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Masters of Science
in Marine Ecology

Geographic variation in the trophic position of the jumbo squid (*Dosidicus gigas*): Insights of interspecific competition with *Sthenoteuthis oualaniensis*

A dissertation
submitted in partial satisfaction of the requirements for the degree
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By:

Nahieli Castañeda Rojas

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A Dissertation Presented by

Nahieli Castañeda Rojas

And approved by the following Committee

Dra. Rocio Iliana Ruiz-Cooley

Director of thesis

Dr. Unai Marcaida Aburto

Dr. Rafael Ramírez Mendoza

Dra. Rosalía Aguilar Medrano

Dr. Rafael Andrés Cabral Tena
Coordinator of Postgraduate in Marine Ecology

Dra. Ana Denise Re Araujo
Director of Studies of Postgraduate

Resumen de la tesis que presenta **Nahieli Castañeda Rojas** como requisito parcial para la obtención del grado de Maestro en Ciencias en Ecología Marina

Variación geográfica en la posición trófica del calamar gigante (*Dosidicus gigas*): un vistazo a su competencia interespecífica con *Sthenoteuthis oualaniensis*

Resumen aprobado por:

Dra. Rocio Iliana Ruiz-Cooley
Directora de tesis

El éxito alimentario depende de la morfología del consumidor, su comportamiento y las condiciones ambientales que sustentan la disponibilidad de presas, así como la presencia de competidores. En este estudio, evaluamos el nicho trófico de *Dosidicus gigas* del Pacífico Tropical Oriental (PTO), el Sistema de la Corriente de California (SCC) y el Golfo de California (GC) mediante análisis de isótopos estables de carbono ($\delta^{13}C$) y nitrógeno ($\delta^{15}N$), así como de aminoácidos individuales (CSIA-AA). También calculamos el traslape de nicho isotópico utilizando el área de la elipse estándar (SEA_C) entre *D. gigas* y *Sthenoteuthis oualaniensis*, un competidor, en el PTO, donde coexisten ambas especies. Nuestros resultados muestran que el tamaño y la posición del nicho isotópico de *D. gigas* varían entre regiones, debido a diferencias en los procesos biogeoquímicos del nitrógeno, así como la composición de la dieta. *D. gigas* del GC presentó valores enriquecidos de $\delta^{15}N$ asociados con los procesos de desnitrificación, mientras que el SCC mostró valores reducidos de $\delta^{13}C$, influenciados por una mayor productividad primaria y una menor temperatura superficial que influyen en la disolución de CO_2. En el PTO, *D. gigas* y *S. oualaniensis* compartieron aproximadamente el 36 % de su SEA_C, lo que indica una superposición de recursos alimenticios. Sin embargo, no se documentó una fuerte competencia interespecífica durante el período de estudio, debido a diferentes estrategias tróficas y/o una buena disponibilidad de diversas presas. El análisis CSIA-AA confirmó que ambas especies habitan regiones con diferentes valores base de nitrógeno. *D. gigas* y *S. oualaniensis* entre 20-35 cm presentaron las posiciones tróficas más altas. En el PTO, *S. oualaniensis* obtuvo posiciones tróficas más altas que *D. gigas*, lo que sugiere una preferencia para capturar presas de niveles tróficos más altos a pesar de tener morfología y tallas similares a *D. gigas*. Inesperadamente, *D. gigas* de tallas grandes obtuvieron posiciones tróficas bajas en el SCC y GC a comparación del PTO sugiriendo que la complejidad de las redes tróficas mesopelágicas y transferencia de energía son fundamentalmente diferentes entre los sistemas geográficos.

Palabras clave: *D. gigas* · *S. oualaniensis* · nicho trófico, análisis de isotopos estables, CSIA-AA.

Abstract of the thesis presented **by Nahieli Castañeda Rojas** as a partial requirement to obtain the Masters of Science degree in Marine Ecology

Geographic variation in the trophic position of the jumbo squid (*Dosidicus gigas*): Insights of interspecific competition with *Sthenoteuthis oualaniensis*

Abstract approved by:

Dra. Rocio Iliana Ruiz-Cooley
Thesis Director

Feeding success depends on consumer morphology, behavior, and environmental conditions that support prey availability, as well as the presence of competitors. In this study, we assessed the trophic niche of *Dosidicus gigas* from the Eastern Tropical Pacific (ETP), the California Current System (CCS), and the Gulf of California (GC) using stable isotope analyses of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), as well as individual amino acids (CSIA-AA). We also calculated isotopic niche overlaps using the standard ellipse area (SEA_C) between *D. gigas* and *Sthenoteuthis oualaniensis*, a competitor, in the ETP, where both species coexist. Our results show that the size and position of the isotopic niche of *D. gigas* vary between regions, due to differences in nitrogen biogeochemical processes as well as diet composition. *D. gigas* from the GC presented enriched $\delta^{15}N$ values associated with denitrification processes, whereas the SCC showed reduced $\delta^{13}C$ values, influenced by higher primary productivity and lower surface temperature that influence CO_2 dissolution. In the ETP, *D. gigas* and *S. oualaniensis* shared approximately 36% of their SEA_C, indicating an overlap in food resources. However, strong interspecific competition was not documented during the study period, due to different trophic strategies and/or good availability of diverse prey. CSIA-AA analysis confirmed that both species inhabit regions with different base nitrogen values. *D. gigas* and *S. oualaniensis* between 20–35 cm presented the highest trophic positions. In the ETP, *S. oualaniensis* obtained higher trophic positions than *D. gigas*, suggesting a preference for prey of higher trophic levels despite having similar morphology and size to *D. gigas*. Unexpectedly, large-sized *D. gigas* obtained lower trophic positions in the SCC and GC compared to the ETP, suggesting that the complexity of mesopelagic food webs and energy transfer is fundamentally different between the geographic systems.

Key words: *D. gigas* · *S. oualaniensis* · trophic niche, stable isotope analysis, CSIA-AA.

Dedication

To my parents and my brother, for their unconditional support and for always being there for me. In memory of my beloved dog Dody (June 22, 2010 – February 18, 2025), my loyal companion and an endless source of love.

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Chapter 1. Introduction

The ability to obtain food resources is influenced by the consumer´s foraging behavior, morphology, and environmental conditions supporting prey populations (MacArthur, 1972; Pianka, 1999). Predators, both specialists and generalists, can develop active and passive behavioral strategies to obtain food resources, selecting specific prey or sizes that are energy-efficient or abundant in their environment (Kolodiuk et al., 2010). This is especially true in marine ecosystems where predators are usually larger than their prey; this predator-prey size drives their feeding strategies and interactions (Cohen et al., 1993). Animal feeding success is critical to continuing their life cycle and depends on the environmental conditions, prey availability, and presence or absence of competitors. Prey availability strongly influences the abundance and spatial distribution of their predators (Elton, 1927; Murcia -Rojas et al., 2016), but this aspect is poorly understood for epi-mesopelagic cephalopods, such as some species of the family Ommastrephidae, given the difficulty in conducting research in their remote deep habitat. Ommastrephids have a short lifespan (~ 1 year) (Rodhouse and Nigmatullin, 1996) and have a significant role in marine ecosystems for energy exchanges and flow (Karpouzi and Stergiou, 2003; Xavier and Croxall, 2007). The jumbo squid (*Dosidicus gigas*, D'Orbigny, 1835) is the largest species of this family (Nigmatullin et al., 2001). The mantle length (ML) is the standard measurement of length in cephalopods and is measured along the dorsal midline from the anterior margin of the mantle to the posterior tip of the body. The largest *D. gigas* measured 120 cm ML (Nesis, 1972). This ommastrephid species is an abundant nektonic squid endemic to the Eastern Tropical Pacific (ETP) with the highest potential fecundity of all cephalopod species (Nigmatullin and Markaida, 2009). Depending on its size, it is an important prey of sperm whales and other odontocete species (Clarke, 1996; Ruiz-Cooley et al., 2004, 2006), and large pelagic fish (Nigmatullin and Shukhalter, 2001; Galván-Magaña et al., 2013). It also represents a voracious predator for anchovies and mackerel in the Humboldt Current and western Baja California (Neira and Arancibia, 2013). In the Gulf of California (GC), it consumes nictoepipelagic micronekton such as myctophids and red crab (Ehrhardt, 1991; Markaida, 2006b, 2006a; Markaida and Sosa-Nishizaki, 2003), while in the California Current System (CCS) it had a wide-range of preys such as invertebrates (mollusks and arthropods) and vertebrates (mainly fish) (Field et al., 2007).

Dosidicus gigas mature at different maximum sizes (a small, medium, and large forms were proposed), across their entire geographical range, or even within the same geographic area (Nesis, 1993). Its geographic distribution and size variation seem to be associated with prey type availability and productivity of the marine systems that inhabit (Nesis, 1972; Nigmatullin, 2001; Jereb and Roper, 2005).

Its regular distributional range is from 30°N to 26°S, and a maximum of 140° W of the equatorial strip (Nigmatullin et al., 2001). However, *D. gigas* can expand its geographical range; the most recent expansion occurred after 1997-1998 covering a distribution from 60°N to 50°S, possibly in response to "El Niño" (Zeidberg and Robison, 2007; Staaf et al., 2008; Ruiz-Cooley et al., 2013), and reaching new areas including Oregon, Canada, and Alaska (Pearcy, 2002; Keyl et al., 2008; Cosgrove and Sendall, 2015). Multiple migrations from the Mexican Pacific or GC could have supported the *D. gigas* population in the Northeast Pacific (NE) (Field et al., 2013; Ruiz-Cooley et al., 2013). In the CCS, *D. gigas* fed on abundant and diverse prey, such as neritic fish (*Merluccius angustimanus*), myctophids (*Myctophum nitidulum*), squid (*Doryteuthis opalescens*) and crustaceans (*Pleuroncodes planipes*) (Field et al., 2013).

Studies based on stomach content analysis (Table 1) have provided valuable and detailed information on prey items consumed by *D. gigas*. Specifically for the CCS during *D. gigas* range expansion, Field et al. (2013) found 98 prey species, including 71 fish, 22 cephalopods, and 5 pteropods in CCS particles in Monterey Bay, Santa Barbara, and San Diego sites in 370 squid. Using demographic data and seasonal patterns, these authors investigated *D. gigas* ontogeny and migration patterns from 2007 to 2010 during spring, summer, fall and winter. In the GC, where *D. gigas* commonly occurred, Markaida and Sosa-Nishizaki (2003) analyzed 533 squid collected between November 1995 and April 1997, and identified *Benthosema panamense* and *Triphoturus mexicanus*, small mesopelagic squid, and shrimp as their main prey and lower presence of anchovies. Subsequent studies confirmed that *D. gigas* feeds mainly on nocturnal pelagic micronekton in the GC (Markaida, 2006b; Markaida et al., 2008), but it has been shown that *D. gigas* can feed both day and night, despite undertaking daily vertical migrations, residing in deeper waters during daylight hours, and ascending to the surface at night (Nigmatullin et al., 2001). Furthermore, it has been suggested that inhabiting a hypoxic environment, such as the oxygen minimum zone (OMZ) during the day, provides jumbo squid with two main advantages: reduced foraging effort and predator avoidance in hostile environments such as the GC and CCS (Stewart et al., 2013).

Table 1. Stomach content analysis studies for *Dosidicus gigas* (*Dg*) and *Sthenoteuthis oualaniensis* (So) in BCS: Baja California Sur, GC: Gulf of California, CCS: California Current System, EW: Ecuadorian waters, ETP: Eastern Tropical, HW: Hawaii. Preys: F (Fish), Cr (Crustaceans), Ceph (Cephalopods), Moll (Mollusks).

System	Specie	Prey		Reference
BCS	*Dg*	F	*Synodus lucioceps*	Bazzino et al. (2010)
			Merluccius angustimanus	
			Prionotus stephanophrys	
		Cr	*Pleuroncodes planipes*	
			Nyctiphanes simplex	
		Ceph	*Lolliguncula sp.*	

			Octopus rubescens	
			D. gigas	
GC	*Dg*	F	Mackerel	Ehrhardt, (1991); Markaida and Sosa-Nishizaki (2003); Markaida, (2006); Markaida et al. (2008)
			Myctophids	
			Benthosema panamense	
			Sardinops sagax	
			Triphoturus mexicanus	
			Engraulis mordax	
		Cr	Shrimp Post Larvae	
			Red Crab	
			Euphausiacea	
			Pleuroncodes planipes	
			Plesionika sp	
		Ceph	*Pterygioteuthis giardi*	
			Gonatus sp	
			D. gigas	
			Octopus sp.	
			Abraliopsis affinis	
CCS	*Dg*	F	Myctophiformes	Field et al. (2013)
			Engraulidae	
			Osmeridae	
		Cr	Euphasiidae	
		Ceph	*Gonatus spp.*	
			D. gigas	
			Onychoteuthis borealijaponicus	
		Moll	*Clio pyramidata*	
			Cresis spp.	
EW	*Dg*	F	*Myctophum sp.*	Rosas-Luis and Chompoy-Salazar (2016)
			Lampanyctus sp	
		Ceph	*Gonatus sp*	
			D. gigas	
Eastern Pacific	*So*	F	*Symbolophorus evermanni*	Shchetinnikov (1992)
			Diogenichthys laternatus	
			Larval Myctophidae	
			Vinciguerria lucetia	
		Ceph	Ommastrephidae	
			S. oualaniensis	
			D.gigas	
			Enoploteuthidae	
		Cr	Amphipoda	
			Copepoda	
			Phrosinidae	
			Euphausiacea	
HW	*So*	F	*S. evermanni*	
			H. rheinhardti	

			C. warmingii	Parry (2006)
		Ceph	*Onychoteuthis sp.*	
			Abraliopsis sp. A	
			S.oualanensis	

The presence of potential competitors could reduce the feeding success of cephalopod species, especially if the competitors are morphologically similar, which can result in strong interspecific competition if species overlap and there is not abundant prey (Volterra, 1928; Hutchinson, 1957). Alternatively, asymmetric competition can occur if species differ in their competitive abilities, leading to one species dominating resource acquisition or space utilization over another (Young, 2004). The presence of competitors can strongly influence trophic positions, food availability, and food web roles, as demonstrated for *Rossia* (Golikov et al., 2020); however, this remains unexplored among *D. gigas* and other mesopelagic squids.

The distribution of *D. gigas* in the ETP overlaps with that of purple squid *Sthenoteuthis oualaniensis*, (Lenson, 1830) (Fig. 1). *Sthenoteuthis oualaniensis* has a wide distribution in the tropical and subtropical Pacific, but its largest range extends from the tropical to the subtropical Indian Ocean (Young et al., 1975), where *D. gigas* does not occur (Roper et al., 1984; Zuyev et al., 2002; Xinjun et al., 2007). The high degree of morphological similarity during the paralarva stage "Rhynchoteuthion" (typical of the family Ommastrephidae) and the overlap in the distribution of both species in the eastern tropical Pacific (Ramos et al., 2017), which could lead to interspecific competition and potentially reduce feeding success. In the long term, this competition could influence the distribution, abundance and behavior of both squid species, as well as the ecological structure in which they are found (Zuev et al., 1985). Also, given the morphological similarity between *S. oualaniensis* and *D. gigas*, they could share trophic niches when prey is highly abundant (Shchetinnikov, 1992). Both species can use the prominent OMZ in the Eastern Pacific (Fig. 1) (Gilly et al., 2006b).

Three intraspecific groups of *D. gigas* may be distinguished on the basis of the size of adult males and females: small-sized adult males with (13–26 cm) and females (14–34 cm) MLs, medium-sized (24–42 cm) and (28–60 cm) MLs, respectively) and large-sized (>40–50 cm and 55–65 cm to ~100 cm MLs and more, respectively) (Nigmatullin et al., 2001). The distribution ranges of both the small and medium sized groups fully or partially overlap, while the ranges of the medium-sized and large-sized groups commonly overlap. Squids of the small-sized group are found predominantly in the near-equatorial area, those of the medium-sized group live within the whole species range (except in the most high-latitudinal parts) and those of the large-sized group occur at the northern and southern peripheries of the range (usually northward of 10°15°N (Nigmatullin et al., 2001).

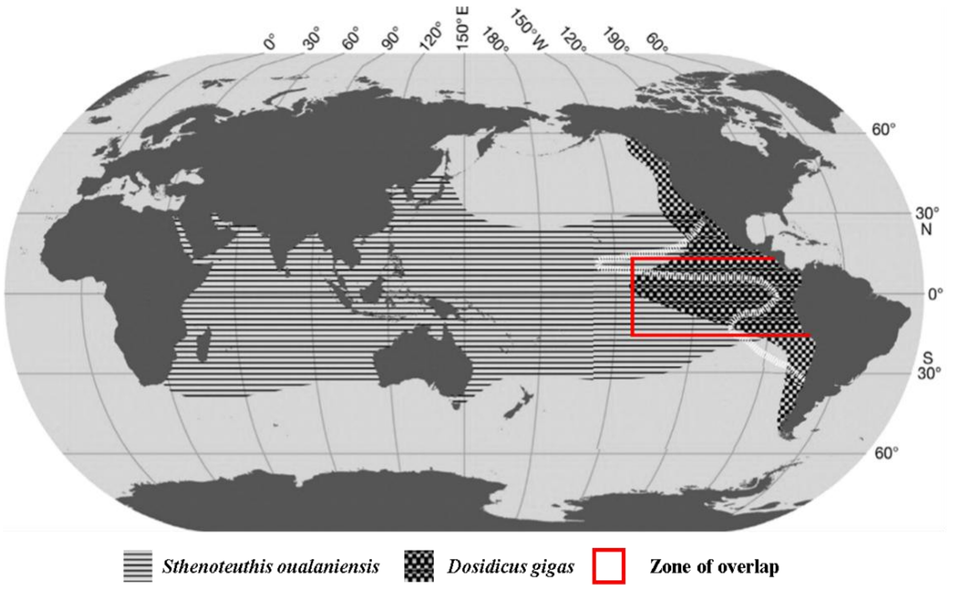

Figure 1. Overlap between *Dosidicus gigas* and *Sthenoteuthis oualaniensis*. Species range illustrating the region of overlap. The minimum oxygen zone of the Eastern Pacific is shown by a white line, indicating 20 µM dissolved oxygen at 300 m depth and the competition zone (red box). Taken and modified Staaf et al. (2010).

Sthenoteuthis oualaniensis is represented by two forms. The dwarf early maturing equatorial form does not have a dorsal photophore (males and females modal ML are 9-10 cm, and 9-12 cm, respectively). Sex ratio on average is equal, and long horizontal migrations have not been documented. The middle-sized form has a dorsal photophore, it is the most common and is widespread (Nigmatullin et al, 2001; Nigmatullin and Shukhalter, 2001). The modal ML of males is 12-15 cm, and females 19-25 cm. A giant form of this species only occurs in the Arabian Sea (Nesis, 1993). So, both dwarf and medium size squid of both species are sympatric to the equatorial and Tropical Eastern Pacific. The medium size group of *D. gigas* dominates during warm and less productive waters, while the large form of this species occurs during cool periods and more productive waters. The medium sized lives for one year while the large form can reach up to two years (Keyl et al., 2008; Arkhipkin et al., 2014; Robinson et al., 2016). These phenotypic groups, their distribution, and their high ability of movement have been related to the prominent use of OMZ in the ETP during the day (Staaf et al., 2010). Their size is influenced by phenotypic plasticity, that is, the ability to modify their growth and development in response to environmental conditions. Factors such as food availability, temperature, and oxygen concentration can affect their growth rate, allowing them to reach varied sizes within the same habitat. This plasticity may improve their ability to exploit resources within the OMZ, including prey that thrive in low oxygen conditions, such as some myctophid species (Kinzer et al., 1993; Snyder, 1998). The OMZ exhibits high biological productivity at the surface; as sinking particulate organic matter (e.g., phytoplankton remains, zooplankton fecal pellets, and detritus) is decomposed by microbial activity, the concentration of dissolved oxygen in the water column decreases (Xinjun et al., 2007). This area may provide refuge for these squid species from hypoxia-intolerant predators and be a good foraging site for catching myctophids (Gilly et al., 2006a).

