships is therefore a key issue in understanding the structure and functioning of marine ecosystems. The trophic role of cephalopods has been examined mainly by stomach contents analysis. 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). Additionally, stomach content analysis is time-consuming and represents the last feeding events only, with no indication of long-term dietary habits (Jackson et al. 2007).

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J. Argüelles (✉) · M. Graco · R. Tafur · A. Alegre ·
P. Espinoza · A. Taipe · P. Ayón
Instituto del Mar del Perú Esq. Gamarra y Gral Valle
s/n Chucuito, Callao, Lima, Peru
e-mail: jarguelles@imarpe.gob.pe

A. Lorrain
IRD, UMR 6539 CNRS/IRD/UBO LEMAR, BP 70,
29280 Plouzané, France

Y. Cherel
Centre d'Etudes Biologiques de Chizé, UPR 1934 du CNRS,
BP 14, 79360 Villiers-en-Bois, France

A. Bertrand
IRD, UMR212 EME, IFREMER/IRD/UM2, Av. Jean
Monnet, BP 171, 34203 Sète, France

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Ecología, pesquería y conservación del jurel (*Trachurus murphyi*) en el Perú.
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Facultad de Ciencias Biológicas **UNMSM**

Ecología del jurel (*Trachurus murphyi*) en el Perú

Ecología trófica del jurel *Trachurus murphyi* en el Perú entre 1977 – 2011

Trophic ecology of Jack mackerel *Trachurus murphyi* in Peru, 1977 – 2011

Ana Alegre, Pepe Espinoza y Marco Espino

Instituto del Mar del Perú, esquina Gamarra y General Valle S/N Chucuito, Callao, Perú.
Email Ana Alegre: palegre@imarpe.gob.pe

Resumen

Se analizó la variabilidad espacio-temporal de la dieta de jurel *Trachurus murphyi* frente a Perú de 1977 a 2011. Un total de 21058 estómagos fueron analizados utilizando métodos bivariados y el Modelo de Árbol de Regresión Multivariado (ARM). Se utilizó como variable respuesta la composición gravimétrica de la dieta, con respecto a diferentes variables predictivas como años, profundidad de la isoterma de 15 °C, Índice de Oscilación del Sur (IOS), Índice de Oscilación Decadal del Pacífico (PDO), anomalía de la temperatura superficial del mar, zona (norte, centro y sur) y distancia de la costa. Nuestros resultados nos permitieron identificar dos escenarios diferentes, uno desde el año 1977 al 2000, donde la dieta del jurel *T. murphyi* estuvo fuertemente dominada por Euphausiidae, y otro escenario después del 2000, donde el jurel *T. murphyi* consumió mayor diversidad de presas, principalmente Euphausiidae, camaroncito rojo *Pleuroncodes monodon* y Zoeas. Se destaca que el primer escenario corresponde a condiciones cálidas y el segundo a condiciones frías, ambas coincidentes con los periodos multidecadales. A diferencia de estudios anteriores que muestran que la anchoveta *Engraulis ringens* es una presa abundante, en este estudio no fue significativamente importante. Espacialmente, los Euphausiidae dominaron la dieta en el norte-centro de Perú, mientras que al sur, la composición de las presas fue más diversa. La dieta también varió significativamente según la distancia a la costa, con mayor proporción de *P. monodon* cerca a la costa y con respecto a su etapas de desarrollo ontogenético.

Palabras clave: Jurel, alimentación, Perú.

Abstract

We analyzed the spatiotemporal variability of Jack mackerel *Trachurus murphyi* diet off Peru from 1977 to 2011. A total of 21058 stomachs were analyzed using bivariate methods and the Multivariate Regression Tree Model (MRT). The gravimetric composition of the diet was used as response variable with respect to different predictor variables such as years, depth of the 15°C isotherm, Southern Oscillation Index (SOI), Index of the Pacific Decadal Oscillation (PDO), sea surface temperature anomaly, zone (north, center and south) and distance to the coast. Our results allowed us to identify two different scenarios. From 1977 to 2000 the Jack mackerel *T. murphy* diet was strongly dominated by Euphausiidae, and since 2000 when *T. murphyi* consumed a greater diversity of prey, mainly Euphausiidae, squat lobster *Pleuroncodes monodon* and Zoea. It is noted that the first scenario corresponds to warm conditions and the second to cold conditions, both coincident with observed multidecadal periods. In contrast to previous studies showing that the anchovy *Engraulis ringens* is an abundant prey, in this study anchovy was not significantly important. Spatially, the Euphausiidae dominated the diet in central-northern Peru, while further south the prey composition was more diverse. The diet also varied significantly according to the distance from the coast (higher proportion of *P. monodon* closer to the coast) and the ontogenic stages.

