Feeding habits of the South Pacific hake, *Merluccius gayi*, in Ecuador, Tropical Eastern Pacific Ocean

Ana R. Hernández-Téllez[1] , Jacqueline M. Cajas-Flores[2] , Alfredo Ordiano-Flores[3] ,
Marcos D. Calle-Morán[4]* , Robert J. Bucheli-Quiñonez[2]

[1] Posgrado en Ciencias en Recursos Acuáticos – Facultad de Ciencias del Mar – Universidad Autónoma de Sinaloa (Av. Paseo Claussen, s/n - Mazatlán - CP 82000 - Mexico).

[2] División de Recursos Bioacuáticos y Ambiente – Instituto Público de Investigación de Acuicultura y Pesca (Letamendi y la Ría, s/n – Guayaquil - CP 90308 - Ecuador).

[3] Universidad del Valle de México (Jiménez Cantú 4 - San Martin - Texcoco de Mora - 56100 - México).

[4] Carrera de Biología, Facultad de Ciencias de la Vida – Universidad Estatal Amazónica (Calle Luis Imacela – El Pangui - CP 190401 - Ecuador).

* Corresponding author: marcalle02@gmail.com

ABSTRACT

The South Pacific hake, *Merluccius gayi*, is an ecologically and economically important species in Ecuador. However, studies regarding its feeding habits remain scarce. This study aimed to characterize the food and feeding habits of *M. gayi* in the Ecuadorian Pacific Ocean by sex, sexual maturity stages, size classes, and years. Hakes obtained (n = 2993) from industrial fishing (captured with seine nets) were analyzed from September 2013 to December 2014. Their diet was composed of 27 prey species. The most important prey was the euphausiid *Nyctiphanes simplex* (52%) and the same hake species (*M. gayi*; 31%) according to the prey-specific index of relative importance (%PSIRI), making this species a cannibal predator. Results show no significant dietary differences between female and male hakes or immature and mature males, but found differences between immature and mature females and individuals from four size classes and hake between 2013 and 2014. According to Levin's Index, the species showed a low trophic niche breadth (*Bi* = 0.03), making it a selective specialist mesopredator with high specialization. The trophic overlap analysis based on Jaccard's index by sex was low (*J* = 0.23) for indetermined individuals, moderate (*J* = 0.59) for males and females, and high (*J* = 0.78) for immature females and males; moderate values were noted for size classes (*J* = 0.42-0.63) and low for years (*J* = 0.31). Based on the Cortés index, the trophic level totaled (*TLk* = 3.22), indicating that this species is a primary and secondary carnivore mesopredator. This information supports the understanding of the relations between predators and prey and the flow of nutrients and energy in marine ecosystems, which serve as a base for ecosystemic fishing management.

Keywords: Feeding habits, Length-body mass relationship, Mesopredator, Diet overlap, Trophic level

INTRODUCTION

The South Pacific hake, *Merluccius gayi* (Guichenot, 1848), belongs to the family Merlucciidae and has a coastal and oceanic (horizontal distribution) and epipelagic and mesopelagic (vertical distribution) habitat. It inhabits depths from 50 to 614 m, forming

dense shoals from Ecuador to Peru, including the Galapagos Islands. Females reach a total length (TL) of 115 cm and males, of 68 cm, averaging 50 cm (Lloris et al., 2005; Guevara-Carrasco and Lleonart, 2008; Robertson and Allen, 2015). It feeds on euphausiids, squids, sardines (*Sardinops sagax sagax*), the Peruvian barbel drum (*Ctenosciaena peruviana)*, the Peruvian anchoveta (*Engraulis ringens)*, the bignose anchovy (*Anchoa nasus*), and hake of its same species (*M. gayi*), which is why it is considered as cannibal (Lloris et al., 2005). This mesopredator consumes prey from several trophic levels, including planctophagous and carnivore organisms.