Dosidicus gigas and *S. oualaniensis* are highly flexible and can adapt to strong variations in environmental parameters such as temperature, dissolved oxygen, and types of prey available (Bazzino et al., 2007). Their high capacity of phenotypic plasticity allows these squids to adjust growth based on environmental conditions and resource availability, optimizing their survival in highly variable environments. Their high phenotypic plasticity is closely related to their extremely rapid growth, while their ability to adjust growth rate in response to environmental conditions allows them to maximize the utilization of available resources and reach their maximum size in a short life span (Hoving et al., 2013). Since both species have a relatively short life cycle (1-2 years), they require a considerably high food intake to maintain rapid somatic growth, reaching maximum growth rates between 181 and 210 days (females) and 151-180 days in males (Chen et al., 2013) (*D. gigas*: ≤ 34 cm ML; *S. oualaniensis*: ≤ 35 cm ML), which in turn influences their ecological success in the eastern tropical Pacific (Shchetinnikov, 1992; Nigmatullin et al., 2001; Markaida et al., 2004).

Table 2. Essential factors (diet, vertical distribution, mantle length) that contribute to interspecific competition between *D. gigas* and *S. oualaniensis*. Oxygen Minimum Zone (OMZ).

Factor	Similarities (competition potential)	Reference
Diet	*Myctophidae, Vinciguerria lucetia, Euphausiidae, Amphipoda*	Shchetinnikov, (1992); Rosas-Luis et al. (2011); Cisneros et al. (2024)
Vertical distribution	Both OMZ associates perform diel migrations	Nesis, (1983); Gilly et al. (2006b); Staaf et al. (2010); Stewart et al. (2013)
Mantle length	*D. gigas*: 13 to 42.2 cm ML *S. oualaniensis*: 9 to 28.3 cm ML	Shchetinnikov, (1992); Staaf et al. (2010)

Both the diet and habitat of *D. gigas* and *S. oualaniensis* change during ontogenesis (Shchetinnikov, 1992; Markaida and Sosa-Nishizaki, 2003; Markaida, 2006a, 2006b). Based on stomach content analysis (Table 1; 2) of *S. oualaniensis* in the Eastern Tropical Pacific, Shchetinnikov (1992) found that juveniles of 4-10 cm

ML fed on euphausiids, amphipods, and ichthyoplankton, while medium-sized squid (10-15 cm ML) fed on myctophids. Adults of 15-36.5 cm ML consumed different species of myctophid fish, such as *Myctophum reticulum* and, to a lesser extent, squid such as *D. gigas, Onychoteuthis banksii,* and juveniles of *S. oualaniensis*. In the southern sub-region in the subtropical waters of the Humbolt Current, *D. gigas* was the main food of *S. oualaniensis* (Shchetinnikov, 1992). In addition, the diet of *D. gigas* also changes in the same area during different environmental setups. *D. gigas* from the GC fed on a slightly different micronekton composition after the 1997-98 El Niño event. Pteropods, micronektonic squid, megalopae, and euphausiids were more important in the diet than in years before this El Niño event, this difference in diet could be due to a smaller squid size or to a change in the pelagic environment (Markaida, 2006b).

Stable isotope analysis (SIA) of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) is a complementary method to stomach content analysis to investigate squid foraging ecology (Ruiz-Cooley et al., 2013). The main function of stable isotopes is to determine the trophic position, to infer trophic relationships and reconstruct the dietary history of squid throughout their ontogenetic cycle (Ruiz-Cooley et al., 2013; Ruiz-Cooley and Gerrodette, 2012; Navarro et al., 2013). In trophic ecology studies, $\delta^{15}N$ is used to estimate trophic position, while $\delta^{13}C$ offers information about the primary source of carbon (Post, 2002). However, these two biochemical tracers provide information on both trophic position and foraging habitats based on the dominant C and N cycling process (Natelhoffer and Fry, 1988; Rau et al., 1989; Ruiz-Cooley and Gerrodette, 2012). For resident consumers, $\delta^{13}C$ and $\delta^{15}N$ increase between predator and prey by 0.4 to 1 ‰ for ^{13}C, and 3 to 4 ‰ for ^{15}N. Using these values, an assessment of the degree of overlap between consumers can provide information on shared feeding resources and habitat (Post, 2002). Predators integrate the isotope ratios of their prey and foraging habitat through diet (Tieszen et al., 1983; Peterson and Fry, 1987). Depending on the tissue analyzed, the diets of predators can be analyzed at different time scales (Tieszen et al., 1983). Animal inert tissue can provide information for longer periods (month to years) than metabolically active tissues like the liver (that provide information for days) (Schell et al., 1989). When using a given tissue, its biochemical composition and metabolism can determine the period in which isotopic signals reflect an average diet composition of its life cycle (Hobson, 1999). Thus, highly migratory species such as squid incorporate diets with different isotope ratios as they grow, and such dietary changes are recorded in the gladius (Ruiz-Cooley et al., 2006, 2010). Gladius is a chitinous structure that is synthesized during the life cycle of the squid and grows by adding chitin along the periostracum (Bizikov, 1991), incorporating part of the assimilated diet and tracking ontogenetic changes in diet and habitat as the squid grows (Ruiz-Cooley et al., 2010). Inferences about horizontal movement can be made if the squid moves between areas isotopically different and can help to distinguish subpopulations based on habitat biochemistry (Ruiz-Cooley et al., 2010, 2013). On the other hand, in the muscle tissue (mantle), the isotopic ratios indicate a recently assimilated diet (< 2 months) (Ruiz-Cooley et al., 2006), compared to the sections along the gladius that represent a continuous nutritional record during ontogenetic growth (Ruiz-Cooley et al., 2010). These tissues have the unique advantage of revealing lifelong life history traits, since the early life stages are difficult to tag (Parry, 2003; Hunsicker et al., 2010). However, SIA cannot recognize the effect of diet or baseline variability. These drawbacks can be solved using compound specific isotope analysis of amino acids (CSIA-AA) (Mcclelland and Montoya, 2002; Chikaraishi et al., 2009).

CSIA-AA disentangle the interrelationships of food webs and can be used to provide more precise trophic position estimates than bulk SIA without the need to isotopically analyze primary producers. The CSIA-AA is based on isotopic values of macromolecules such as amino acids or fatty acids (Chikaraishi et al., 2009). It is an analytical method used to obtain complete information on nutrition, food webs, primary production patterns, migrations, physiology, and metabolic pathways (nutrients) (Ruiz-Cooley et al., 2013, 2024; McMahon and McCarthy, 2016). The isotopic values of amino acids quantified from any animal tissues follow the classification of "source and trophic" for $\delta^{15}N$ (Chikaraishi et al., 2009) and "essential and non-essential" for of $\delta^{13}C$ (O´Brien et al., 2002). To date, CSIA-AA has been applied to a few species of squids that include *D. gigas* (Ruiz-Cooley et al., 2013; Gong, et al., 2018) The $\delta^{15}N$ values of phenylalanine (Phe; an essential-AAs) from consecutive gladii sections revealed different geographic origins and migration patterns of *D. gigas* collected in the CCS during its range expansion (Ruiz-Cooley et al., 2013), but $\delta^{15}N_{AAs}$ results were not used to provide estimates of *D. gigas* trophic position. Because *D. gigas* can be a voracious predator, but also an important prey of many consumers, It is essential to understand the complexity of trophic interactions and predict how *D. gigas* role in the food web varies across different ecosystems. Although CSIA-AA provides more accurate estimates than bulk, it also has limitations where variations in baselines, metabolic routing, and differences between tissues can complicate the interpretation of results (Chikaraishi et al., 2009; McMahon and McCarthy, 2016). Estimating the trophic positions of species allows us to obtain information about the diets of animals, understand their role in food webs and the energy flow of an ecosystem that is associated with abundance and trophic interactions (Post, 2002), as well as their growth and survival, developing interspecific and intraspecific interactions, particularly in species with commercial importance (Mcclelland and Montoya, 2002). Squids with similar phenotypes, such as *D. gigas* and *S. oualaniensis*, could compete interspecifically for shared resources (food and habitat) while at the same time maintaining unique niches that facilitate their coexistence (Hutchinson, 1957; Rodhouse and Nigmatullin, 1996). Given the complexity of trophic ecology, the implementation of $\delta^{15}N$ of individual amino acids has been crucial to understanding the feeding habits of different marine species (Ruiz-Cooley et al., 2004, 2006, 2010, 2013; Ruiz-Cooley and Gerrodette, 2012) and to assess aspects of their trophic ecology that allow them to survive. In this thesis, SIA in bulk tissues of *D. gigas* and *S. oualaniensis* were analyzed by individuals inhabiting different ecosystems to understand their trophic niche. For the first time, $\delta^{15}N$ of individual AAs were used to estimate the trophic position of *D. gigas and S. oualaniensis* to investigate variability in TP based on size and geographic area. Since both species of squid are important fishery resources and play a critical role in pelagic food webs, it is essential to understand how their trophic position varies in different geographic areas and in the presence of a potential strong competitor. So far, interspecific competition has only been studied in the genus *Rossia* through bulk (Golikov et al., 2020). Evaluating differences in the trophic position of *D. gigas* in the absence and presence of *S. oualaniensis* as a potential competitor is unknown.

1.1 Hypothesis

The trophic position of *D. gigas* varies depending on size, feeding grounds, and the presence or absence of potential competitors. Therefore, the trophic position of each cephalopod species would be higher in geographic areas where neither *D. gigas* nor *S. oualaniensis* is found. In contrast, different trophic positions are expected in areas where both species overlap as a possible strategy to reduce interspecific competition.

1.2 Objetives

1.2.1 Main objetive

Evaluate geographic variation in the trophic position of *Dosidicus gigas* in areas of overlap and lack of overlap with *Sthenoteuthis oualaniensis* by using stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$ and CSIA-AA.

1.2.2 Specific objetives

Determine the isotopic niche of *Dosidicus gigas* as an approximation of its trophic niche.

To estimate the degree of overlap and the differences in trophic position between *Dosidicus gigas* and *Sthenoteuthis oualaniensis.*

Chapter 2. Methodology

2.1 Experimental design

In this study, muscle, and gladius tissue from *D. gigas* and *S. oualaniensis* were collected and processed primarily for stable carbon and nitrogen isotope analysis. The methodology and data analysis were based on previously established protocols (Ruiz-Cooley et al., 2010, 2013; Ruiz-Cooley and Gerrodette, 2012), with adaptations according to the research objectives. In general, sample processing was based on the traditional stable isotope methodology of Bulk and CSIA-AA (Fig. 2). These procedures allowed for the assessment of the isotopic niche, trophic position, and interspecific competition.

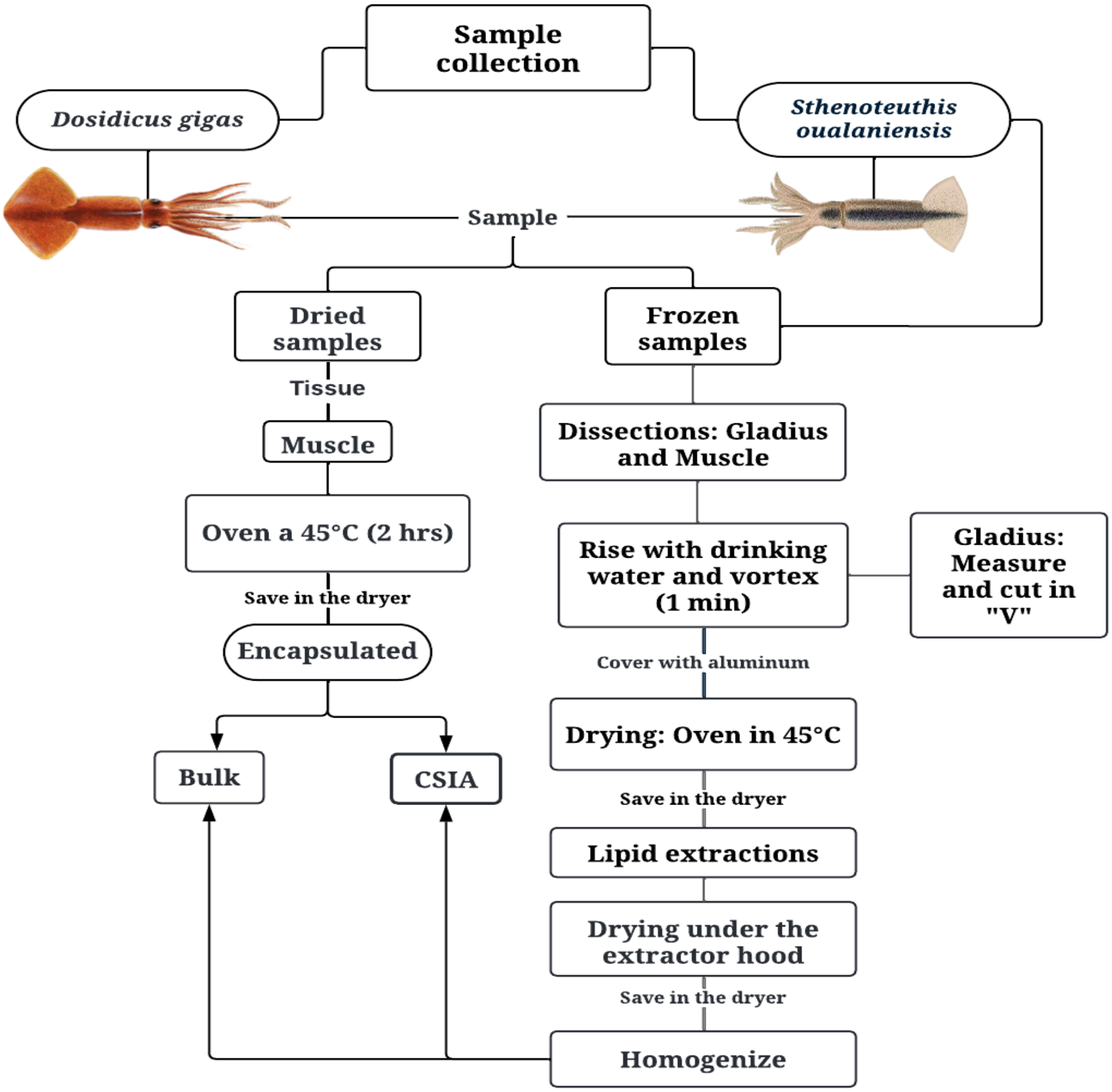

Figure 2. Processing of muscle and gladius samples in the laboratory for Bulk and CSIA-AA.

2.2 Study area

Squid were collected in four different systems: Eastern Tropical Pacific (ETP), GC, Current California System (CCS), Gulf of California (GC) and Hawaii (HW). The ETP extends from the Southern limit of Colombia to Mexico on the western coast of Baja California and at the northern end of the GC (Spalding et al., 2007). It includes approximately 9,975 km of continental coasts, distributed across eight countries, Colombia, Panama, Costa Rica, Nicaragua, Honduras, El Salvador, Guatemala, and Mexico (Fig. 3) (Wang and Enfield, 2001). This region presents a circulation of oceanographic currents located in the northern part by the CCS, the Humboldt Current to the south, and the South Equatorial Current in the center (Lavín et al., 2006). These currents form intertropical northern and southern gyres that, in turn, cause a countercurrent called the Equatorial Countercurrent that travels from the east (Wyrtki, 1974). The eastern boundary currents feature a circulation toward the CCS and the Humboldt Current. Surface waters have average temperatures between 16° and 27°C and an average salinity between 32 and 35 ppm (Fiedler and Talley, 2006) and represent around 23% of the primary production of the Pacific Ocean (Lavín et al., 2006). The warm (>27.5 °C) eastern Pacific lies along the southwestern coast of Mexico and Guatemala, and cold surface waters are found in the equatorial cold tongue and eastern boundary current along Humboldt Current and the Baja California to the north (California Current) (Wang et al., 2001; Fiedler and Talley, 2006). This area is characterized by the presence of OMZ and intense denitrification processes, which significantly enrich the nitrate (NO_3^-) levels available for primary production. Furthermore, the convergence between equatorial surface and subsurface waters, along with the interannual variability associated with El Niño or La Niña, also influences the $\delta^{13}C$ and $\delta^{15}N$ values of the trophic base (Kessler, 2006).

The CCS (Fig. 3) it extends from the North Pacific Current (NPC) (50°N) to Baja California, Mexico (15°N) where its circulation is in an equatorward flow that is affected by winds and the pressure system along the west coast of the North American continent (Ueno et al., 2023). It is known as a transition zone because masses of subarctic water that circulate to the south converge with tropical and subtropical waters that go to the north (Durazo, 2015). However, in its movement towards the south, it crosses regions with different topographic characteristics. Along its path, it mixes with other water masses; therefore, its subarctic identity is lost, and the percentage of subtropical water increases progressively towards the south and west (Moser et al., 1954). It has its own subtropical and warm-temperature biota, which is influenced by the North Pacific Current and the Central Pacific Anticyclonic Gyre (Brinton and Reid, 1986). This current presents one of the five coastal upwelling zones of the world's oceans, which supports a productive and diverse fishery that depends on nutrient-rich waters in the euphotic layer (Checkley and Barth, 2009; Capone and Hutchins, 2013). This current presents one of the four coastal upwelling zones of the world's oceans, which supports a productive and diverse fishery that depends on cold, nutrient-rich waters in the euphotic layer (Checkley and Barth, 2009a; Capone and Hutchins, 2013), where the mixing of subarctic and subtropical waters influences isotopic values, due to the partial consumption of nitrate in areas of high productivity (Checkley and Barth, 2009a).

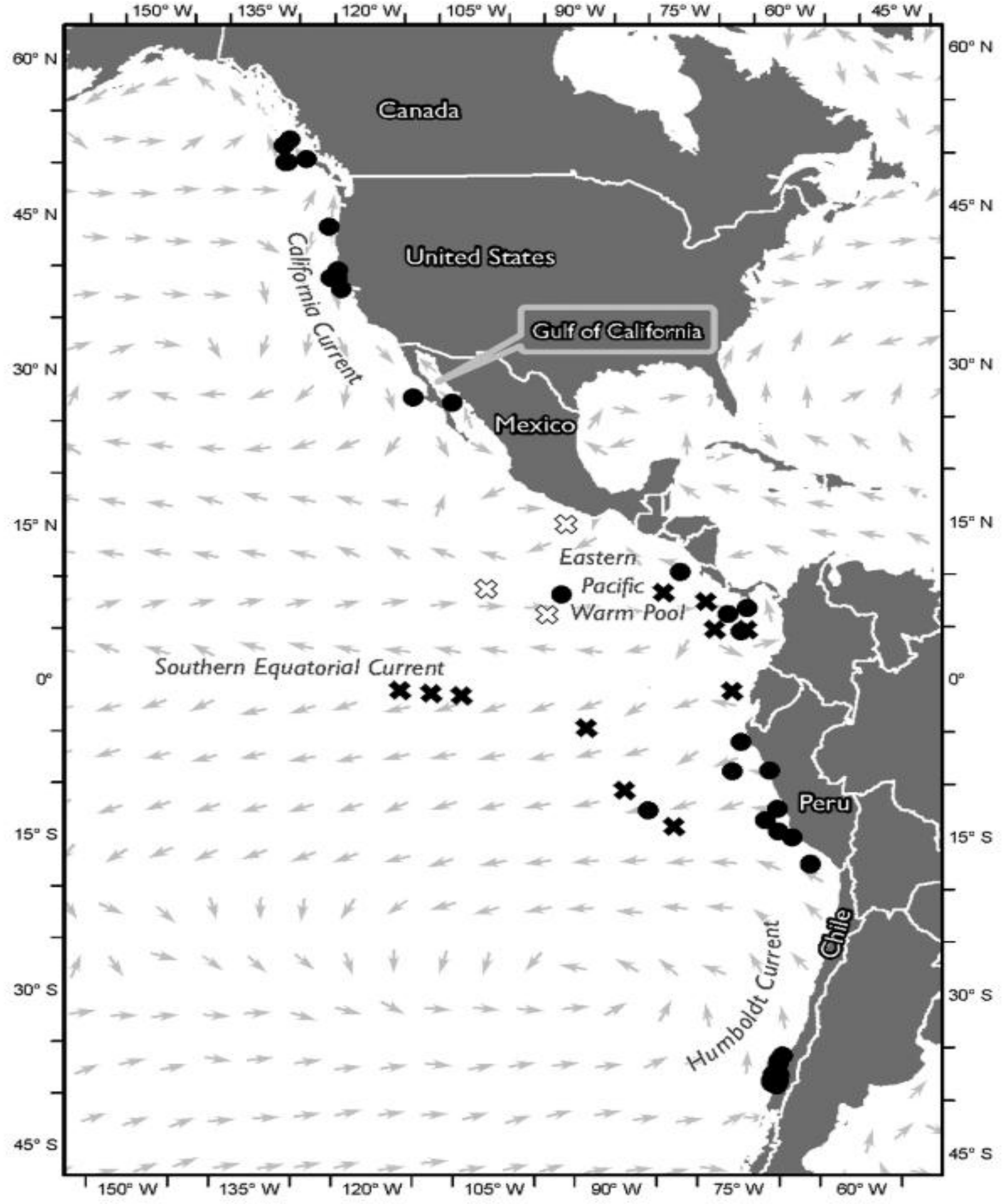

Figure 3. Different geographic systems: *Dosidicus gigas* (solid crosses), *Sthenoteuthis oualaniensis* (open crosses) and sites were both species *D. gigas* and *S. oualaniensis* were collected simultaneously (solid crosses). Taken from Ruiz-Cooley & Gerrodette, (2012). Some tissue samples and data from some sites are used in the current study.