Keywords: Jack mackerel, food, Peru.

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Introducción

El jurel *Trachurus murphyi* Nichols 1920 es uno de los componentes de la red trófica marina peruana que se asocia principalmente con el subsistema pelágico oceánico, y junto a la anchoveta *Engraulis ringens*, sardina *Sardinops sagax sagax* y caballa *Scomber japonicus* han posibilitado el desarrollo de una de las principales actividades pesqueras del ámbito mundial, localizada frente al Perú.

Cada vez con mayor frecuencia se recomienda que los administradores pesqueros deban tener en cuenta las más amplias consideraciones ecológicas en el manejo de los

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Comprehensive Model of Jumbo Squid *Dosidicus gigas* Trophic Ecology in the Northern Humboldt Current System

Ana Alegre[1,2], Frédéric Ménard[2], Ricardo Tafur[1], Pepe Espinoza[1], Juan Argüelles[1], Víctor Maehara[3], Oswaldo Flores[1], Monique Simier[2], Arnaud Bertrand[2]*

1 Instituto del Mar del Perú (IMARPE), Callao, Peru, **2** Institut de Recherche pour le Développement (IRD), UMR212 EME IFREMER/IRD/UM2, Sète, France, **3** Universidad Nacional Agraria La Molina, La Molina, Lima, Peru

Abstract

The jumbo squid *Dosidicus gigas* plays an important role in marine food webs both as predator and prey. We investigated the ontogenetic and spatiotemporal variability of the diet composition of jumbo squid in the northern Humboldt Current system. For that purpose we applied several statistical methods to 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. Our results evidenced a large variability in prey composition as already observed in other systems. However, our data 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, multinomial model predictions showed that stomach fullness increased with the number of prey taxa, while most stomachs with low contents contained one or two prey taxa only. Our results therefore question the common hypothesis that predators seek locally dense aggregations of monospecific prey. In addition *D. gigas* consumes very few anchovy *Engraulis ringens* in Peru, whereas a tremendous biomass of anchovy is potentially available. It seems that *D. gigas* cannot reach the oxygen unsaturated waters very close to the coast, where the bulk of anchovy occurs. Indeed, even if jumbo squid can forage in hypoxic deep waters during the day, surface normoxic waters are then required to recover its maintenance respiration (or energy?). Oxygen concentration could thus limit the co-occurrence of both species and then preclude predator-prey interactions. Finally we propose a conceptual model illustrating the opportunistic foraging behaviour of jumbo squid impacted by ontogenetic migration and potentially constrained by oxygen saturation in surface waters.

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* E mail: Arnaud.Bertrand@ird.fr

Introduction

The ommastrephid jumbo squid *Dosidicus gigas* is the most abundant nektonic squid in the surface waters of the world ocean [1,2] and supports the largest cephalopod fishery. This squid, endemic to the Eastern Tropical Pacific, is mainly distributed in the oceanic domain [3] over a wide bathymetric range [4]. *D. gigas* is a large squid with high fecundity [2], a rapid growth rate and a short life span (up to ~32 months [5,6]). The tolerance of this species to a wide range of environmental factors (temperature and oxygen) facilitates its geographic expansion [7 9], such as the recent invasion into California waters [4,10].

D. gigas plays an important role in marine food webs both as predator and prey [11]. This abundant and voracious squid forages on a large variety of prey using prehensile arms and tentacles coupled with an efficient sensory system [12,13]. The impact on exploited marine resources can be strong [4] 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 [2,7,14,15]. In addition, its presence within anoxic or hypoxic waters was validated by tagging experiments in the Californian Current System [15,16]. Indeed, the eastern tropical Pacific is characterised by the presence of an oxygen minimum zone (OMZ) [17] and *D. gigas* is a part-time resident of the OMZ thanks to adapted behavior and specific metabolic characteristics [18,19]. Jumbo squid vertical migrations impact the vertical energy flow, providing an efficient energy transport from the surface to deeper waters [7,15].