The economic importance of this species stems from its capture in Ecuador and Peru distribution areas by artisanal and industrial fishing (Lloris et al., 2005). In Ecuador, it is captured by bottom longlines and trawls, and its main landing ports are Manta and Puerto López in the Manabí province; Anconcito, La Libertad, and Santa Rosa in the Santa Elena province; Posorja, El Morro, General Villamil Playas, and Guayaquil in the Guayas province; and Puerto Bolívar and El Palmar in the El Oro province. It is sold fresh, frozen, whole, or filleted due to its high value (García-Domínguez et al., 2014; Jiménez-Prado and Béarez, 2004). During 2012-2013, 20 183.60 tons were captured eight miles from the coast of Manabí to El Oro, valued at US $ 16,385,340 in exportations. From 2014-2016, the species was captured over the continental platform and in 29.5-614-m depths over the continental slope, producing a value of US $ 16,400,000 (García-Domínguez et al., 2014; Pesquería…, 2014; Global Marine Commodities, 2018).

Trophic studies of *M. gayi* in Ecuador remain scarce. Varela and Pincay-Mendoza (2019) - the only study for this species in Ecuador - included 232 individuals collected with bottom trawlers from Manabí to El Oro. That study found *C. peruviana*, the long-finned butterfish, *Peprilus medius*, and other bony fish, crustaceans, and cephalopods to constitute main prey of this species. It also found spatial differences in the diet composition by sampling zone, cataloguing the species as an opportunistic predator that consumes a wide variety of vertebrates and invertebrates. Conversely, diet and feeding habits

in Peru are well documented since Fuentes (1983), Muck et al. (1988), Castillo et al. (1989), Fuentes et al. (1989), Castillo et al. (1995, 1997), Álamo and Blaskovic (1994), Álamo and Espinoza (1996, 1997), Espinoza (2000, 2001), Blaskovic and Espinoza (2011), Orrego and Mendo (2012), and Castillo (2018, 2019). In Chile, Bahamonde and Carcamo (1959), Hermosilla (1959), Arana and Williams (1970), Meléndez (1984), Stobberup (1992), Fuentealba (1993), Vidal et al. (1997), Aguayo-Hernández (1995), and Cubillos et al. (2003, 2007), among others, have documented the diet of this species.

The problem with *M. gayi* lies in the fact that the International Union for Conservation of Nature has cataloged it as data deficient with an unknown population tendency (Iwamoto et al., 2010), thus entailing studies on how fishery affects its actual populations. Conversely, Ecuador regulates fishery and includes a management plan since 2013, even though this species has been exported since 1999 (García-Domínguez et al., 2014). However, due to its catch reduction during the 2010s, Ecuador changed this fishery to a small pelagic one. This could continue since these fish populations have remained stable by their constant landing volumes (Global Marine Commodities, 2018).

The relevance of feeding studies (or the analysis of a species diet and feeding habits) lies in evaluating a species ecological role and trophic position in ecosystemic trophic chains (Allan and Castillo, 2007). Fish stomach content analysis provides an idea regarding feeding patterns and the quantitative evaluation of feeding habits, is an essential aspect of fishery management. The study of fish diet integrates some relevant ecologic components, between them, the behavior, condition, habitat use, energy consumption, and intraspecific and interspecific interactions (Sagar et al., 2018). Furthermore, diet data supports aquatic resource management, especially in aquaculture and conservation issues (Saikia, 2015). In aquaculture, one of the most significant aspects of the success of any species used to culture refers to the management and knowledge of diet composition, feeding habits, and nutrition of the species of interest (Cahu, 2004; De Silva et al., 2012; Serrano et al., 2014).

Traditionally, one of the basic methodologies to study the nutritional requirements of wild fish lies in determining the feeding preferences of the species of interest and characterizing its natural diet components and the nutritional value of each (Amezaga-Herrán, 1988). Regarding ecology and conservation, studies that describe diets and feeding habits can explain the trophic structure and ecological dynamics of a marine community involving key species (Riccioni et al., 2018). These studies help prevent a decline in trophic levels of the marine food web due to fishery (Shackell et al., 2010), establishing the conscious exploitation of trophic levels (García et al., 2014). Furthermore, knowing predator-prey relations and their changes over time is essential to understanding the population dynamics of multispecies and complex ecosystem models (Carrozzi et al., 2019).