On the other hand, the GC (Fig. 3) is a semi-enclosed sea of great interest because it is the unique evaporation basin of the Pacific. The northern region is characterized by high surface salinities and temperatures that range from 10°C to 32°C from winter to summer (Sverdrup and Urdang, 1941). The seasonal circulation in the GC is dominated by the forcing of the Pacific Ocean and by the wind regime (Alvarez-Sánchez et al., 1978). The islands region, delimited to the south, constitutes important features for the GC, where the lowest surface temperatures are present due to intense tidal mixing (Roden, 1964a). This region that allows the entry of the Eastern Tropical Pacific Ocean into the interior of the GC through the mouth, has a complicated hydrographic structure due to the confluence of different water masses. The water circulation is seasonal where the water enters during spring and summer and leaves during autumn and winter (Ripa and Marinone, 1989). Its variation over time shows that the surface circulation is cyclonic in summer and anticyclonic in winter (Beier, 1997). This area is highly productive due to the mixing of nutrient-rich deep waters with surface waters, influenced by upwelling and the California Undercurrent. This interaction can modify basal carbon and nitrogen levels through the remineralization and denitrification characteristics of the region (Rau et al., 1982, 1989).

The Hawaiian (HW) archipelago has strong influence from oceanic and atmospheric circulations (Fig. 4). The northeast trade winds blow constantly most of the year, with greater force during the summer (Calil et al., 2008). In this region, there are strong obstacles to atmospheric flow such as the islands of Maui and HW, whose mountains, Haleakala (3055 m) in Maui, and Mauna Kea (4201 m) and Mauna Loa (4169 m) in HW, penetrate the trade wind inversion layer that extends from 1700 to 5000 m (Calil et al., 2008). The trade winds and islands exert a distinctive and constant oceanic forcing (Fig. 4). Located around 19°N, the Hawaiian Leeward Countercurrent (HLCC) is an eastward current that transports warm water toward HW Island (Fig. 4). The interaction between converging winds and elevated sea surface temperature (SST) along the zonal extent of the HLCC generates an extensive wake region (Xie et al., 2001). This circulation is composed of two consistent areas: a cyclonic region to the north and anticyclonic region to the south (Calil et al., 2008). The time-varying North Hawaiian Ridge Current (NHRC) influences the northeast of the islands, which behaves as a western boundary current (Godfrey, 1989), whereas the North Equatorial Current (NEC) plays an important role in the North Pacific subtropical gyre, moving from south of the HW Islands with velocities exceeding 0.25 ms^{-1}. Additionally, mesoscale cyclonic eddies transport nutrient-rich waters toward the euphotic zone, which enhances biological activity (Seki et al., 2001). However, Hawaii is considered an oligotrophic zone, characterized by low nutrient availability (Seki et al., 2001; Montoya et al., 2002) which influences nitrogen isotope values.

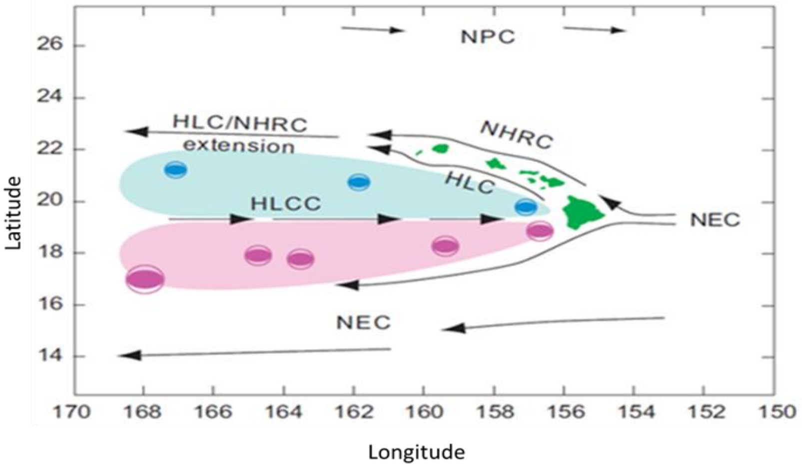

Figure 4. Major surface currents around the Hawaiian Islands, as well as the predominant paths of cyclones (blue) and anticyclones (magenta). HLCC: Hawaiian Lee Counter Current, NHRC: North Hawaiian Ridge Current, NECC: North Equatorial Current, HLC: Hawaiian Lee Current. Modified from Lumpkin, (1998).

2.3 Specimen collection

Squid were collected at a total of 26 sampling stations in different years (Table 3). Squid were collected using jigs and a hand net to capture small individuals. At night, vertical lights were used to attract them close to the vessel. Both squid species were collected at eight ETP stations. *D. gigas* were collected in the GC and CCS. At HW, only *S. oualaniensis* was collected (Fig. 5, Table 3). Whole specimens of small squid or tissue samples of *D. gigas* and *S. oualaniensis* from all sites were immediately frozen at -20 °C.

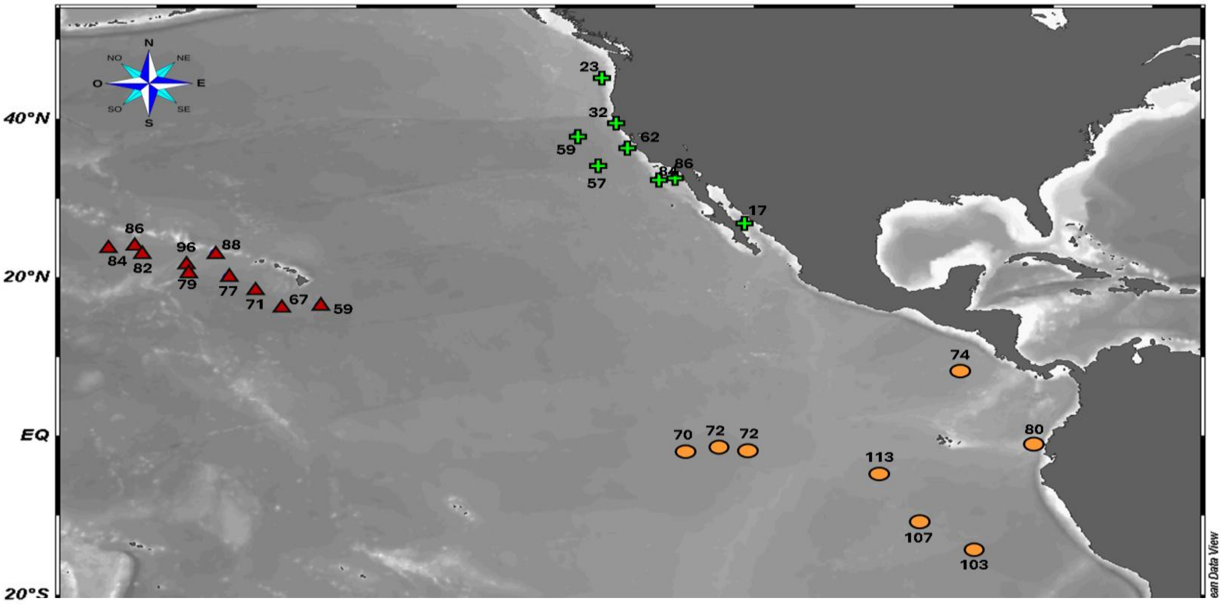

Figure 5. Study area and sampling stations. *Dosidicus gigas* (Green crosses), *Sthenoteuthis oualaniensis* (red triangles), Stations where both species were collected (Orange circles).

Table 3. Location, dates, positions (Latitude, Longitude), oceanographic cruise, and species. ETP: Eastern Tropical Pacific; GC: Gulf California; CCS: California Current System; HW: Hawaii.

Location	Date	Latitude	Longitude	Oceanographic cruise	Species
ETP	Sep, 2006	1° 10'00.0" S	82° 27'00.0" W	McArthur II	Both species collected
	Sep, 2006	1° 59'01.0" S	116° 59'02.2" W		
	Sep, 2006	8° 22'05.8" N	89° 28'07.9" W		
	Sep, 2006	1° 38'00.0"S	110° 39'00.0"W		
	Oct, 2006	4° 43'00.0"S	97° 34'00.0"W		
	Sep, 2006	1° 25'00.0"S	113° 43'00.0"W		
	Oct, 2006	10° 48'00.0"S	93° 27'00.0"W		
	Oct, 2006	14° 14'00.0"S	88° 06'00.0"W		
GC	Aug, 2006	26° 55'47.4"N	111°09'16.1"W		*D. gigas*
CCS	Oct, 2008	34° 08'00.0"N	125° 50'00.0"W	ORCAWALE	*D. gigas*
	Sep, 2008	39° 33'17.4"N	124°00'08.4"W		
	Oct, 2008	36° 26'00.0"N	122° 56'00.0"W		
	Aug, 2008	45° 16'00.0"N	125° 21'06.0"W		
	Oct, 2008	37° 58'00.0"N	127° 54'00.0"W		
HW	Oct, 2010	20° 56'06.7"N	167°02'56.4"W	HICEAS Sette	*S. oualaniensis*
		16° 29'03.6"N	15343'01.8"W		
		18° 25'27.6"N	160° 13'45.0"W		
		22° 55'59.4"N	171° 33'45.1"W		

2.4 Laboratory work

Published results from stable isotope ratios of carbon ($\delta^{12}C$) and nitrogen ($\delta^{15}N$) from bulk muscle tissue samples from Ruiz-Cooley and Gerrodette (2012), and some results from gladii by Ruiz-Cooley et al., (2010), were used in this study (Table 4). A portion of the mantle muscle tissue or gladius section was collected (the gladius, throughout its ontogenetic cycle, adds material forming chitin layers) and preserved frozen in Eppendorf tubes. The mantle length (ML) was measured in centimeters, and this measurement was used as the primary morphometric indicator to represent the average size of the squid. Since this study aimed to compare the trophic niche of squids at relatively similar sizes (except for CCS, which were only considered at sizes > 54 cm ML), gladius sections of *D. gigas* in the GC were considered to reconstruct their trophic positions from small to large sizes. The gladius total length (GL) was measured to the nearest 1 mm. According to Bizikov (1991), the gladius has three morphological parts: proostracum, conus, and rostrum; however, for this study, only the proostracum was used for stable isotope analysis. The proostracum was carefully cleaned with double-distilled water and KimWipes measured, and marks were made every 3 cm from the anterior edge to the to the narrowest posterior section (Fig. 6). The sections were cut with fine scissors following the "V" shape of the growth line

Table 4. General information on *D. gigas* and *S. oualaniensis* samples from the Gulf of California (GC), California Current System (CCS), Eastern Tropical Pacific (ETP), and Hawaii (HW). Laboratory: Analyzed for the first time in the laboratory.

Location	Specie	Analysis	Tissue	Reference
GC	*D. gigas*	Bulk	Muscle	Ruiz-Cooley et al. (2010)
		CSIA-AA	Gladius Muscle	Laboratory
CCS	*D. gigas*	Bulk CSIA-AA	Muscle	Ruiz-Cooley et al. (2013)
ETP	Both species collected	Bulk	Muscle	Ruiz-Cooley et al. (2010)
		CSIA-AA	Muscle	Laboratory
HW	*S. oualaniensis*	Bulk CSIA-AA	Muscle	Laboratory

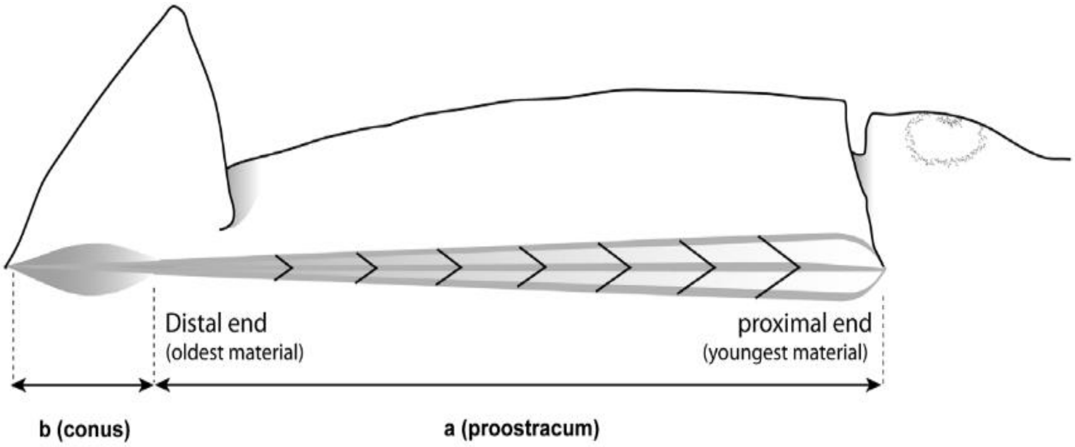

Figure 6. Gladius. A) Proostracum, B) Conus. In this study, the proostracum was used by measuring and cutting 3 cm sections following the direction of the growth lines. Taken from Lorrain et al. (2011).

2.5 Stable isotope analysis (SIA) in Bulk tissue

Muscle tissue and gladius sections were dried in a GCA/PRECISION SCIENTIFIC oven at 40° - 45°C. Drying lasted 3 days for muscle tissue and 1 day for gladius sections. In both tissues, adherent surface lipid residues were removed by lipid extraction with a chloroform-methanol mixture (2:1) in previously treated vials (Bligh and Dyer, 1959). They were then mixed in a VORTEX-2 GENIE and placed in a VEVOR ultrasonic machine for 20 min at 23°C. This procedure was repeated twice for muscle and once for gladius to ensure the removal of all lipids. Samples were placed in a desiccator at room temperature and homogenized using a mortar and pestle to obtain a fine powder. On a SARTORIUS microbalance, 1.5 mg of the powdered sample was weighed to the nearest 0.0001 g where the samples were placed in small Costech Analytical Technologies Inc. tin capsules, for solid samples of 3.5 x 5 mm and stored in a 96-well plate for shipment to perform stable isotope analysis at the UC Davis Stable Isotope Facility.

Isotopic compositions ($\delta^{13}C$ and $\delta^{15}N$) were measured using a mass spectrometer. Values are expressed as ratios relative to international standards: The Vienna Pee Dee Belemnite (VPDB) value was used for ^{13}C and Atmospheric nitrogen (N_2) for ^{15}N. The isotopic ratios (δ) of ^{13}C and ^{15}N of the samples were calculated using the equation:

$$\delta^{\mathrm{H}}\mathrm{X} = [((\mathrm{X}^{H}/ X^{L})_{sample}/ (X^{H}/X^{L})_{standard}) - 1] * 1000 \tag{1}$$

X represents carbon (C) or nitrogen (N), H is the heavy isotope ($\delta^{13}C$ or $\delta\,^{15}N$), and L represents the lighter isotope ($\delta\,^{13}C$ or $\delta\,^{15}N$). The international standards were Vienna Pee Dee Belemnite for C and atmospheric Nitrogen (N_2), and values are expressed in ‰.

2.6 Compound specific isotope analysis of individual amino acids for nitrogen (CISA-AA)

Ten composite samples (one tissue sample containing equal proportions of tissue from different individuals of the same species collected at the same station) of 5 mg well-homogenized powder samples of muscle tissue or gladii were considered for CSIA-AA. These samples were selected considering a ML range of 20 to 35 cm for each system. Likewise, in ETP, three sampling sites were determined, defined according to the previously established size range (Fig. 7). These samples were selected considering an ML range of 20 to 35 cm for HW, ETP, and GC. Likewise, in ETP, three sampling sites were determined, defined according to the previously established size range (Fig. 7). In GC, three size ranges were considered for *D. gigas*: small (20-35 cm), medium (44.3-50.8 cm), and large (52.5-64.3 cm). In contrast, for the CCS, only large specimens (54.3 to 75 cm ML) were included. CSIA-AA performed using the N-acetylmethyl (NACME) method according to the methodology of Corr et al. (2007), where amino acids methylated with 1 ml of an acidified methanol solution for one hour. Then the reagents will be evaporated under a gentle stream of nitrogen, and carbon in an ice bath where dichloromethane (DCM) (2 0.25 ml) integrated to remove excess methanol and water. The amino acid methyl esters will be dissolved in 100 ml of 50 mM (millimolar) ammonium bicarbonate and acetylated in 1 ml of acetic anhydride. Again, the reagents evaporated and for this study, gas chromatography/combustion/isotope ratio mass spectrometry (GC/C/IRMS) was used. The δ^{15}N values were classified as "trophic" protein AA (glutamic acid: Glx; aspartic acid: Asp; alanine: Ala; isoleucine: Ile; leucine: Leu; proline: Pro; valine: Val) or "source" amino acids (AA) (phenylalanine: Phe; methionine: Met; lysine: Lys; tyrosine: Tyr).

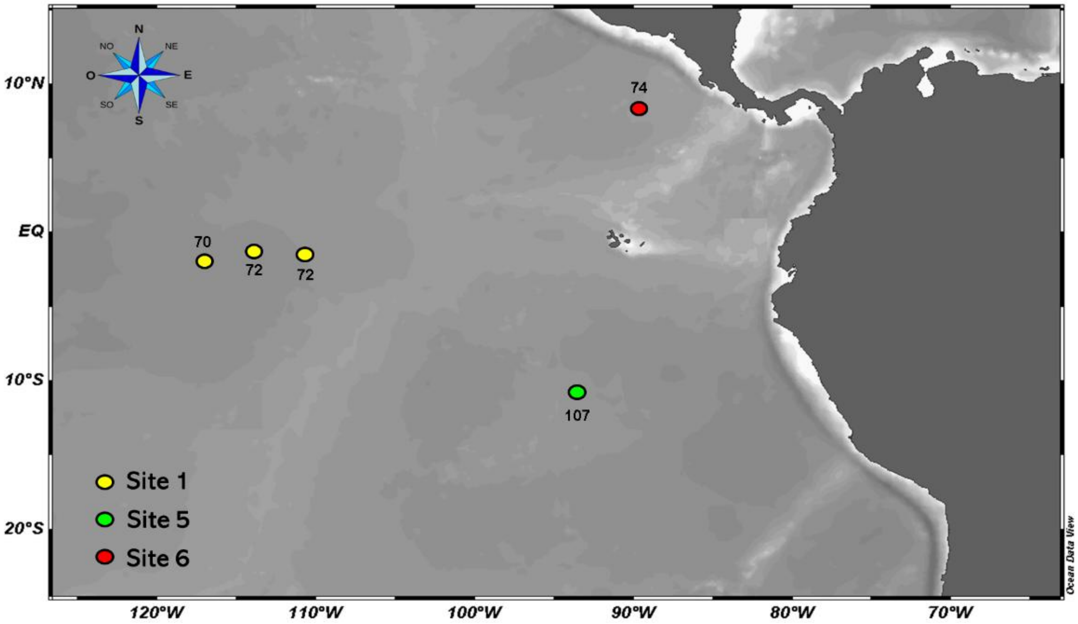

Figure 7. Eastern Tropical Pacific (ETP) sites for *Dosidicus gigas* and *Sthenoteuthis oualaniensis* of 20-35 cm ML.