Previous studies showed that the feeding ecology of jumbo squid is highly variable in time and space [20,21]. The feeding ecology of jumbo squid was investigated in the eastern Pacific from stomach content [22 25] and stable isotopes [26 29]. By investigating stable isotope signatures along gladius, [28] 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, were confirmed by [29] who analysed carbon and nitrogen stable isotopes of individuals collected during 2008 2010. Here, we used an

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Ontogenetic and spatiotemporal variability in anchoveta *Engraulis ringens* diet off Peru

P. Espinoza*† and A. Bertrand‡

**Instituto del Mar del Perú, Esquina Gamarra y Gral. Valle s/n, Apartado 22, Callao, Lima, Peru and ‡Institut de Recherche pour le Développement (IRD), UMR212 EME IFREMER/IRD/UM2, Avenue Jean Monnet, BP 171, 34203 Sète Cedex, France*

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In this study, historical data available since 1954 were used to get new insight to ontogenetic and spatiotemporal variability in Peruvian anchovy or anchoveta *Engraulis ringens* diet. Whatever the period, *E. ringens* foraged mainly on macrozooplankton and the importance of euphausiids in *E. ringens* diet appears directly related to euphausiids abundance. This bottom-up effect is also observed at smaller scale because the euphausiids fraction increased with *E. ringens* total length and euphausiids accessibility. Selecting the largest prey, the euphausiids, provides an energetic advantage for *E. ringens* in its ecosystem where oxygen depletion imposes strong metabolic constraints on pelagic fishes. This study illustrates the plasticity of *E. ringens* that allows it to cope with its highly variable environment.

Key words: euphausiids; Humboldt Current system; oxygen; Peruvian anchovy; spatiotemporal variability; trophic ecology.

INTRODUCTION

The Peruvian anchovy, or anchoveta, *Engraulis ringens* Jenyns 1842 is the dominant pelagic nekton species in the coastal Northern Humboldt Current system (NHCS) off Peru. This fish has great ecological importance in channelling energy flow from primary and secondary production to higher trophic levels (Pauly *et al.*, 1989). For decades *E. ringens* was considered to depend mainly on phytoplankton (Ryther, 1969; Rojas de Mendiola, 1989; Alamo & Espinoza, 1998). These studies were based on counts of *E. ringens* prey, a method considered to be inadequate for estimating dietary importance (James, 1987; Konchina & Pavlov, 1995). By applying an analytical method based on the estimation of prey carbon content, Espinoza & Bertrand (2008) showed that *E. ringens* forage mainly on macrozooplankton, in particular euphausiids and large copepods. Such trophic behaviour is common for *Engraulis* spp. (van der Lingen *et al.*, 2009).

Engraulis ringens diet may have changed over time. Indeed, the *E. ringens* population was assumed to be dominated by individuals with higher affinity for

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†Author to whom correspondence should be addressed. Tel.: +51 1 6250800; email: pespinoza@imarpe.gob.pe

Utilisation de contenus stomacaux et d'isotopes stables pour une nouvelle vision des dynamiques trophiques dans le nord du système du Courant de Humboldt

RÉSUMÉ

Le nord du système du Courant de Humboldt (NHCS), le long des côtes péruviennes, est l'une des régions océaniques les plus productives au monde avec l'anchois *Engraulis ringens* comme espèce emblématique. Comparé aux autres systèmes d'upwelling de bord Est, la forte productivité en poissons ne peut être expliquée par une productivité primaire plus élevée. Par contre, le NHCS est la région où *El Niño*, et la variabilité climatique en général est la plus notable. D'autre part, les eaux de surface oxygénées recouvrent une zone de minimum d'oxygène extrêmement intense et superficielle. L'objectif principal de ce travail est de mieux comprendre les relations trophiques au sein du NHCS en combinant l'analyse de contenus stomacaux et d'isotopes stables.

Les analyses des contenus stomacaux d'anchois et de sardine (*Sardinops sagax*) ont permis de revisiter l'écologie de ces espèces. En effet, bien que le phytoplancton domine largement les contenus stomacaux en termes d'abondance numérique, le zooplancton est de loin la composante alimentaire la plus importante pour ces deux espèces en termes de carbone. Dans le cas de l'anchois, les euphausiacés contribuent à plus de 67,5 % du carbone ingéré, suivis par les copépodes (26,3 %). Sélectionner les proies les plus grandes telles que les euphausiacés procure à l'anchois un avantage énergétique dans cet écosystème où les carences en oxygène imposent de fortes contraintes métaboliques. La sardine se nourrit de zooplancton plus petit que l'anchois. Ainsi, la compétition trophique entre les sardines et les anchois est minimisée dans le NHCS. Ces résultats remettent en question la compréhension première de la position des petits poissons pélagiques (zooplanctonophage et non phytoplanctonophage) dans la chaîne trophique ce qui implique de reconsidérer le fonctionnement et les modèles trophiques du NHCS.