We utilized the essential amino acid Phenylalanine (Phe) as an indicator of average δ^{15}N of source AA since it is the most stable source and shows little trophic fractionation between $\delta^{15}N_{basal}$ values and values measured in higher trophic level consumers (Chikaraishi et al., 2009; McMahon and McCarthy, 2016). To differentiate between trophic position and feeding location of squid's species, their trophic and source AA δ^{15}N values were averaged to estimate trophic position following the equation of Chikaraishi et al. (2009):

$$TL_{Glu/Phe} = \frac{\delta^{15}N_{Glu} - \delta^{15}N_{Phe} - 3.4}{7.6 + 1} \qquad (2)$$

Where $\delta^{15}N_{Glx}$ represents the trophic AA of glutamic acid (Glx) and $\delta^{15}N_{Phe}$ represents an organism's parent AA value for phenylalanine (Phe). The value (-3.4) represents the isotopic difference between Glx and Phe; 7.6 means the ^{15}N enrichment factor of Glx and Phe amino acids.

2.7 Statistical analysis

Data analysis was performed using R version 4.2.1 (R Core Team, 2022). Multivariate homogeneity was assessed using the PERMDISP. A Permutational Multivariate Analysis of Variance (PERMANOVA) was used to identify significant differences between the mean values of $\delta^{13}C$, $\delta^{15}N$, and ML according to their geographical distribution. A Post Hoc test was determined to examine pairwise comparisons (with Bonferroni correction to produce adjusted significance levels) to identify which systems differed. Likewise, the differences in trophic positions with their respective tissues (muscle and gladius) and their geographical distribution of AIS should be applied. The aim is to determine if there are significant differences with a probability of α=0.05, where the null hypothesis assumes that the population means are the same, while the alternative hypothesis assumes that they are different:

$$Ho: \mu 1 = \mu 2 = \mu 3 = \dots \mu c \qquad (3$$

On the other hand, linear regression models performed to examine the mantle length and the isotopic values between $\delta^{13}C$ and $\delta^{15}N$ where the estimators calculated based on the linear regression model:

$$Y_i = b_0 + b_1 X_i + E_i \qquad (4)$$

Where:

Y_i= Dependent variable

X= Independent variable

b0= Intercept

b_1= Slope

E_i= Estimation error

Subsequently, the coefficients of determination calculated to know the number of data that represent the model, as well as the degree to which the variables vary together in a linear manner. However, to estimate that we have a good model, a residual analysis performed where the assumptions to be met are randomness, normality with the Shapiro-Wilks test, homoscedasticity (Breusch-Pagan), independence (Durbin-Watson) and zero mean (Table A1).

A hierarchical dendrogram was included for the AAsSrc data (excluding Thr) following the criteria of Schonlau (2002), using Pearson's coefficient of estimation as a similarity measure and the average linkage clustering method (UPGMA). A similarity threshold of 80% was set to delimit the clusters.

2.8 Trophic position estimates and the isotopic niche: SIBER-Standard Ellipse Areas

To determine the isotopic niche of each species, $\delta^{13}C$ and $\delta^{15}N$ data were analyzed following the approach of Jackson et al. (2011). The standard ellipse areas (SEA) was calculated to infer the breadth of the trophic isotopic niche of both squid species, using the SIBER (Stable Isotope Bayesian Ellipses in R) package in the R programming language. The ellipse works as an ordering method in Euclidean space as a geometric model consisting of two variables ($\delta^{13}C$ and $\delta^{15}N$) with the same unit of measurement, parts per thousand (‰). The SEA, Bayesian standard ellipse areas (SEA_B) and corrected standard ellipses for sample size (SEA_C) were calculated with the covariance matrix, where the eigenvalues (λ) and eigenvectors (v) define the amplitude of the major axis (a = λ1−1) and the minor axis (b = λ1− 1) and the location is defined by the means of the variables x = $\delta\ ^{13}C$ y = $\delta\ ^{15}N$. SEA_B and isotopic niche parameters were calculated with 95% of the data using the JAGS package, through Monte Carlo simulation. Using Bayes' Theorem, the probable distribution of the population parameter can be estimated, in this case, the area of the standard ellipse, using the a priori information of the parameter and the likelihood function of the data to estimate the a posteriori probability . The mean area and overlap of the isotopic niche are expressed in area units that represent the 95% probability as a graph with the meaning of the posterior area of the SEA_B and the respective credibility intervals.

Chapter 3. Results

3.1 Bulk stable isotope analysis

A total of 99 squids were captured (n = 69 for *Dosidicus gigas* and n = 30 for *Sthenoteuthis oualaniensis*). The largest sizes were recorded in the CCS and the GC, while the smallest were observed off HW. Table 5 presents mantle length (ML) values and their variability for both species, captured in four different systems over different years. Also included are $\delta^{13}C$ and $\delta^{15}N$ values, which reflect differences in carbon and nitrogen isotopic composition between species and locations.

Table 5. Maximum and minimum mantle length (ML) of *D. gigas* and *S. oualaniensis* in ETP: Eastern Tropical Pacific; GC: Gulf of California; CCS: California Current System; HW: Hawaii. The mean and standard deviation (SD±) for ML, $\delta^{13}C$ and $\delta^{15}N$ are shown.

System	**Year**	**Species**	**n**	**ML Range (cm)**		**ML Median and SD**	**$\delta^{13}C$ (‰)**	**$\delta^{15}N$ (‰)**
				Min	**Max**			
ETP	2006	*D.gigas*	22	13.5	42.8	29.4 ± 7.38	-17.04 ± 0.74	11.6 ± 2.06
ETP	2006	*S. oualaniensis*	12	12.1	28.3	20.97 ± 5.23	-17.07 ± 0.48	11.42 ± 2.95
GC	2006	*D.gigas*	27	27.2	64.3	47.41 ± 10.19	-16.38 ± 0.42	18.68 ± 0.88
CCS	2008	*D.gigas*	20	54.3	75	65.11 ± 5.53	-19.1 ± 0.38	13.91 ± 0.81
HW	2010	*S. oualaniensis*	18	13.5	27.1	18.57 ± 4.04	-16.91 ± 0.27	8.26 ± 8.26

3.1.1 Isotopic variation of $\delta^{13}C$ and $\delta^{15}N$ as a function of mantle length

The $\delta^{13}C$ values at all sites ranged between -19‰ and -16‰ (Table 6), indicating a depletion in $\delta^{13}C$ compared to the international standard (VPDB). The most enriched $\delta^{13}C$ values were recorded in the GC, in organisms with a ML of 27.2 to 64.3 cm. In contrast, *D. gigas* from the CCS had the most depleted $\delta^{13}C$ values, despite having a ML between 54 and 75 cm (Table 6, Fig. 21a). On the other hand, the highest $\delta^{15}N$ values were observed in the GC (45 to 75 cm ML), while the lowest (<10‰) were recorded in organisms shorter than 40 cm, predominantly in HW (Table 6, Fig. 22b). The strength and direction of the relationship between $\delta^{13}C$ and $\delta^{15}N$ isotopic values and mantle length (ML) varied among the analyzed geographic systems. *Dosidicus gigas* in the GC and the CCS, as well as *S. oualaniensis* in HW, showed highly significant differences in the relationship between $\delta^{13}C$, $\delta^{15}N$, and ML (Table 6, Fig. 21, 22). However, in all analyzed systems, the linear relationship between these variables was weak ($r^2 \leq 0.3$) (Table 6).

Table 6. Results of the linear regression analysis between squid isotopic values and mantle length from different systems. Notes: r^2: coefficient of determination; *p*-value: statistical significance; *p*-value < α (α = 0.05). * indicate statistically significant differences.

	Eastern Tropical Pacific		**California Current System**		**Gulf of California**		**Hawaii**	
	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
r^2	0.04	0.03	0.09	0.2	0.3	0.07	0.01	0.3
p-value	0.2	0.2	0.1	0.04*	<0.01*	0.1	0.6	<0.01*

Isotopic values and ML showed homogeneous variances (*p*-value = 0.0824 > 0.05), indicating that the null hypothesis of homogeneity of variances is not rejected. This suggests that the variations between the geographic systems are similar, which is suitable for the multivariate PERMANOVA analysis. The PERMANOVA results showed highly significant differences between the factors evaluated (p-value = 0.001 < 0.05). In addition, the Post-Hoc test revealed significant differences in all pairs of geographic systems analyzed (p = 0.006 < 0.05) (Table 7).

Table 7. Post-Hoc test to examine pairwise comparisons of groups (with Bonferroni correction to produce adjusted significance levels). ETP: Eastern Tropical Pacific; GC: Gulf of California; CCS: California Current System; HW: Hawaii. *p*-value: statistics.

Systems	***p*-value**
ETP vs GC	< 0.01
ETP vs CCS	< 0.01
ETP vs HW	< 0.01
GC vs CCS	< 0.01
GC vs HW	< 0.01
CCS vs HW	< 0.01

3.1.2 Isotopic niche with Bulk in SIBER

The $\delta^{15}N$ and $\delta^{13}C$ isotopic values (n = 99) from muscle tissue samples of *D. gigas* and *S. oualaniensis* were used to calculate standard ellipses per species and geographic area (Fig. 8). *Dosidicus gigas* of the GC and CSS showed no overlap with the results of any other system, except between the GC and the ETP. *D. gigas* from the GC had the highest $\delta^{15}N$ values, while *D. gigas* from the CCS had the most negative $\delta^{13}C$ values compared to the other systems. In GC and CCS, the SEA_B presented relatively similar isotopic areas, but in ETP, they were smaller in *D. gigas* than in *S. oualaniensis* (Fig. 8). Furthermore, the SEA_B of *D. gigas* from the ETP overlapped with the *S. oualaniensis* ellipse, but notable differences were observed in the shape and position of the ellipses. The SEA$_C$ of *S. oualaniensis* from the ETP had a narrower range in δ^{13}C but a wider range in δ^{15}N, whereas *D. gigas* showed a wider range in δ^{13}C. *S. oualaniensis* from HW was located near the ETP overlap zone, standing out for presenting the lowest δ^{15}N values (Fig. 8).

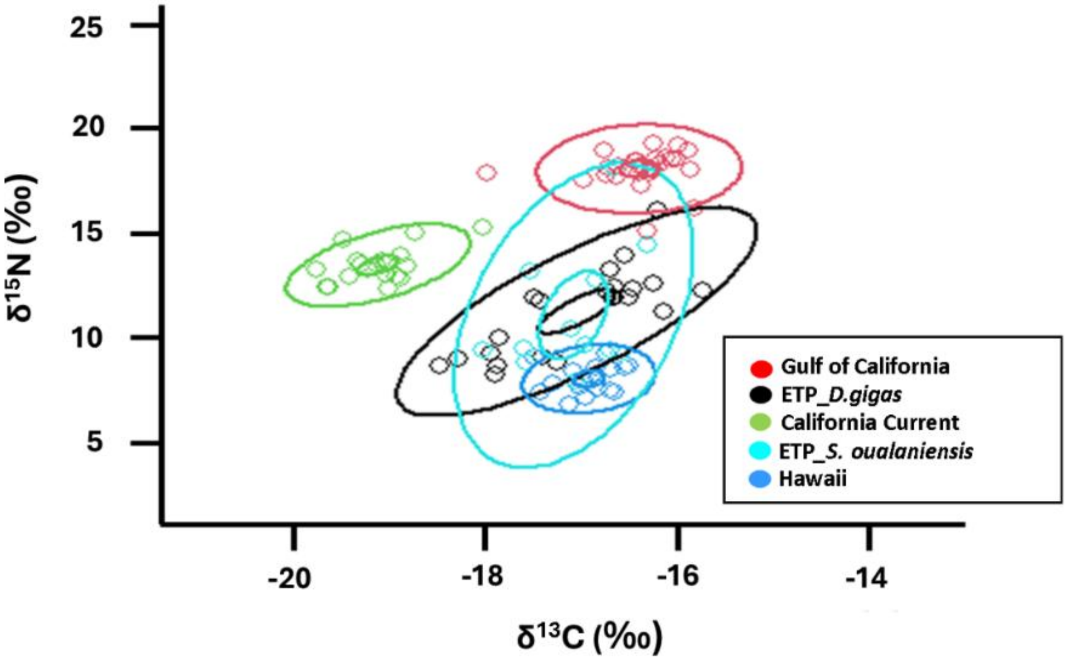

Figure 8. Standard ellipse of the isotopic niches of *D. gigas* and *S. oualaniensis* in different systems.

The isotopic niche between ETP-*D. gigas* and ETP-*S. oualaniensis* overlapped by 31%, and the SEA$_B$ varied between both species and geographic systems (Fig. 9). GC and CCS had similar SEA$_B$ values; HW had the lowest value, while ETP-*S. oualaniensis* had the highest value, followed by ETP-*D. gigas*. Isotopic niche metrics obtained for the five groups analyzed showed that ETP-*S. oualaniensis* had the largest total area (TA), followed by ETP-*D. gigas*, while HW had the smallest area. Similarly, in the SEA$_C$, ETP-*S. oualaniensis* had the largest amplitude, followed by ETP-*D. gigas*, and HW the smallest (Table 7).

Table 8. Statistical summary of each group based on Total Area (TA), Standard Ellipse Area (SEA), and Corrected Standard Ellipse Area (SEA$_C$).

Systems	**Isotopic niche breadth ranges and trophic overlap**		
	TA	SEA	SEA$_C$
ETP-*D. gigas*	8.78	3.18	3.34
ETP-*S. oualaniensis*	9.56	4.49	4.93
GC	5.43	1.23	1.28
CCS	2.95	0.86	0.91
HW	1.82	0.60	0.64

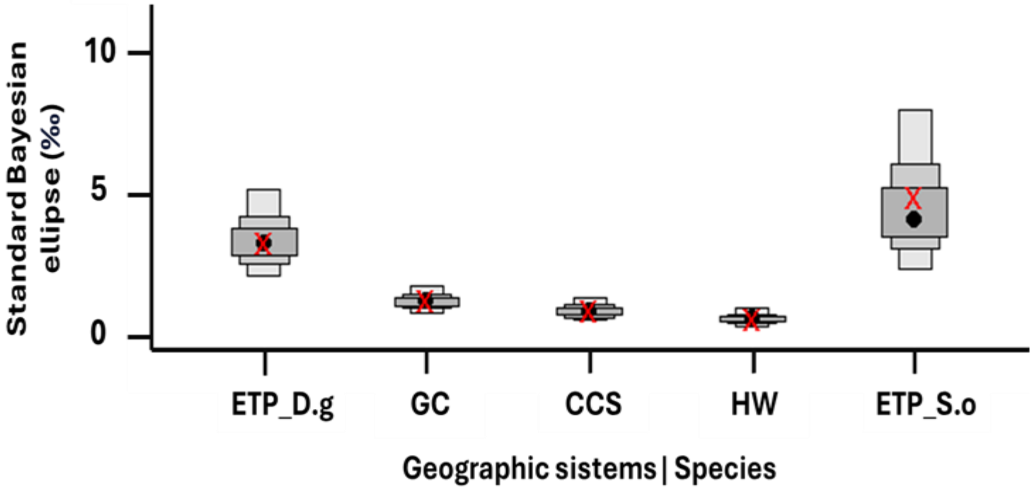

Figure 9. Standard Bayesian ellipse (SEA_B) areas from squid species by geographic areas. Red dots indicate the average value of the SEA_B for each geographic system**.** ETP_D.g: *D. gigas,* ETP_S.o: *S.oualanensis*, GC: Gulf of California, CCS: California Current System, HW: Hawaii.

To obtain a finer resolution of potential competition between squid species in the ETP, six stations at relatively similar latitudes (Fig. 10) were used to assess isotopic niche overlap between *D. gigas* (n = 13) and *S. oualaniensis* (n = 10). The samples were grouped considering the number of specimens per species and MLs (20-35 cm).

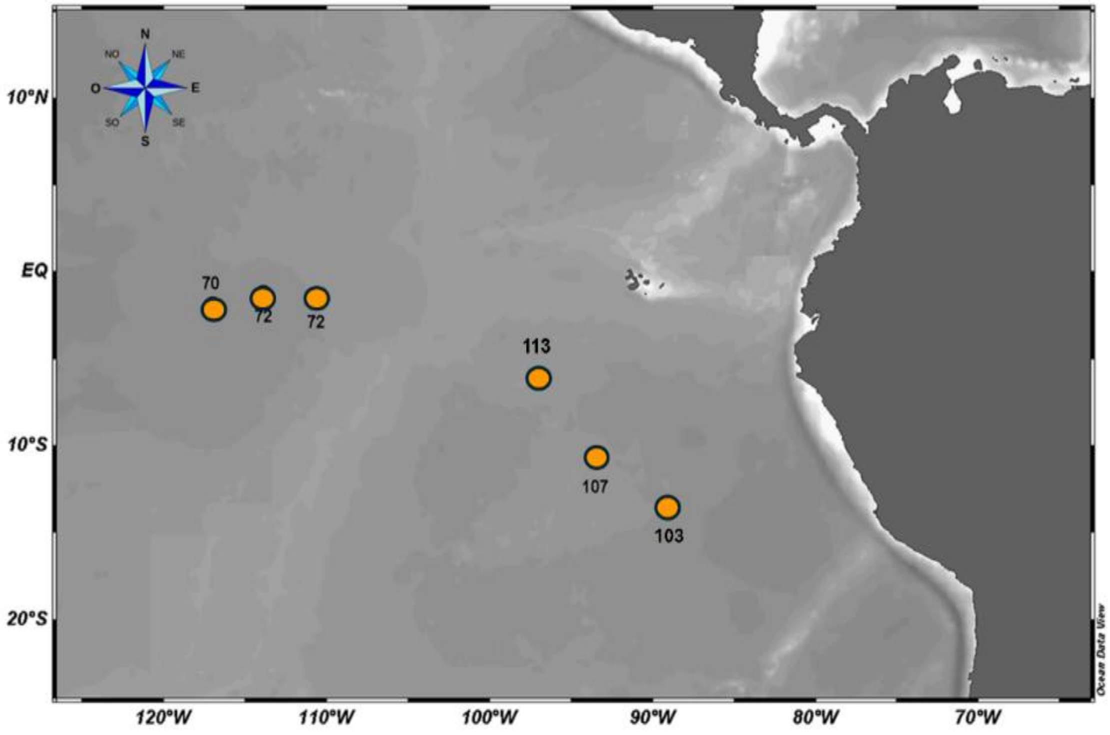

Figure 10. Subgroups to evaluate interspecific competition between *D. gigas* and *S. oualaniensis.*

The percentage for overlaps (36%) (Figs. 11, 12) was a little bit higher in comparison to the calculated overlap considering all samples from ETP (Fig. 10). These isotopic niches per species exhibited differences in the position, amplitude, and width for *S. oualaniensis*, characterized by a lower variation in δ^{15}N and a smaller total area (TA = 4.92) in contrast to *D. gigas*. On the other hand, *D. gigas* presented a greater variation in both δ^{15}N and δ^{13}C, with a larger total area (TA = 8.75). *D. gigas* had a larger SEA_C (4.30 ‰) than *S. oualaniensis* SEA_C (3.20 ‰) (Fig. 12).

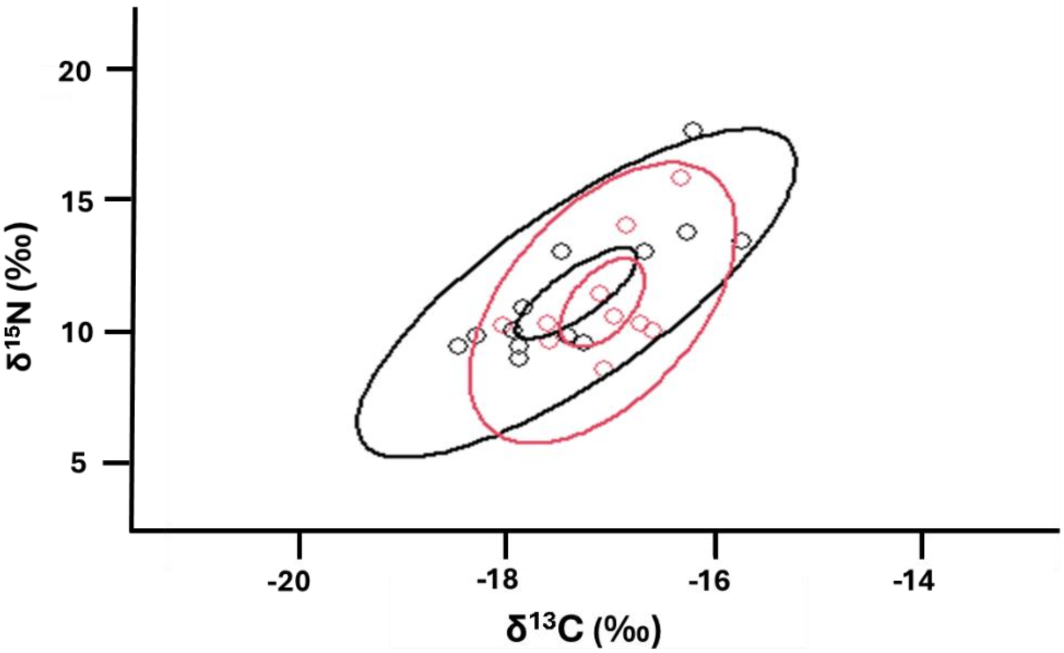

Figure 11. Standard Bayesian Ellipses of *D. gigas* and *S. oualaniensis* from relatively similar latitudes at the Eastern Tropical Pacific.

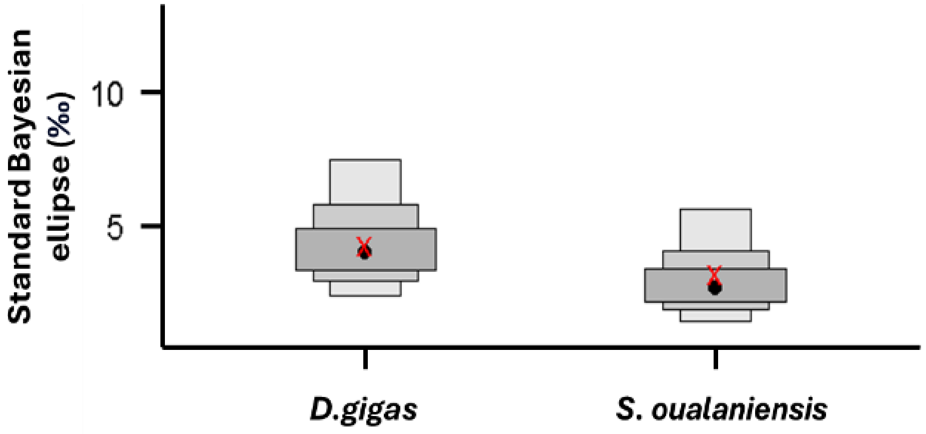

Figure 12. Standard ellipse of isotopic niches. Subgroups of *D. gigas* (black) and *S. oualaniensis* (red) in the Eastern Tropical Pacific (ETP).

3.2 Compound specific stable isotope analysis of amino acids (CSIA-AA)

The average values of $\delta^{15}N$ for each AA considering both species together were represented in a box plot, which varies from -20‰ to 26‰ and showed substantial variability between the Aas (Fig. 13). In general, trophic amino acids (AAs_{Tro}) exhibited the highest $\delta^{15}N$ enrichment, whereas source amino acids (AAs_{Src}) had the lowest values. Thr showed the lowest average $\delta^{15}N$ values (median reaching approximately -20‰) among all AAs. Met exhibited the highest variability among AAs_{Srs} with a median close to 10‰; but this AA was not detected in *D. gigas* specimens from the CCS and GC regions. Due to these inconsistencies and because Thr, Ser, and Gly values do not consistently follow the expected behavior of source AAs in other taxonomic groups (McMahon and McCarthy, 2016), they were excluded from further statistical analysis. Phe and Lys were selected as the main AAs_{Src} due to greater stability across samples. In total, nine AAs were included in our analysis to calculate trophic proxies: seven AAs_{Tro} (i.e. Glx, Asx, Ala, Ile, Leu, Pro, and Val) and two AAs_{Src}, i.e. Phe and Lys.

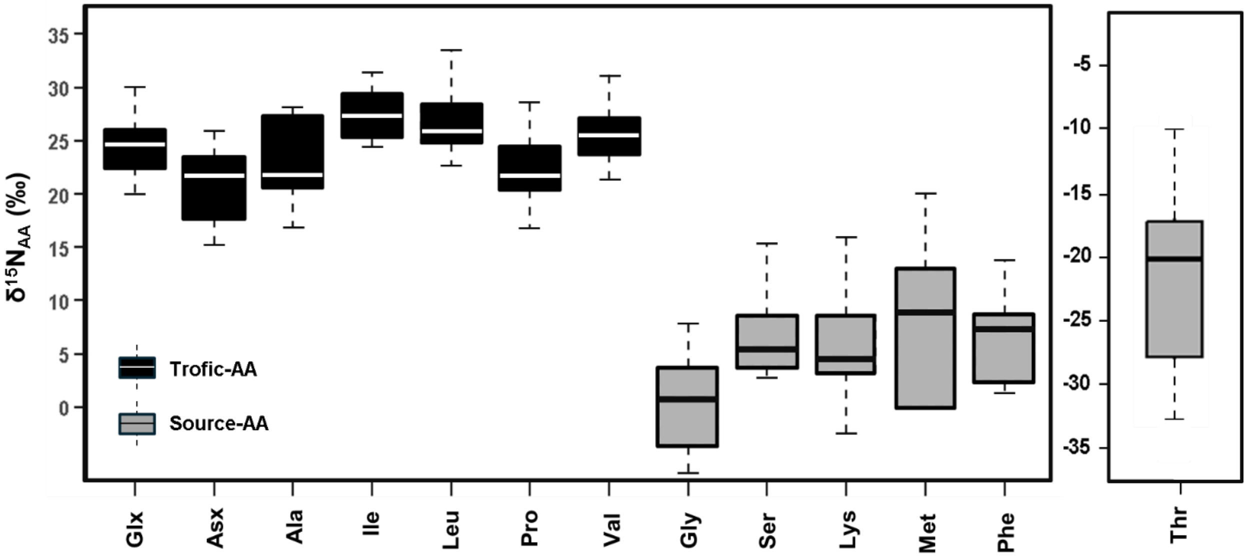

Figure 13. Box plots of $\delta^{15}N_{AA}$ data of 13 trophic and source amino acids in the muscle tissue of *D. gigas* and *S. oualaniensis*.

Consistent differences in $\delta^{15}N_{AA}$ values were observed between *D. gigas* and *S. oualaniensis* across the four systems evaluated (Fig. 14). $\delta^{15}N_{Src\text{-}AA}$ corresponded to the average of the source amino acids (e.g., Phe, Lys), while $\delta^{15}N_{Tro\text{-}AA}$ was obtained from the average of the trophic amino acids (e.g., Glx, Ala, Leu, Val, Pro, Asxp, Ile). Individually, Phe (source amino acid) and Glx (trophic amino acid) values were the highest mean. $\delta^{15}N_{Src\text{-}AA}$ values for *D. gigas* from the GC were the highest across all geographic areas, with estimates ranging from approximately 13‰ to 14‰. $\delta^{15}N_{Src\text{-}AA}$ and Phe values for *D. gigas* from the CCS were variable, ranging from 2‰ to 10‰. In contrast, $\delta^{15}N_{Src\text{-}AA}$ values were consistently lower at HW and the ETP (1‰ to 7‰), with the lowest values found at Site 1. *Dg* and Site 5. *Dg* (~1‰) (Fig. 14). The variability in Glx and $\delta^{15}N_{Tro\text{-}AA}$ values was pronounced for *D. gigas*, with the highest values in GC being for larger individuals. In particular, Glx and $\delta^{15}N_{Tro\text{-}AA}$, an ontogenetic change associated with the growth of squid in GC, was observed, where small sizes (GC. S = 20 to 35 cm ML), medium sizes (GC. M = 44.3 to 50.8 cm ML) and large sizes (GC. L = 52.5 to 64.3 cm ML) showed a progressive increase in Glx and $\delta^{15}N_{Tro\text{-}AA}$ values as size increased. In contrast, squid from ETP and HW had Glx, and $\delta^{15}N_{Tro\text{-}AA}$ values ranged from 20‰ to 27‰; *S. oualaniensis* had slightly higher $\delta^{15}N_{Tro\text{-}AA}$ and Glx values at Site 1. So, Site 5. So, and Site 6. So, than *D. gigas* at Site 1. *Dg*, Site 5. *Dg*, and Site 6. *Dg* (Fig. 14).

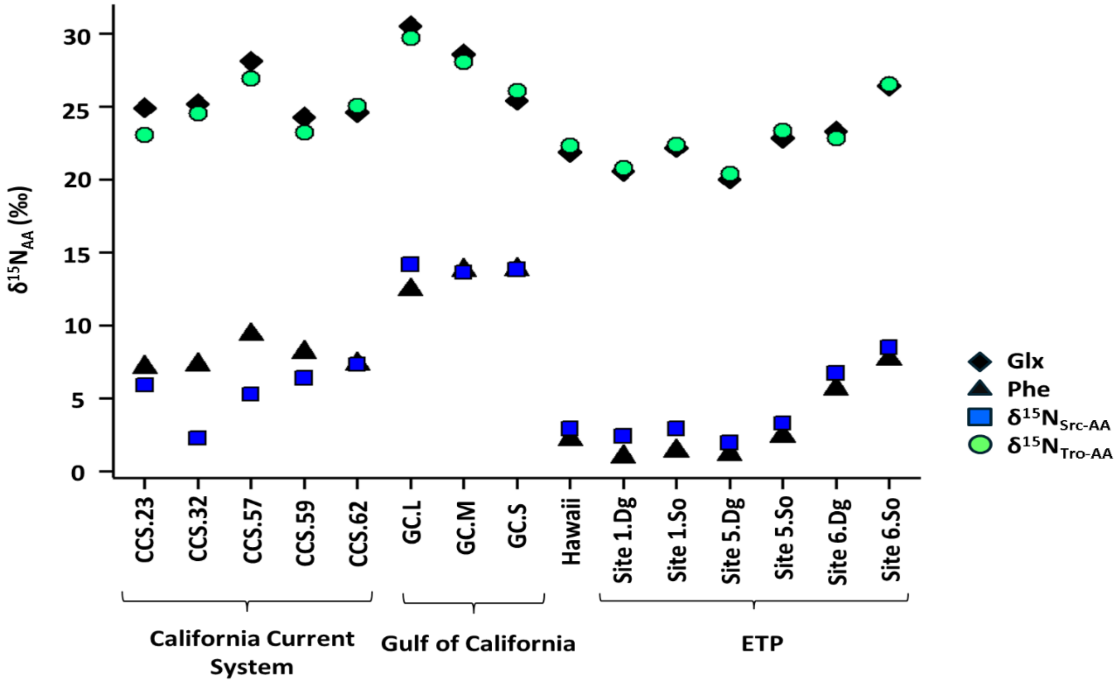

Figure 14. Comparison of $\delta^{15}N_{AA}$ between *D. gigas* (Dg) and *S. oualaniensis* (So) to support the use of Glx as the most reliable trophic amino acid for estimating trophic position. Sites as defined in Figure 6.

The two trophic position proxies ($\delta^{15}N_{Glx\text{–}Phe}$ and $\delta^{15}N_{Tro\text{–}Phe}$) exhibited similar patterns of variation regardless of squid species and geographic areas indicating that both tracers are consistent trophic proxies (Fig. 15). Although the $\delta^{15}N_{Glx\text{–}Phe}$ values tended to be slightly higher than $\delta^{15}N_{Tro\text{–}Phe}$. *Dosidicus gigas* from the CCS (only large sizes were worked with in this system) exhibited relatively low variability among sites, with CCS.59 presenting the lowest values for both $\delta^{15}N_{Glx\text{–}Phe}$ and $\delta^{15}N_{Tro\text{–}Phe}$ (15–18.5 ‰), corresponding to large individuals (66.9–72.4 cm ML), while the highest values were found in CCS.57 for small sizes (31 cm

ML). In contrast, *D. gigas* from the GC exhibited a clear increase in both indicators ($\delta^{15}N_{Glx–Phe}$ and $\delta^{15}N_{Tro–Phe}$ values = 11.5–18 ‰) with increasing body size (Fig. 15). The highest trophic position indicators ($\delta^{15}N_{Glx–Phe}$ and $\delta^{15}N_{Tro–Phe}$ values = 17.7 to 21.01‰) were found for *D. gigas* and *S. oualaniensis* from the ETP and HW. Among the species, *S. oualaniensis* exhibited the highest $\delta^{15}N_{AA}$ values (Fig. 16) for both trophic indicators; trophic indicators for *S. oualaniensis* were similar in the ETP and HW. Notably, *D. gigas* from the ETP had relatively lower or comparable values to *S. oualaniensis* from the same sites. In contrast, the lowest $\delta^{15}N_{AA}$ values were observed for *D. gigas* from the CCS, followed by those from the GC (Fig. 16).

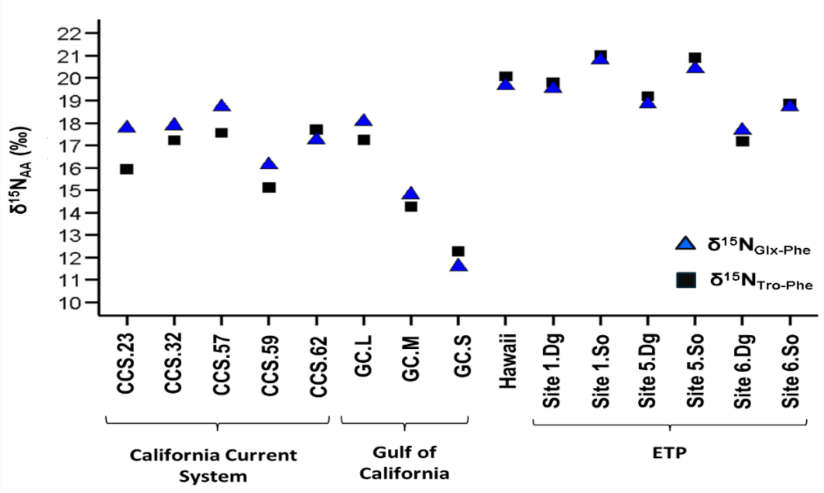

Figure 15. Use of $\delta^{15}N_{Tro-Phe}$ and $\delta^{15}N_{Glx-Phe}$ as indicators of trophic position for *D. gigas* (Dg) and *S. oualaniensis* (So) in different systems.

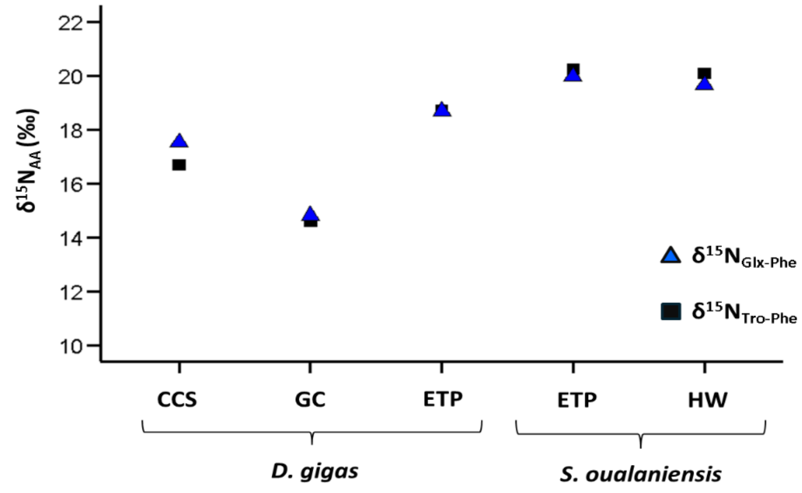

Figure 16. Average $\delta^{15}N_{Tro–Phe}$ and $\delta^{15}N_{Glx–Phe}$ values by system, representing trophic position of *D. gigas* and *S. oualaniensis* across different regions.

Considering the relationship in $\delta^{13}C_{Bulk}$ values (indicating primary producers) and $\delta^{15}N_{Tro}$ in *D. gigas* and *S. oualaniensis* from the CCS, GC, HW and ETP, distinct geographic clusters emerge separated mainly by $\delta^{13}C_{Bulk}$ (Fig. 17). The most enriched values of $\delta^{15}N_{Tro}$ and $\delta^{13}C_{Bulk}$ were found in GC for *D. gigas*, followed by specific ETP sites: Site 6. So, Site 1. So, Site 5. So, and HW with *S. oualaniensis*. In contrast, *D. gigas* from the CCS had the most depleted $\delta^{13}C_{Bulk}$ values, and a slight trend toward higher $\delta^{15}N_{Tro}$ values similar than those from the GC. There was a notable variability in trophic position (TP) between *D. gigas* and *S. oualaniensis* (Fig. 18). Interestingly, higher TP values were recorded at several ETP sites and HW, suggesting high trophic positions in small individuals (20–35 cm ML). Similarly, only *D. gigas* at site CCS.57, corresponding to small sizes (31 cm ML), presented the highest trophic level of all CCS sites. In the GC region, *D. gigas* showed an ontogenetic increase in TP with increasing body size. Furthermore, *S. oualaniensis* consistently presented higher trophic positions than *D. gigas* in most systems.

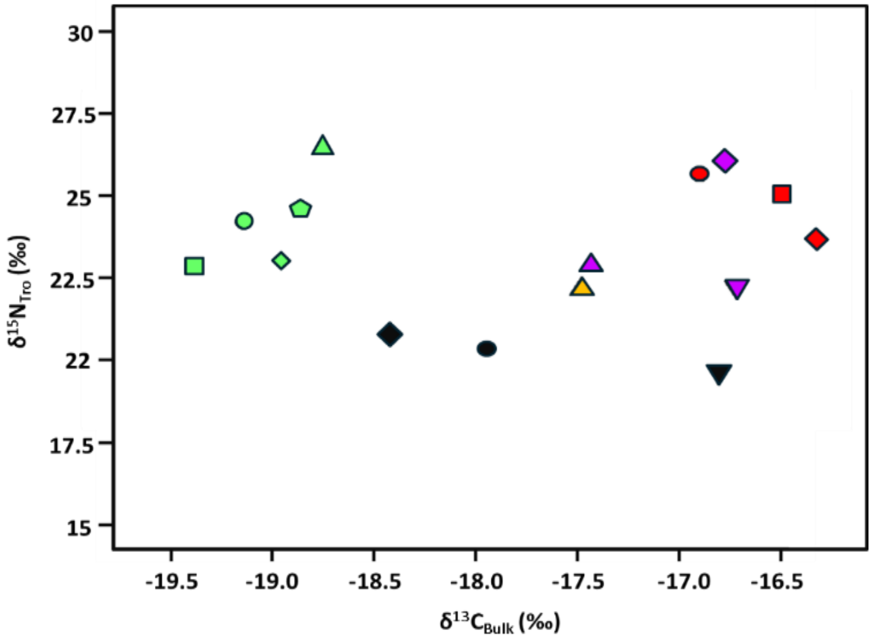

Figure 17. Variability of $\delta^{15}N_{Tro}$ versus $\delta^{13}C_{Bulk}$ values in *D. gigas* and *S. oualaniensis* across different systems. CCS (green), GC (red), ETP. Dg (black), ETP. S.o (purple), and Hawaii (orange).

Hierarchical clustering analysis showed a clear separation between *D. gigas* and *S. oualaniensis* in the different geographic systems, according to the $\delta^{15}N_{Src}$ (Phe, Lys, Met, Ser, and Gly) values (Fig. 19). The first group includes the ETP sites (Site 5. *So*, Site 1. *So*, Site 1. *Dg*, Site 5. *Dg*, Site 6. *Dg* and Site 6. *So*) and HW; the second group includes the CCS sites (CCS57, CCS59, CCS23, CCS32 and CCS62) and the third group is composed of the GC sites (GC.S and GC.M). However, GC.L shows a clear clustering of the first group of ETP and HW (Fig. 19).