Afin d'obtenir une compréhension plus globale de la position trophique relative des principaux composants du NHCS, une approche basée sur des analyses d'isotopes stables (δ^{13}C et δ^{15}N) a été utilisée. Pour ce faire, la signature isotopique d'échantillons de 13 groupes taxonomiques (zooplancton, poissons, calmars et prédateurs supérieurs) prélevés entre 2008 et 2011 a été déterminée. Les valeurs de δ^{15}N obtenues sont fortement impactées par l'espèce, la taille et la latitude. Le long de la côte péruvienne, la zone de minimum d'oxygène devient en effet plus intense et plus superficielle au sud de ~7,5° S impactant fortement la valeur de δ^{15}N de la ligne de base. Nous avons donc utilisé un modèle linéaire à effet mixte afin de prédire la position trophique relative des composants-clés de l'écosystème. Ces analyses isotopiques confirment les résultats issus des contenus stomacaux sur le régime alimentaire de l'anchois et mettent en évidence l'importance potentielle d'une composante souvent négligée de l'écosystème, la galathée pélagique *Pleuroncodes monodon*. En effet, nos résultats supportent l'hypothèse selon laquelle cette espèce s'alimenterait en partie d'œufs et de larves de poissons, donc des premiers stades de vie des espèces exploitées.

MOTS CLÉS

Système Nord du Courant de Humboldt **Écologie trophique** **Zone de minimum d'oxygène** **Anchois *Engraulis ringens*** **Sardine *Sardinops sagax***
Calmar géant *Dosidicus gigas* ***Pleuroncodes monodon*** **Isotopes stables** **Contenus stomacaux**

Trophic dynamics in the northern Humboldt Current system: insights from stable isotope and stomach content analyses

ABSTRACT

The northern Humboldt Current system (NHCS) off Peru is one of the most productive world marine regions, with the Peruvian anchovy or anchoveta Engraulis ringens as emblematic fish resource. Compared with other eastern boundary upwelling systems, this higher fish productivity cannot be explained by a corresponding higher primary productivity. On another hand, the NHCS is the region where El Niño, and climate variability in general, is most notable. Also, surface oxygenated waters overlie an intense and extremely shallow Oxygen Minimum Zone (OMZ). In this context, the main objective of this study is to better understand the trophic flows in the NHCS using both stomach content and stable isotope analyses. The study focuses on a variety of organisms from low trophic levels to top predators.

Revisiting anchovy and sardine (Sardinops sagax) trophodynamics we show that whereas phytoplankton largely dominated their diets in terms of numerical abundance, the carbon content of prey items indicated that zooplankton was by far the most important dietary component. Indeed for anchovy euphausiids contributed 67.5% of dietary carbon, followed by copepods (26.3%). Selecting the largest prey, the euphausiids, provide an energetic advantage for anchoveta in its ecosystem where oxygen depletion imposes strong metabolic constrain. Sardine feed on smaller zooplankton than do anchoveta, with sardine diet consisting of smaller copepods and fewer euphausiids than anchoveta diet. Hence, trophic competition between sardine and anchovy is minimized by their partitioning of the zooplankton food resource. These results suggest an ecological role for pelagic fish that challenges previous understanding of their position in the foodweb (zooplanktophagous instead of phytoplanktophagous), the functioning and the trophic models of the NHCS.

Finally to obtain a more comprehensive vision of the relative trophic position of NHCS main components we used stable isotope analyses. For that purpose we analyzed the δ^{13}C and δ^{15}N stable isotope values of thirteen taxonomic categories collected off Peru from 2008 - 2011, i.e., zooplankton, fish, squids and air-breathing top predators. The δ^{15}N isotope signature was strongly impacted by the species, the body length and the latitude. Along the Peruvian coast, the OMZ get more intense and shallow south of ~7.5° S impacting the baseline nitrogen stable isotopes. Employing a linear mixed-effects modelling approach, we provide a new vision of the relative trophic position of key ecosystem components. Also we confirm stomach content-based results on anchoveta Engraulis ringens and highlight the potential remarkable importance of an often neglected ecosystem component, the squat lobster Pleuroncodes monodon. Indeed, our results support the hypothesis according to which this species forage to some extent on fish eggs and larvae and can thus predate on the first life stages of exploited species.

KEYWORDS

Northern Humboldt Current system **Trophic ecology** **Oxygen minimum zone** ***Anchoveta Engraulis ringens*** **Sardine *Sardinops sagax*** **Jumbo squid *Dosidicus gigas***
Squat lobster *Pleuroncodes monodon* **Stable isotope analysis** **Stomach content**

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