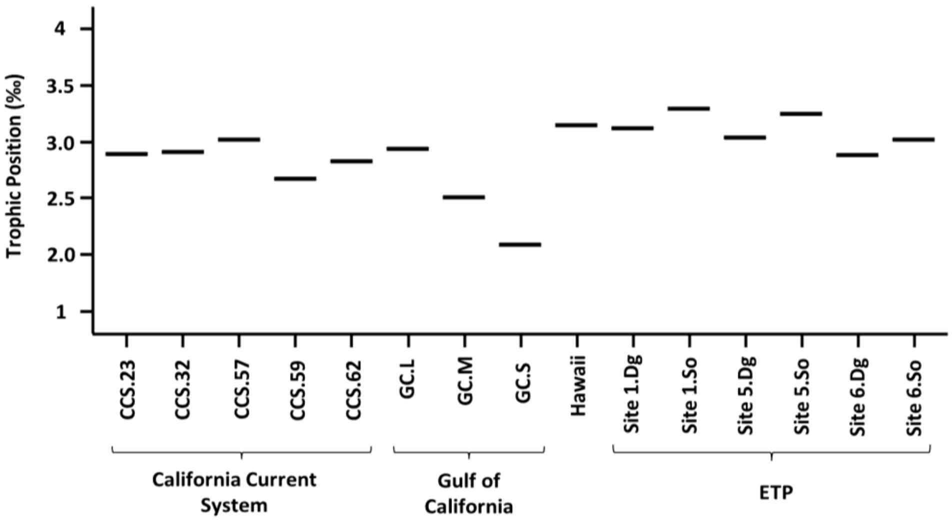

Figure 19. Estimated trophic position of *D. gigas* (Dg) and *S. oualaniensis* (So) using δ^{15}N values of amino acids and equation 2 (see methods) .

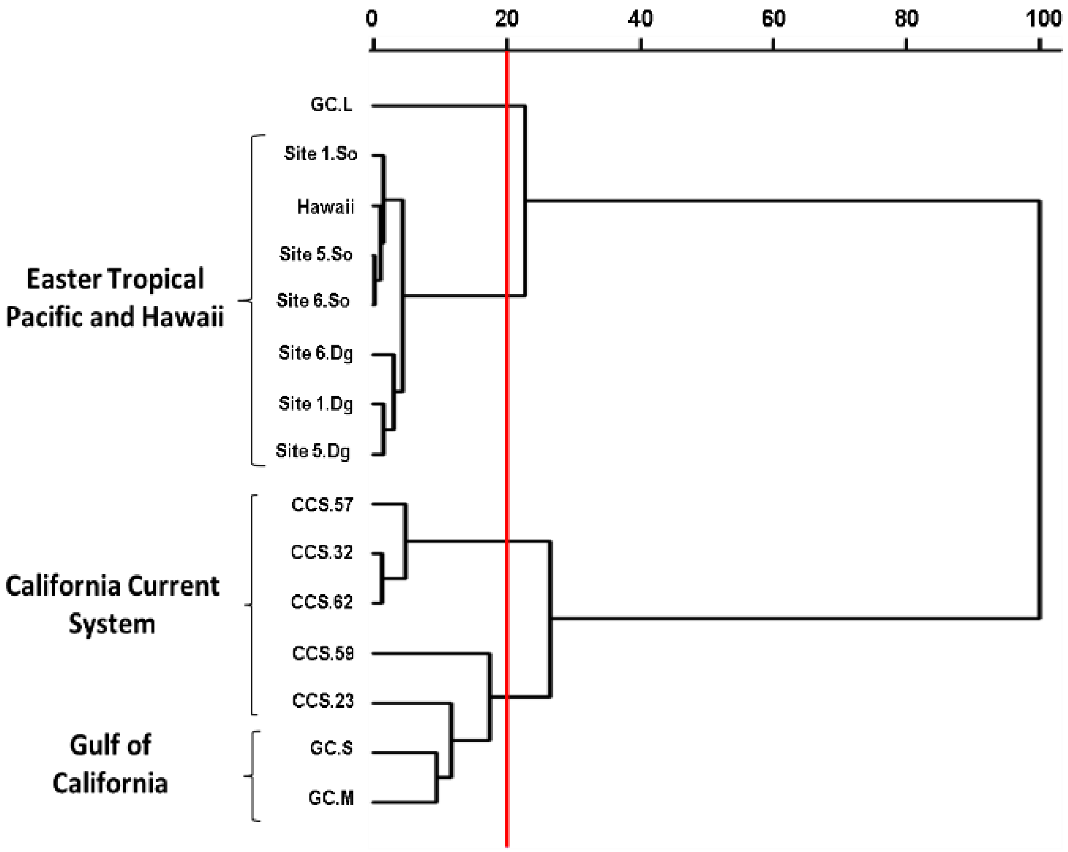

Figure 18. Resultant dendrogram from hierarchical clustering analysis of *D. gigas* and *S. oualaniensis* in different geographical systems based on δ^{15}N$_{Src\text{-}AA.}$

Chapter 4. Discussion

4.1 Relationship between squid mantle length and $\delta^{13}C$ and $\delta^{15}N$

The relationships between *D. gigas* mantle length (ML) and $\delta^{13}C$ or $\delta^{15}N$ values were variable among study sites, suggesting different ontogenetic shifts in diet, habitat, or movement (Table 5; Fig. A1, A2, A3). *D. gigas* exhibited a clear ontogenetic enrichment in $\delta^{15}N$ values with increasing ML in the GC and the CCS, indicating that larger squid feed at successively higher trophic levels. These results are consistent with previously documented ontogenetic enrichment in $\delta^{15}N$ values among individuals from the GC, supporting earlier observations with a gradual shift toward higher trophic level prey as *D. gigas* grow (Ruiz-Cooley et al., 2004, 2006, 2010; Ruiz-Cooley and Gerrodette, 2012). However, the relationship between mantle length (ML) and $\delta^{13}C$ and $\delta^{15}N$ values was relatively weak, probably due to the limited size range in our samples. In the ETP, the analyzed specimens mainly presented lengths between 20 and 35 cm ML and, in the case of the CCS, only large sizes (Table 5, Fig. A2, A3). In contrast, in the GC, a wider range was included, from small to large sizes, although still narrower than that reported in previous studies for this region, where organisms from 22 to 82 cm M were analyzed (Ruiz-Castro, 2002; Ruiz-Cooley et al., 2004, 2006, 2010; Ruiz-Cooley and Gerrodette, 2012). Stomach content analysis, reflecting the most recent diet and conducted during intense El Niño periods (1995–1997, 1998–2000, 2005–2007, and 2016–2017) in the GC and Pacific off Baja California Sur consistently found myctophids such as *Synodus lucioceps* (California lizardfish) and *Merluccius angustimanus* (Panama hake), *Benthosema panamense*, *Triphoturus mexicanus*, and *Diogenichthys laternatus* as the main prey of *D. gigas* from 14.5 to 87.5 cm ML (Markaida and Sosa-Nishizaki, 2003; Markaida, 2006a; Rosas, 2007; Markaida et al., 2008; Bazzino et al., 2010; Portner et al., 2020). This preference for mesopelagic fishes appears linked to the GC´s high productivity which produce a well-defined oxygen minimum zone (OMZ; where O_2 falls below ~ 1 ml l^{-1}) between 400 and 800 m in the GC, which provides a vertically favorable mesopelagic habitat that concentrates lanternfishes (Lavenberg and Ebeling, 1967; Robison, 1972; Moser et al., 1974). Evidence from electronic tagging indicates that *D. gigas* feeds during the day at depths greater than 200 m (Gilly et al., 2006a). Consequently, prey consumed in deep waters could be partially digested or even excreted before the squid rises to the surface, where it is captured by the fishing fleet mainly at night (Ruiz-Cooley et al., 2010). However, digestion times in *D. gigas* are not well documented, and the few studies carried out mention that in squid, it ranges between 2 and 10 hrs at temperatures of 16 to 22 °C (Ponte et al., 2017). This behavior is consistent with its diurnal vertical migration pattern and that of other species, such as myctophids, which also move to shallow waters at night, e.g., *B. panamense* in the GC (Robison, 1972; Moser et al., 1974; Markaida and Sosa-Nishizaki, 2003; Alegre et al., 2014). This could explain the high presence of epi-mesopelagic fish recorded in the squid stomach content analysis, which reflects the most recent diet, corresponding to the hours prior to capture (probably less than 24 hours) (Ruiz-Cooley et al., 2006). Measurements of $\delta^{15}N_{Bulk}$ in squid muscle, which reflect the integrated diet over 1–3 months (Ruiz-Cooley et al., 2006). Consistent with previous research in the same region (Ruiz-Cooley et al., 2004, 2006, 2010; Ruiz-Cooley and Gerrodette, 2012). This pattern suggests that the observed ontogenetic enrichment of $\delta^{15}N$ could be due to *D. gigas* fast grow; as it becomes bigger, it consumes larger prey at progressively higher trophic positions. CSIA-AA analysis supports this trend; the two trophic position (TP) indicators calculated from individual AA $\delta^{15}N$ ($\delta^{15}N_{Glx\text{-}Phe}$ and $\delta^{15}N_{Tro\text{-}Phe}$), together with the estimated TP, reveal lower values for small individuals (20–35 cm ML) and higher values for large individuals (52.5 to 64.3 cm ML) (Figs. 15-18). These results confirm the ontogenetic shift in diet in the GC (Figs. 15-18).

In the CCS, a weak relationship is observed between mantle length (ML) and the values of $\delta^{15}N$ ($r^2 = 0.2$) and $\delta^{13}C$ ($r^2 = 0.09$) of *D. gigas*, however, a slight ontogenetic enrichment is shown for larger specimens (Fig. A2b, A3b), which could be conditioned by the absence of small and medium-sized individuals in the area, making it difficult to identify a progressive pattern in the $\delta^{15}N$ associated with growth, given that *D. gigas* found in the CCS were considered migratory (Ruiz-Cooley et al., 2013). In various stations from the Eastern North Pacific, Ruiz-Cooley et al. (2010) documented increasing but highly variable $\delta^{13}C$ and $\delta^{15}N$ values along bulk tissue samples of *D. gigas* proostracum, indicating an opportunistic feeding pattern based on prey availability. In the CCS, as *D. gigas* grows (> 50 cm ML), it consumes organisms of higher trophic position, such as *Merluccius productus, Tarletonbeania crenularis, Stenobrachius leucopsarus,* and *Engraulis mordax* according to stomach content analysis (Field et al., 2007). According to these authors, the species moves opportunistically towards coastal areas during the winter to feed on resources such as Pacific hake and rockfish (*Sebastes spp.*), coinciding with the seasonal migration of Pacific hake (Holmes et al., 2008) also documented coastal movements, where baseline $\delta^{15}N$ values differs notably from those of oceanic waters. *D. gigas* consumes larger prey, despite the remarkable dietary plasticity of this species, it feeds on prey of different sizes, including post juvenile stages, but its diet is mainly composed of small fish and invertebrates (Ehrhardt, 1991; Nigmatullin et al., 2001; Markaida and Sosa-Nishizaki, 2003; Markaida, 2006a; Field et al., 2007; Field et al., 2013). A previous study in the CCS, found high variability in $\delta^{15}N$ values with *D. gigas* growth, where different individual squid exhibited increases, decreases or flat $\delta^{15}N$ values as squid became bigger (Ruiz-Cooley et al., 2013). These authors interpreted these patterns as evidence of opportunistic predation while migrating from geographic areas with distinct $\delta^{15}N$ baseline values (as indicated by $\delta^{15}N_{Phe}$) towards the CCS; once they established in this ecosystem, the $\delta^{15}N$ values homogenized at large sizes. Hence, isotopic patterns throughout the proostracum encompass the entire dietary history and habitats utilized by squid throughout an individual´s life (Ruiz-Cooley et al., 2010), while $\delta^{15}N$ in muscle represents an average value of its diet consumed for at least two months (Ruiz-Cooley et al., 2006). Stomach content analysis is based only on individuals captured at night and represents a snapshot of the diet. Because *D. gigas* seems to remain within the GC (Markaida et al., 2005; Gilly et al., 2006a; Gilly et al., 2006b), and no large shifts in $\delta^{15}N$ baseline variation are expected given that denitrification seems to be the dominant N cycling process (Rafter et al., 2012a), the observed ontogenetic changes in $\delta^{13}C$ and $\delta^{15}N$ reflect shifts in diet associated with growth. In contrast, no clear ontogenetic isotopic trend associated with size was evident in the CCS, since large *D. gigas* $\delta^{15}N_{Bulk}$ (Fig. A2b, A3b), trophic position indicators ($\delta^{15}N_{Glu\text{-}Phe}$ and $\delta^{15}N_{Tro\text{-}Phe}$), and TP estimates remained relatively constant among sites (CCS.23 to CCS.62, Fig. 15-18).

Considering the ETP results, a marked variability in $\delta^{13}C$ and $\delta^{15}N$ was observed along *D. gigas* MLs (Fig. A2c, A3c), suggesting a diverse diet for smaller individuals (Table 4). This interpretation is consistent with the stomach content analysis performed in Santa Rosa, Ecuador, where small specimens (15–20 cm ML) presented a varied diet dominated by fish (*Lampanyctus spp., Myctophum spp.*); in medium specimens (25–45 cm ML), the consumption of cephalopods (Gonatidae, Ommastrephidae, Onychoteuthidae) predominated, and in large specimens (45–55 cm ML), *Myctophum spp*. became prominent again (Rosas-Luis and Chompoy-Salazar, 2016). In more coastal waters off Peru, Alegre et al. (2014) documented a progressive increase in cephalopod consumption as *D. gigas* grew. Euphausiids also increased their share with size, except in the smallest individuals. In contrast, the proportion of mesopelagic fishes such as *Vinciguerria lucetia* and *Myctophum spp*. decreased markedly with size, from 21% to 5.6% and from 7.2% to 1.3%, respectively. More recent studies in the same system reveal a distinctive pattern where small specimens (20 to 40 cm ML) feed mainly on euphausiids (*Nictiphanes simplex*) and teleosts (*Vinciguerria lucetia*), while medium (41 to 60 cm ML) and large specimens (61 to 80 cm LM) also include cephalopods and pelagic fishes such as *Engraulis ringens* and *Anchoa nasus* (Cisneros et al., 2024). At ETP sites near Ecuador, including coastal and oceanic areas, variable $\delta^{15}N$ values were detected, but with an increasing trend with increasing size, supporting their opportunistic behavior and tendency to consume higher trophic level prey (Ruiz-Cooley et al., 2004, 2006, 2010; Ruiz-Cooley and Gerrodette, 2012). Other studies in Peruvian waters have also reported increases in $\delta^{13}C$ and $\delta^{15}N$ with growth, especially in individuals >20 cm ML, along with high variability in these isotopic signatures (Argüelles et al., 2012). This suggests that both juveniles and adults explore a wide range of habitats and maintain flexible trophic strategies (Shchetinnikov, 1992; Markaida and Sosa-Nishizaki, 2003; Markaida, 2006a; Field. et al., 2007; Ibáñez et al., 2008; Ruiz-Cooley et al., 2010). Furthermore, it has been observed that small specimens (≈20 cm ML) can present $\delta^{15}N$ values similar to those of much larger individuals (≈80 cm ML), which indicate that, at certain ontogenetic stages, both access comparable trophic resources (Argüelles et al., 2012). Therefore, the variability in $\delta^{15}N$ values as a function of size in *D. gigas* in the ETP (Fig. A2c, A3c) could reflect a diverse diet, encompassing different types and sizes of prey, from euphausiids to cephalopods and fish (Rosas-Luis and Chompoy-Salazar, 2016), especially in small individuals (20–35 cm ML).

In *S. oualaniensis* from HW, $\delta^{15}N$ and $\delta^{13}C$ values increased with body size, supporting the existence of ontogenetic shifts in diet (Fig. A2d, A3d). Analyses of stomach contents from 16.8 to 23.4 cm ML consuming a variety of mesopelagic fishes (Myctophidae, Anoplogasteridae, Omosudidae) and cephalopods (Enoploteuthidae, Onychoteuthidae, Ommastrephidae) (Parry, 2003, 2006, 2008). This is evidence of a marked ontogenetic shift towards higher trophic levels with growth in HW. In other systems, such as the ETP, small individuals (4 to 10 cm ML) fed primarily on euphausiids, amphipods, and fish larvae. At the juvenile stage (10 to 15 cm ML), their diet became predominantly oriented towards myctophids, whereas adults (15 to 36.5 cm ML) incorporated lanternfish and other squids (Shchetinnikov, 1992). Taken together, variation in prey type and size could explain the increase in $\delta^{15}N$ even at relatively small sizes (20–35 cm ML). This pattern is also reflected in the CSIA-AA results, which indicate that *S. oualaniensis* in HW and the ETP exhibits high TPs (Fig. 15-18) and high values for TP estimators ($\delta^{15}N_{Glx-Phe}$ $\delta^{15}N_{Tro-Phe}$), likely associated with both food availability and preference for higher trophic level prey.

4.2 Geographic variation of $\delta^{13}C$ and $\delta^{15}N$ and isotopic niches

The significant differences in $\delta^{13}C$ and $\delta^{15}N$ values of *D. gigas* tissues between geographical areas (Table 6) are probably due to variations in carbon and nitrogen cycling processes, primary productivity, and dietary composition of the squid. In the case of $\delta^{15}N$, its variability occurs at both spatial and temporal scales (Goering et al., 1990), in response to changes in physical and chemical factors (Dawson and Brooks, 2001), such as N_2 fixation and assimilation (Hoering and Ford, 1960), the manipulation and remineralization of organic matter (Miyake and Wada, 1971; Tieszen et al., 1983; Checkley and Miller, 1989) and oxidation-reduction processes, such as nitrification and denitrification (Miyake and Wada, 1971). For its part, variations in $\delta^{13}C$ are linked to carbon cycle processes, particularly carbon fixation through the photosynthesis process and remineralization by bacterial activity (Farquhar et al., 1989; Brugnoli and Farquhar, 2000). Previous studies on *D. gigas* muscle and gladius, conducted along a broad latitudinal gradient in the ETP, indicate that geographic differences in $\delta^{15}N$ depend on both location and assimilated diet, in addition to the variability in organic deposits, remineralization of organic matter, and physicochemical properties between regions (Ruiz-Cooley et al., 2010; Ruiz-Cooley and Gerrodette, 2012). These results provide strong evidence of the marked spatial variation in the species. A determining factor is the availability of NO_3^- in the euphotic zone and the surface isotopic signal of $\delta^{15}N_{NO_3^-}$, since phytoplankton incorporate it during photosynthesis, thus fixing the value of $\delta^{15}N$ (Wada and Hattori, 1991; Somes et al., 2010). Differences in the source and extent of NO_3^- utilization can be transmitted along the food web through diet, from primary consumers to top predators (Ruiz-Cooley and Gerrodette, 2012; Ruiz-Cooley et al 2012). In this context, the isotopic niche of *D. gigas* reflects a clear variation in $\delta^{13}C$ and $\delta^{15}N$ across the ETP (Fig. 8), highlighting regional contrasts, such as the particularly high $\delta^{15}N$ values in the GC (Ruiz-Cooley et al., 2010; Ruiz-Cooley and Gerrodette, 2012) or the very low $\delta^{13}C$ values in the CCS (Rau et al., 1989; Ruiz-Cooley et al., 2010), a consequence of the biogeochemical characteristics of each ecosystem. This is confirmed in our hierarchical clustering analysis, where systems were grouped according to biochemical and ecological processes reflected in the $\delta^{15}N_{Src\text{-}AA}$ values (Fig. 19). These results (Fig. 8) are consistent with those reported by Ruiz-Cooley et al. (2010) and Ruiz-Cooley and Gerrodette, (2012), who attribute the enrichment of $\delta^{15}N$ in *D. gigas* (6.5‰ and 7‰) relative to the $\delta^{15}NO_3^-$ sediments of the Guaymas basin to the denitrification process (conversion of NO_3^- and NO_2 to N_2O by microbial activity) that is characteristic of the GC (Altabet et al., 1999). Denitrification elevates nitrate $\delta^{15}N$ ($\delta^{15}N_{NO_3}^-$) values due to the influence of the California Undercurrent, which transports deep nitrate-rich waters with elevated nitrate concentrations (Liu' and Kaplan, 1989, Altabet et al., 1999). During this process, ^{15}N poor NO_3^- is preferentially removed, leaving an enriched residual nitrate pool (Naqvi et al., 2000; Voss et al., 2001). The GC is distinguished by its high nutrient availability in the surface layer, largely derived from the recycling of particulate organic matter (POM) and transported by wind or tidal current-generated upwellings (Badan-Dangon et al., 1985). Our CSIA-AA results corroborate this pattern, showing an increase in the isotopic values of $\delta^{15}N_{Phe}$ and $\delta^{15}N_{Src}$ (Fig. 14) across the different sizes of *D. gigas* in the GC. These values represent the highest enrichments in $\delta^{15}N_{AA}$ among all the systems analyzed (CCS, ETP, HW), confirming a substantial input of ^{15}N enriched nitrogen in this region and supporting the influence of intense denitrification processes in the GC.

Within the isotopic niche, the CCS system showed the greatest impoverishment in $\delta^{13}C$ (Fig. 8), a phenomenon that could be linked to variations in primary production rates and the composition of primary producer communities mainly dominated by large microphytoplankton like diatoms and dinoflagellates. This pattern had previously been reported by Ruiz-Cooley et al. (2014) for this region, where they observed that, within the latitudinal range of *D. gigas* and *Physeter macrocephalus*, $\delta^{13}C$ values progressively decreased from the southern to the northern hemisphere, suggesting recent changes in the dynamics of the trophic basis. These latitudinal isotopic variations were associated with oceanographic and biogeochemical factors, such as light intensity, average surface nutrient status, sea surface temperature (SST), CO_2 solubility, isotopic kinetic effects on phytoplankton metabolism, and, in particular, high primary production (Rau et al., 1982, 1989; Sackett and Moore, 1996; Ruiz-Cooley and Gerrodette, 2012). The CCS is part of the four main eastern margin upwelling systems (Checkley and Barth, 2009b). In this area, coastal winds displace surface waters offshore, favoring the upwelling of deep, cold, nutrient-rich waters into the photic zone, which boosts primary productivity (Bakun and Nelson, 1991). Thus, it is one of the most productive oceanic regions on the planet, with year-round upwelling and high rates of primary production (Huyer, 1983; Dorman and Winant, 2000). In this context, the combination of strong upwelling, high nutrient availability, high productivity and low SST (Checkley and Barth, 2009b), increases CO_2 solubility, which increases available carbon and allows phytoplankton to discriminate more efficiently between ^{13}C and ^{12}C, favoring the incorporation of ^{12}C and generating more depleted isotopic signals (Rau et al., 1982, 1989; Bograd et al., 2009). This often results in reduced $\delta^{13}C$ values in phytoplankton (Ruiz-Cooley et al., 2014). In general, when surface nitrate (NO_3^-) concentrations are high, its proportional uptake by phytoplankton tends to be lower (Wada and Hattori,1991). During periods of intense upwelling in the CCS, the abundance of NO_3^- can lead to incomplete assimilation, without fully depleting the resource, resulting in lower $\delta^{15}N$ values at the base of the food web, which are integrated by consumers like squid. The CCS also showed the highest variability in $\delta^{15}N_{Glx}$, $\delta^{15}N_{Phe}$, $\delta^{15}N_{Tro\text{-}AA}$, and $\delta^{15}N_{Src\text{-}AA}$ recorded in *D. gigas* muscle (Stations CCS.23 to CCS.59; Fig.14), which could reflect differences in nitrogen assimilation rates by primary producers (Décima et al., 2013). The variation between $\delta^{15}N_{Glx}$ and $\delta^{15}N_{Phe}$ suggests spatial heterogeneity in the nitrogen source and in the degree of isotopic fractionation during its incorporation into the trophic base. At some stations (e.g., CCS.57 and CCS.59), the slightly elevated $\delta^{15}N_{Phe}$ values in Phe could indicate a predominance of nitrogen from processes such as remineralization or upwelling of deep water enriched in ^{15}N (Sigman et al., 2005). In contrast, other locations (e.g., CCS.23 and CCS.32) recorded lower values, possibly associated with the influence of newly fixed nitrogen or with conditions under which NO_3^- uptake by phytoplankton is incomplete (Needoba et al., 2007).

Dosidicus gigas and *S. oualaniensis* in the ETP showed the most variable values in $\delta^{15}N$ compared to HW, GC, and CCS (Fig. 8, Table 4). There are high surface NO_3^- levels (5-8 µM) in the ETP, which is attributed to the upward injection of nitrate driven by the warm Equatorial Counter Current (NECC) and the Southern Equatorial Current (SEC), where it progressively decreases towards northern and southern latitudes due to phytoplankton utilize NO_3- (Altabet and Francois, 1994; Somes et al., 2010) and a prominent OMZ with high denitrification rates in the water column (Cline and Richards, 1972; Codispoti and Richards, 1976). Likewise, a notable influence of SEC (Sites 1 and 5) and NECC (Site 4) is observed in our different ETP study sites (Fig. 7). For example, the SEC cools and transports nutrient-rich waters because it is strongly influenced by the Humboldt Current and equatorial upwelling, which brings nutrient-rich water from high latitudes (Altabet and Francois, 1994). Therefore, the baseline values in this area exhibit higher $\delta^{15}N$ values, resulting from the advection of waters with an isotopic signature influenced by denitrification (Rafter et al., 2012; Peters et al., 2018). Furthermore, residual nitrate rising to the surface has undergone isotopic fractionation due to incomplete nutrient utilization as these waters are advected away from upwelling areas. As a consequence, surface $\delta^{15}N_{NO_3^-}$ values in the equatorial region reach very high levels, between 13‰ and 18‰ ($\delta^{15}N$), in the sector between 155° W and 170° W, before gradually decreasing northwards towards the subtropical gyre (Rafter and Sigman, 2016; Peters et al., 2018). On the other hand, the NECC also contributes to the nutrient dynamics of the area due to its own oceanic transport and mixing characteristics (Lavín et al., 2006). Surface nutrient levels in the NECC are low and comparable to those in the subtropical gyres (Fiedler and Talley, 2006), but the nutricline is much shallower so the euphotic zone of the NECC could receive some nutrients from the depth (Lavín et al., 2006). However, within the entire *D. gigas* distribution analyzed in this study, *D. gigas* from the ETP presented the lowest $\delta^{15}N$ values (Table 4, Fig 8), possibly due to the presence of low chlorophyll but high nutrient levels, where iron (Fe) limits between 40% and 60% of NO_3^- utilization by phytoplankton (Altabet, 2001), as previously proposed by Ruiz-Cooley and Gerrodette (2012), who observed depleted nitrogen values in *D. gigas* near the equator and in the warm zone of the Eastern Tropical Pacific (EPWP). Furthermore, NO_3^- fixation in the ETP has been documented to be higher than previously reported, even with low Fe deposition (Moore et al., 2001). However, our collection sites (Fig. 7) are usually influenced by the SEC where low N_2 fixation rates occur due to iron limitation, as this current is one of the most extensive and extreme high nutrient content and low chlorophyll (HNLC) areas in the world's oceans (Behrenfeld and Kolber, 1999). Fixation generates low $\delta^{15}N$ values due to minimal isotopic fractionation (Karl et al., 1997). Therefore, if N_2 fixation, incomplete NO_3^- utilization by phytoplankton, and intense denitrification in the water column occur in the same geographic area, the $\delta^{15}N$ values in primary producers would average, resulting in low to intermediate nitrogen values at the base of the food web (Ruiz-Cooley and Gerrodette, 2012). This could be in line with our CSIA-AA results, as reference $\delta^{15}N_{Phe}$ and $\delta^{15}N_{Src}$ values for the different ETP sites (Fig. 14) are shown to be highly similar to HW, which is an N_2 fixation-dominated system.

The $\delta^{15}N$ values observed in *S. oualaniensis* in HW were lower than those recorded in any other study system (Fig. 8), likely reflecting differences in reference baseline isotopic values between regions influenced by biogeochemical, oceanographic, and nutrient availability conditions. This decrease in $\delta^{15}N$ was previously reported by Parry (2008), who found an average value of 8.2 ‰ in *S. oualaniensis* individuals in HW, associated with nitrogen fixation by cyanobacteria of the genus *Trichodesmium spp.*, which thrive in oligotrophic waters due to their ability to absorb nutrients at very low concentrations (Seki et al., 2001) and release nitrogen into the environment (Minagawa and Wada, 1986). In fact, HW is characterized as an oligotrophic region, where N_2 fixation contributes to the decline in $\delta^{15}N$ values at the base of the food web (Montoya et al., 2002). Furthermore, isotopic fractionation during surface nitrate assimilation favors the incorporation of the lighter isotope (^{14}N), further contributing to this $\delta^{15}N$ depletion (Minagawa and Wada, 1986). These processes, together with other oceanographic factors, modulate the variability in nitrogen sources, which is reflected in consumers, whose tissue $\delta^{15}N$ values directly depend on the nitrogen source used at the base of the food web (Hannides et al., 2009). On the other hand, the average values of $\delta^{13}C$ and $\delta^{15}N$ for *S. oualaniensis* in the ETP (Table 4, Fig. 8) differed from those reported by Takai et al. (2000) off the coast of Peru, where higher values were recorded for both $\delta^{13}C$ (−15.6 ± 0.3 ‰) and $\delta^{15}N$ (16.3 ± 0.6 ‰). These differences may be attributed to the geographic distance between our study area in the ETP, which is more oceanic (Fig. 5, Table 3), and the Peruvian coast, which implies variations in environmental conditions such as terrestrial input, precipitation, and temperature, factors that influence the isotopic composition of the biota (Fiedler and Talley, 2006). Furthermore, the values reported by Takai et al. (2000) come from a coastal region influenced by OMZ that tend to enrich the reference isotopic signal, particularly for $\delta^{15}N$ (Minagawa and Wada, 1986), and a Peruvian coastal upwelling is characterized by low surface temperatures, high primary production rates, and nutrient input to the euphotic zone, such that coastal phytoplankton experience optimal nutrient conditions (Guillén and Calienes, 2013). In contrast, our study covers a wider area in the ETP (Fig. 5, Table 3) rather than a localized zone like the Peruvian coast, so this greater spatial integration may attenuate extreme signals associated with the OMZ. Similar observations have been documented for *D. gigas*, where individuals inhabiting more oligotrophic waters off the ETP show lower isotopic values compared to specimens caught along the western coast of South America (Gong, et al., 2018). This is consistent with CSIA-AA, where the lowest $\delta^{15}N_{Phe}$ and $\delta^{15}N_{Src\text{-}AA}$ values are shown for HW (Fig. 14), suggesting that regional differences in primary productivity, oceanographic conditions, and biogeochemical processes may strongly influence the isotopic composition of consumers.

4.3 Differences in the trophic niche and feeding strategies of *Dosidicus gigas* and *Sthenoteuthis oualaniensis*

The results of the SIBER analysis showed that the standard ellipses (SEA_C) presented marked differences in the isotopic values of $\delta^{13}C$ and $\delta^{15}N$ (Figs. 8, 9), indicating variations in resource exploitation associated with different trophic strategies of *D. gigas* among the geographical systems evaluated (GC, CCS, ETP).

According to (Schoener, 1971), the feeding strategies adopted by a species in a given area arise from its interaction with the available prey. The breadth of the trophic niche is determined by the degree of similarity or divergence in these variations, reflecting whether the organisms act as generalists that consume prey based on its availability and present high ecological plasticity or as specialists that systematically select or avoid part of the prey spectrum (Feinsinger et al., 1981; Giller, 1984). In our study, the isotopic niche of *D. gigas* was narrower in GC and CCS than in ETP (Fig. 8, 9), suggesting a narrower trophic spectrum. This pattern does not contradict its opportunistic nature reported in the literature (Ehrhardt, 1991; Nesis, 1993; Nigmatullin et al., 2001; Markaida and Sosa-Nishizaki, 2003; Markaida, 2006a; Ruiz-Cooley et al., 2010; Field et al., 2013), but probably reflects the intensive exploitation of a dominant resource, such as mesopelagic fishes (*Benthosema panamense, Triphoturus mexicanus, Diogenichthys laternatus*) Markaida and Sosa-Nishizaki, 2001, 2003; Markaida, 2006a; Markaida et al., 2008; Portner et al., 2020), which are abundant in the center of GC and characterized by daily vertical migrations associated with the upper limit of the OMZ (Robison, 1972; Reid et al., 1991). This limit is located at depths less than 250 m (Roden, 1964; Alvarez-Borrego and Lara-Lara, 1991;), coinciding with the vertical migrations of *D. gigas* in search of food, which favors its trophic success in this region (Gilly et al., 2006b; Markaida et al., 2008). Studies with electronic tagging have documented that, although *D. gigas* is a generalist and opportunistic predator capable of colonizing new habitats and exploiting emerging resources such as the high biomass of myctophids (Markaida and Sosa-Nishizaki, 2003; Markaida, 2006a; Rosas, 2007; Markaida et al., 2008; Camarillo-Coop et al., 2013; Field et al., 2013), its diet can become temporarily more specialized, concentrating on small and abundant prey that form large aggregations in the GC (Portner et al., 2020). Similarly, the $\mathrm{SEA_C}$ of CCS (Table 7; Figs. 8, 9) showed an isotopic niche comparable to that of GC, suggesting a similar trophic breadth for *D. gigas*. In this region, the species appears to maintain a feeding strategy focused on demersal prey, even in coastal waters (Field et al., 2007). Its main prey items include Pacific hake, rockfish, Pacific flounder (*Citharichthys sordidus*), and slender sole (*Lyopsetta exilis*) (Hobson and Chess, 1986). However, it was suggested that larger hake and rockfish might be consumed more frequently by *D. gigas* in the CCS during certain seasons (Field et al., 2007). The morphological characteristics of the species, such as the long, sharp tips of its arms, which have between two and eight times more suckers than other ommastrephids, facilitate the capture and manipulation of small prey. (Jereb and Roper, 2005; Portner et al., 2020). However, the relatively narrow size of the isotopic niche in the GC and SCC (Table 7; Figs. 8 and 9) does not seem to be directly explained by the morphological characteristics of *D. gigas*, since its morphology could facilitate the capture of prey of different sizes, thus broadening the isotopic niche. Nevertheless, these particular characteristics, such as the number of suckers in *D. gigas*, could distinguish this species from *S. oualaniensis* in the ETP (In communication with Markaida).This morphology, combined with its diet and feeding strategy, likely contributes to the ecological success of *D. gigas*, since by focusing on smaller prey, it avoids competition with similarly sized fish as it grows (Portner et al., 2020). Bulk results (Table 7; Figs. 8, 9) show that the breadth of the isotopic niche in the different geographical systems (GC and CCS) suggests trophic specialization during certain periods. This indicates that niche variability is strongly influenced by resource availability and the feeding strategies employed in each area.

In HW, *S. oualaniensis* displayed a relatively narrow isotopic niche breadth (Table 7; Figs. 8, 9), suggesting a more specialized trophic strategy, similar to the isotopic niche observed for *D. gigas* in CCS and GC. This pattern could be linked to a strong preference for certain resources available in the region, such as myctophids (*S. evermanni, Ceratoscopelus warmingii,* and *Hygophum proximum*) (Parry, 2003, 2006, 2008), and feeding habits. In HW, the coexistence of *S. oualaniensis* with *Ommastrephes bartramii* has been documented, where δ^{15}N values for both species showed a sigmoidal relationship, probably attributed to different feeding strategies (Parry, 2003, 2006, 2008). According to these authors, *O. bartramii* exhibits a more generalist and diversified predatory behavior, whereas S. *oualaniensis* maintains a more homogeneous diet. Furthermore, no direct trophic interactions between the two species have been recorded, and current competition for resources in the North Central Pacific appears to be low, indicating that the niche breadth of *S. oualaniensis* in HW responds primarily to dietary specialization rather than competitive pressure. In this sense, our results (Table 7; Figs. 8, 9) are consistent with Parry, (2003, 2006, 2008) where *S. oualaniensis* from HW could maintain high fidelity to specific prey and consistent trophic behavior over time, reflecting an adaptation to the availability and stability of certain key resources.

4.4 Different trophic positions between *Dosidicus gigas* and *Sthenoteuthis oualaniensis*

At the global scale, CSIA-AA results for the trophic level and position estimators (Fig.15, 16) showed minimal variation between $\delta^{15}N_{Glx\text{-}Phe}$ and $\delta^{15}N_{Tro\text{-}Phe}$ in the four systems analyzed (GC, CCS, ETP, HW) for *D. gigas* and *S. oualaniensis*. This suggests low geographic heterogeneity in the trophic position of both species, possibly related to the characteristics of food webs in eutrophic coastal systems and oligotrophic open ocean (Chavez et al., 2002). In coastal areas, higher phytoplankton biomass, mainly composed by dense diatom blooms (Chavez et al., 1990, 1996; Fiedler, 2002), favored by high availability of nutrients to the euphotic zone through the rise of the thermocline and local wind-driven upwellings (Pennington et al., 2006). The high coastal biomass is maintained because diatoms often outgrow macrozooplankton predators, allowing primary production to be rapidly transferred to small, abundant fish (Ryther, 1969). Although these food chains are usually shorter and more efficient in energy transfer, they also exhibit losses (Chavez et al., 2011). A significant proportion of production may be exported (Muller-Karger et al., 2005), either by sinking, sustaining abundant benthic fauna or, in some cases, generating anoxia conditions (Margalef, 1978), or by horizontal advection, transporting organic matter away from the coast (Olivieri and Chavez, 2000). Ruiz-Cooley, et al. (2017) observed that in the CCS, the food chain length, estimated with Glx-Phe, was shorter under high nitrate concentrations and cooler surface temperatures; in contrast, with reduced nitrate and intermediate temperatures, the chain lengthened. This pattern was associated with variations in phytoplankton size and species composition. These observations are consistent with our results on trophic position (Fig. 18), where at the most coastal sites (Fig. 5, Table 3), such as GC and CCS, which include the largest *D. gigas* (Table, 4), the estimates of $\delta^{15}N_{Glx\text{-}Phe}$ and $\delta^{15}N_{Tro\text{-}Phe}$ were lower. This suggests that larger individuals may occupy lower trophic levels due to shorter food chains, and higher trophic energy transfer. In contrast, in the oligotrophic open ocean, characterized by limited nutrient supply and low primary productivity, picoplanktonic organisms and the so-called microbial food web predominate (Pomeroy, 1974; Azam et al., 1983). There, the availability of fishery resources and high-trophic level consumers is lower due to lower nutrient supply, and the fact that the energy generated by picoplankton must undergo more trophic steps before being converted into biomass usable by marine consumers (Chavez et al., 2011). According to Seki et al. (2001), longer food webs are common in oligotrophic ocean waters, since small phytoplankton require protozoa as intermediary links between themselves and zooplankton. For example, during periods when upwelling is weak, but there is still a high zooplankton biomass and the presence of top predators such as *Delphinus delphis*, food webs can be sustained and extend from lower trophic levels to higher levels (Ruiz-Cooley et al., 2017). Our results show that the highest estimates of trophic position (Fig. 15-18) based on $\delta^{15}N_{Glx\text{-}Phe}$ and $\delta^{15}N_{Tro\text{-}Phe}$ were recorded at different sites in the ETP and in HW, corresponding to more oceanic systems (Fig. 5, Table 3). In these areas, *D. gigas* and *S. oualaniensis* were relatively small (20–35 cm ML), suggesting that, in these systems, smaller individuals may occupy relatively high trophic levels compared to the larger individuals located in GC and CCS (Fig. 15-18), possibly due to a higher complexity in the mesopelagic food web driven perhaps by higher species diversity across trophic levels.

4.5 Isotopic niche and resource overlap in *Dosidicus gigas* and *Sthenoteuthis oualaniensis* in the Eastern Tropical Pacific

Isotopic niche analysis using SIBER revealed a moderate overlap between *D. gigas* and *S. oualaniensis* (~36% SEA_C overlap; Fig. 10, 11), suggesting shared use of food resources and habitat in the ETP. This moderate overlap suggests that these species may exhibit different diet composition, foraging behavior despite similar morphology, habitat use and movement patterns, which could promote coexistence between the two Ommastrephid species, resulting in differentiation in their isotopic niches. For example, Golikov et al. (2020) showed that isotopic overlap between *Rossia palpebrosa, R. megaptera,* and *R. moelleri* does not necessarily indicate direct competition, as these species can coexist through mechanisms such as trophic partitioning, ontogenetic differences, and distinct feeding behaviors due to food availability. These mechanisms are associated with factors such as diving depth, diet composition, and foraging area, which can vary both within and between closely related species (Pinaud and Weimerskirch, 2007; Páez-Rosas and Aurioles-Gamboa, 2010). Similarly, trophic niche partitioning between sympatric predators is commonly interpreted as an ecological strategy that reduces competition for resources and allows coexistence within shared habitats (Páez-Rosas and Aurioles-Gamboa, 2010; Pinela et al., 2010). The low overlap detected between *D. gigas* and *S. oualaniensis* (~36% SEA_C overlap; Fig. 11) in ETP could be strongly influenced by prey availability. This factor plays a crucial role in the overlapping zones between both squids, as it directly influences their growth, distribution, and trophic strategies (Shchetinnikov, 1992; Markaida and Sosa-Nishizaki, 2003). In the ETP, mesopelagic fishes play a fundamental role as key components of the food web. Their high abundance and wide oceanic distribution (Ahlstrom et al., 1976) make them an essential food source for numerous organisms, including *D. gigas* and *S. oualaniensis* (Shchetinnikov, 1992; Markaida, 2006a; Markaida et al., 2008; Portner et al., 2020; Cisneros et al., 2024). Furthermore, mesopelagic fish daily vertical migrations and high biomass suggest that they are important mediators of organic carbon transfer across trophic levels and in the water column (Brodeur et al., 1999; Hidaka et al., 2001). The ecological success of these mesopelagic fish lies in their rapid population growth, which makes them not only essential prey for *D. gigas* and *S. oualaniensis* in the ETP (Rosas-Luis et al., 2011) but may allow coexistence between individuals of similar sizes for both species.

Although our isotopic niche suggests that *D. gigas* and *S. oualaniensis* do not fully compete for the same trophic resources (~36% SEA_C overlap; Fig. 10), stomach content analyses of both species indicate that they may share certain groups of mesopelagic fishes at different depths in the ETP water column (Shchetinnikov, 1992; Liu et al., 2013; Rosas-Luis and Chompoy-Salazar, 2016). These fishes, which dominate in terms of biomass and abundance in the mesopelagic ecosystems of the ETP (Gjosaeter and Kawaguchi, 1980; Irigoien et al., 2014), represent a key resource within the system. A notable example is *Vinciguerria lucetia*, the most frequently identified species in the diets of both squids (Shchetinnikov, 1992; Markaida and Sosa-Nishizaki, 2003; Markaida, 2006a; Rosas-Luis et al., 2011; Alegre et al., 2014; Xiaodi et al., 2022; Cisneros et al., 2024), which is abundant in the warm tropical waters of the ETP (Ahlstrom et al., 1976) and is one of the most important fishes within the Humboldt Current system in Peru (Cornejo and Koppelmann, 2006), which is influenced by this current at our Site 5, where both species were collected. Cornejo and Koppelmann (2006) reported that the highest concentrations of *V. lucetia* are found above 100 m and between 200 and 400 m, overlapping with the OMZ and nocturnal migration of *D. gigas* and *S. oualaniensis* (Gilly et al., 2006b; Field. et al., 2007; Bazzino et al., 2010; Sakai et al., 2017), in which *D. gigas* has been documented to reach depths greater than 1200 m, tolerating daily temperature fluctuations of 15–20 °C and extreme hypoxic conditions (<0.8 kPa at 10 °C), allowing it to actively inhabit and forage within the OMZ during the day, ascending to surface waters at night (Seibel, 2013, 2015). In the case of *S. oualaniensis*, most available studies have focused on the Indian Ocean (South China Sea and Arabian Sea), where diel vertical migration was reported (Harman et al., 1989; Fan et al., 2021, 2023) and its ontogenetic cycle seems to be more influenced by thermal gradients (16 and 32 °C) (Han et al., 2023; Zhou et al., 2018). Although, Staaf et al. (2010), point out that it is not yet clear whether this species uses the OMZ in the ETP; there is evidence from other regions, such as the Arabian Sea, indicating that large sizes could be associated with the OMZ (Nesis, 1993). Therefore, both species may adjust their vertical migratory behavior based on prey distribution. Acoustic studies have also demonstrated a strong predator-prey relationship between *D. gigas* and *V. lucetia*, with overlapping biomass patterns (Rosas-Luis et al., 2011). Indeed, in the ETP, this prey represents the third most abundant biomass after the northern anchovy (*Engraulis mordax*) and the Pacific hake (*Merluccius productus*) (Smith, 1995). Feeding on small prey can be an effective strategy to reduce competition with similarly sized predators by exploiting a different ecological resource (Field et al., 2013). Given the high availability of mesopelagic fish in the ETP, low probability of cannibalism in *D. gigas* (Rosas-Luis et al., 2011; Alegre et al., 2014; Rosas-Luis and Chompoy-Salazar, 2016; Xiaodi et al., 2022) and *S. oualaniensis* (Shchetinnikov, 1992) is expected, while strong predation on mesopelagic fish or other invertebrates may occur (Ibáñez and Keyl, 2010); cannibalism represent a complementary feeding strategy during periods of food scarcity or high ecological pressure (Caddy, 1983). This may explain the breadth of our squid isotopic niche (Fig. 11) and the low overlap between both species (36%), as *D. gigas* and *S. oualaniensis* likely minimize interspecific competition, cannibalism and concentrate on more available food resources.

In the ETP sites at similar latitudes, *D. gigas* exhibited a broader isotopic niche ($SEA_C = 4.30$) than *S. oualaniensis* ($SEA_C = 3.20$) (Fig. 11, 12), suggesting a higher trophic variability and a more flexible diet in *D. gigas* that include OMZs (Rosa and Seibel, 2010; Seibel, 2013), and possibly because *S. oualaniensis* presents a more restricted distribution in the central ETP compared to the typical Pacific group (Staaf et al., 2010). Furthermore, several studies support this opportunistic behavior for *D. gigas* (Ulloa et al., 2006;

Ibáñez et al., 2008; Rosas-Luis et al., 2011; Liu et al., 2013; Alegre et al., 2014; Rosas-Luis and Chompoy-Salazar, 2016; Xiaodi et al., 2022; Cisneros et al., 2024) and *S. oualaniensis* (Shchetinnikov, 1992) in the ETP, which would explain the wide breadth of the isotopic niche for both species. However, our CSIA-AA results, based on the $\delta^{15}N_{Tro\text{-}Phe}$ and $\delta^{15}N_{Glx\text{-}Phe}$ estimators (Figs. 15-17) and TP (Fig. 18), indicate that, despite the greater trophic breadth of *D. gigas*, *S. oualaniensis* consistently reaches higher TPs in the ETP. In terms of food web structure, *S. oualaniensis* occupies a higher position than *D. gigas* in the overlapping zone, which could confer a competitive advantage and preference in exploiting higher trophic level prey in the areas where they coexist, possibly due to a high abundance and diversity of prey that support different feeding strategies. A distinctive morphological feature of *D. gigas* is the long, sharp tips of its arms, which have two to eight times more suckers than other Ommatopehids, facilitating the capture and manipulation of small prey (Jereb and Roper, 2005; Portner et al., 2020). This could explain the differences in isotopic niche and PTs between the two species.

The results obtained from bulk and CSIA-AA allow us to evaluate the hypothesis regarding the variation in *D. gigas* TP based on its ecological and biological characteristics. It was observed that the TPs estimated with $\delta^{15}N_{Tro\text{-}Phe}$ and $\delta^{15}N_{Glx\text{-}Phe}$ in large *D. gigas* specimens from the GC and CSS were lower compared to those of small individuals (20–35 cm ML) of both *D. gigas* and *S. oualaniensis* in Hawaii and the ETP (Fig. 15-18), confirming that both size and foraging areas influence food web length. Furthermore, slight differences in their TPs were recorded in the overlap zone between both species in the ETP (Fig. 15-18), which coincides with the low degree of isotopic overlap reported at the bulk level (36%) and in the isotopic niche (Fig. 11). This pattern, combined with the widespread food availability and differentiation strategies fostered in this region, suggests that both squids can coexist, reducing the intensity of interspecific competition. Furthermore, in the ETP, *S. oualaniensis* consistently occupies a higher trophic position than *D. gigas* (Fig. 15-18), supporting the hypothesis that anticipated trophic differences in overlap zones as a strategy to reduce competition. However, in areas without coexistence (GC and CSS), the opposite pattern to that expected was observed, where *D. gigas* presented lower TPs, while the highest TPs corresponded to regions where they coexist. This result suggests that, in addition to interspecific competition, other factors such as ontogeny and biological and biogeochemical differences between coastal and oceanic zones significantly influence TP variation.

Chapter 5. Conclusions

This is the first study to provide information on the trophic position of *Dosidicus gigas* and *Sthenoteuthis oualaniensis* from different ecosystems of the Eastern Pacific by using SIA in bulk tissue and $\delta^{15}N$ from individual AAs. These biochemical tracers reveal squid ontogenetic patterns by species within the same ecosystem, and low interspecific competition in sites where both species overlap.

The results showed an increase in $\delta^{15}N$ and $\delta^{13}C$ with squid growth, reflecting a shift in the diet toward higher trophic levels. This pattern was confirmed by CSIA-AA for *D. gigas* from the GC, where an ontogenetic shift is evident, suggesting that its diet is not limited to myctophids throughout its life cycle as previously suggested by stomach content analysis, which mostly use specimens collected at night. *Dosidicus gigas* diet during the daytime has not been described yet.

The breadth of the isotopic niche varied among different ecosystems, influenced by biogeochemical processes and diet. The CSIA-AA analysis reinforced this idea, showing differences between $\delta^{15}N_{Phe}$ and $\delta^{15}N_{Src}$, although in the ETP and HW the AA_{Src} were very similar, indicating comparable nitrogen biogeochemical characteristics, a finding supported by hierarchical clustering. The trophic position estimators $\delta^{15}N_{Glx\text{-}Phe}$ and $\delta^{15}N_{Tro\text{-}Phe}$ indicated that small individuals (20–35 cm ML) in HW and different ETP sites reached the highest trophic levels in comparison to large-sized *D. gigas* from the GC and CCS. Therefore, it is suggested that this pattern could be related to environmental differences associated with biogeochemical cycles primary production and food web length (driven by species diversity). In oceanic zones, lower productivity but higher zooplankton diversity may favor longer food chains, while shorter chains are expected in highly productive areas like the CCS.

In ETP, *D. gigas* and *S. oualaniensis* shared approximately 36% of their SEA_C, reflecting some overlap in food and habitat resource use. However, interspecific competition was moderate due to a high availability of mesopelagic fish in the ETP, which possibly induces different foraging strategies. Furthermore, CSIA-AA revealed that both $\delta^{15}N_{Glx\text{-}Phe}$ and $\delta^{15}N_{Tro\text{-}Phe}$ were consistently higher in *S. oualaniensis*, indicating that this species occupies higher trophic positions than *D. gigas* in the overlapping sites.

Taken together, these findings highlight the remarkable flexibility of *D. gigas* to adapt to variable environments and exploit different resources even in the presence of a potential competitor.

This hypothesis is partially supported, as in areas of overlap, *D. gigas* and *S. oualaniensis* showed trophic differences that suggest a reduction in competition. However, in areas without overlap, such as the GC and CCS, *D. gigas* exhibited lower trophic levels than expected. We propose that this variation is due to environmental differences between coastal and oceanic regions, which influence the structure of the food web, generating longer or shorter food chains.

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Anex

Table 9. δ^{13}C and δ^{15}N residuals in relation to mantle length (ML) of *D. gigas* and *S. oualaniensis* in different geographic systems.

Residuals	**ETP**		**GC**		**CCS**		**HW**	
	δ^{13}C	**δ^{15}N**	**δ^{13}C**	**δ^{15}N**	**δ^{13}C**	**δ^{15}N**	**δ^{13}C**	**δ^{15}N**
Normal (Shapiro-Wilk)	0.88	0.07	0.0098	0.0002	0.49	0.86	0.71	0.96
Homoscedasticity (Breusch-Pagan)	0.16	0.12	0.07	0.66	0.60	0.46	0.19	0.82
Independence (Durbin Watson)	0.002	0.005	0.28	0.26	0.17	0.01	0.51	0.43
Average 0	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01

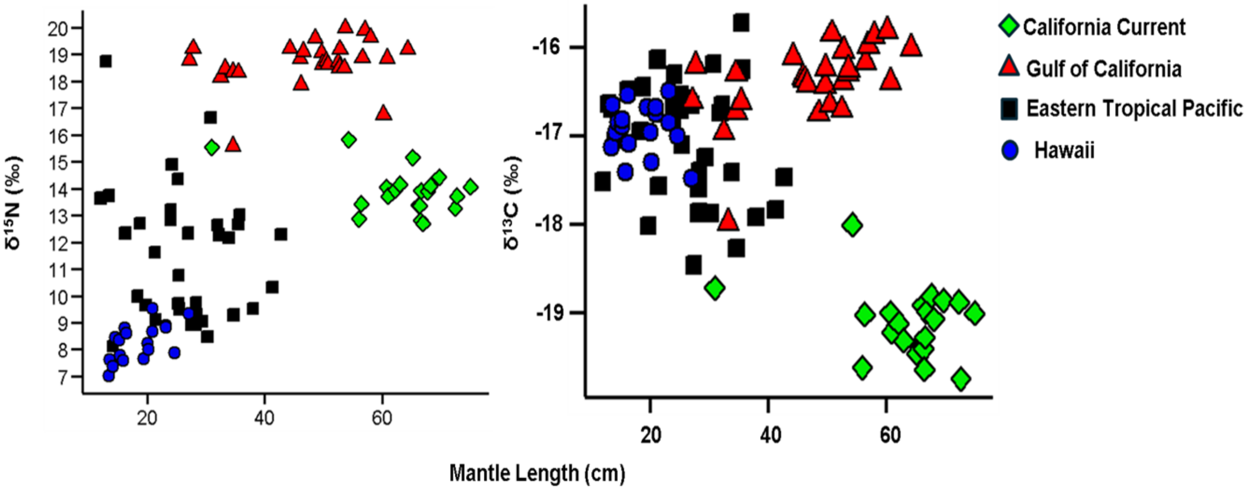

Figure 20. Mantle length variation as a function of (a) δ^{13}C (%) and (b) δ^{15}N (%) values in the muscle of *D. gigas* and *S. oualaniensis*.

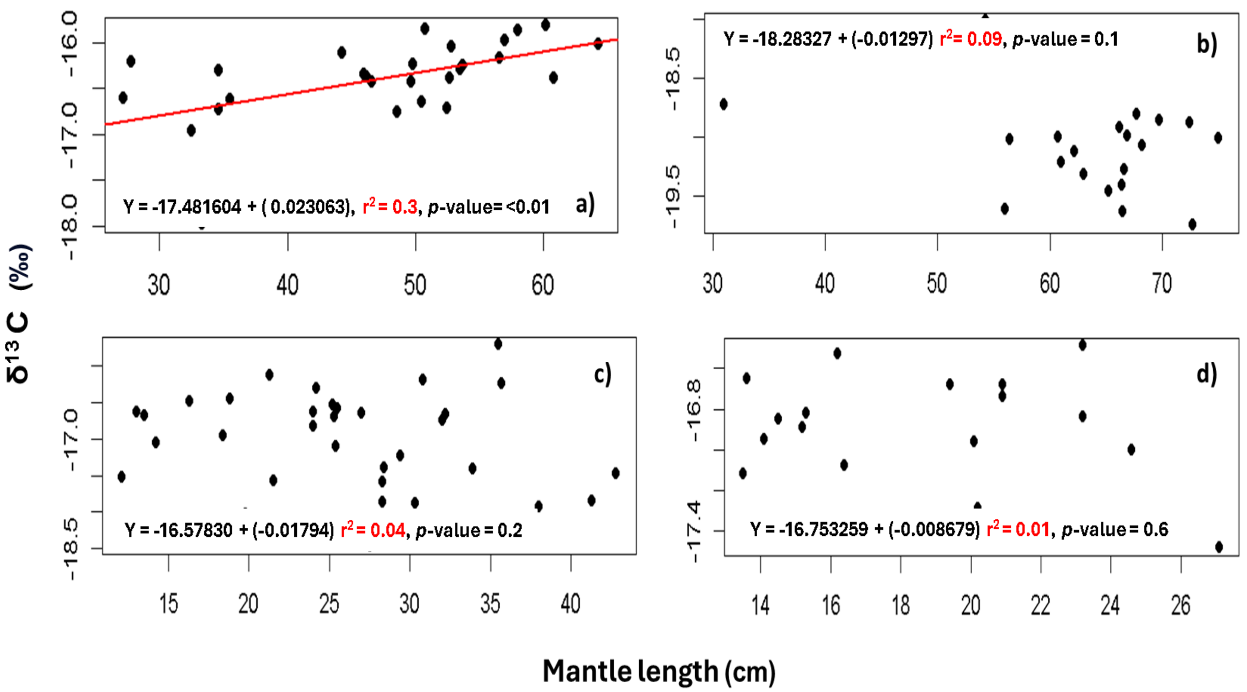

Figure 22. Linear regression between δ^{13}C and mantle length (ML) of *D. gigas* and *S. oualaniensis* in different geographic systems a) Gulf of California b) California Current System c) Eastern Tropical Pacific d) Hawaii. r^2: Coefficient of determination.

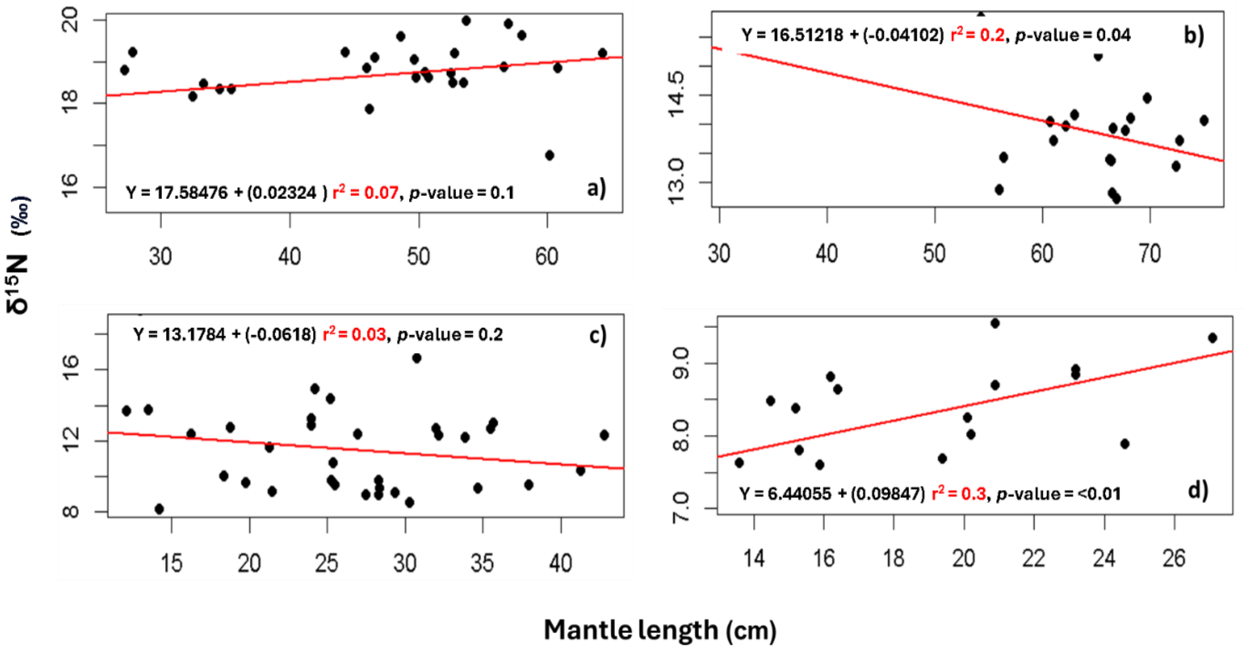

Figure 21. Linear regression between δ^{15}N and mantle length (ML) of *D. gigas* and *S. oualaniensis* in different geographic systems a) Gulf of California b) California Current System c) Eastern Tropical Pacific d) Hawaii. r^2: Coefficient of determination.