Ecuador has neither current studies on the feeding ecology of *M. gayi*, including diet comparisons between females and males, immature and mature individuals, and years, nor on the characterization of its feeding behavior and trophic level. Therefore, it is essential to generate information related to

these topics and their subsequent contribution to the knowledge of nutrient and energy flow in this region of the Pacific Ocean. Moreover, knowledge of the trophic structure of an ecosystem is an essential tool for fisheries and the role biological groups play in energy transference, which indicates ecosystem dynamics (Christensen and Pauly, 1995; Proulx et al., 2005). Thus, this study aimed to characterize the diet composition and feeding habits of *M. gayi* on the coasts of Manabí, Santa Elena, and Guayas in the Ecuadorian Tropical Eastern Pacific and its relation to sex, sexual maturity stages, size classes, and temporality.

METHODS

STUDY AREA AND SAMPLE COLLECTION

The four sampled localities included Puerto López in the Manabí province, Anconcito, and Santa Rosa in the Santa Elena province, and Posorja in the Guayas province, Ecuador (Figure 1). Samples were obtained from artisanal and industrial fleet landings using seine nets from September 2013 to December 2014 (Table 1).

Figure 1. Landing locations of the South Pacific hake, *Merluccius gayi*, Ecuador, Tropical Eastern Pacific Ocean from September 2013-December 2014.

Total, fork (FL), and standard length (SL; cm, ± 0.1 cm) were recorded for each individual, as well as their total mass (TM; g), sex, and maturity stage according to the scale modified from Perea et al. (2015): 1) virginal, 2) maturing, 3) mature, 4) spawning for females and evacuating for males, and 5) spawned for females and evacuated for males. In total, three sex categories were considered: indetermined individuals, females, and males;

individuals were classified as indetermined if they had small, thin, and whitish gonads. Additionally, the state of gastric repletion was estimated from individual stomachs considering reference values from the scale by Stillwell and Kohler (1982): 0 (empty), 1 (25% full), 2 (50% full), 3 (75% full), and 4 (100% full). Then, stomach contents were placed in plastic bags with ice for transfer to the laboratory.

Table 1. Number of South Pacific hake, *Merluccius gayi*, sampled by sex for each month in the Ecuadorian Pacific during September 2013-December 2014.

Time (months)	Indetermined	Females	Males	Total
2013				
September	13	28	2	43
October	0	60	37	97
November	0	0	0	0
December	0	0	0	0
2014				
January	2	41	20	63
February	1	114	113	228
March	3	113	92	208
April	4	115	58	177
May	3	94	117	214
June	2	142	128	272
July	3	268	148	419
August	0	0	0	0
September	2	296	94	392
October	4	206	230	440
November	0	60	9	69
December	2	270	99	371
Total	39	1807	1147	2993

Laboratory work

Samples were thawed to separate the species in the stomach of collected individuals by taxonomic groups and counted, measured (cm), and weighed (g). Content was grouped concerning their digestion state according to Olson and Galván-Magaña (2002): state 1 or fresh (easily identifiable individuals with complete morphological characteristics), state 2 or partially digested, state 3 or remains (individuals without a head, body parts, or axial skeleton), and state 4 or completely digested (fish otoliths and structures;

cephalopod beaks and gladii; and crustacean eyes, cephalothorax, legs, and chelae).

Prey was identified by the lowest possible taxa using zooplankton-specific key guides by Boltovskoy (1981), Cajas-Flores et al. (1998), Prado-España and Cajas-Flores (2010), and Naranjo and Tapia (2013); the guides used for ichthyoplankton included Ahlstrom (1972), Beltrán-León and Ríos (2000), and Calderón (2011). Crustaceans were identified using the guide by Hendrickx (1995) and cephalopods by that from Iverson and Pinkas (1971), Wolff (1982, 1984), Clarke (1986), Roper et al. (1995), Jereb

and Roper (2010), and Jereb et al. (2014). Fish were identified with the guides by Clothier (1950), Clothier and Baxter (1969), Fischer et al. (1995), García-Godos (2001), Jiménez-Prado and Beárez (2004), Muñoz (2012), Robertson and Allen (2015), and Vinueza (2015).

DATA ANALYSIS

Data normality was assessed by the Kolmogorov-Smirnov test (KS), showing an abnormal distribution. Variance was evaluated by the Levene method. Due to its heterogeneity, non-parametric tests were used to analyze data. The Mann-Whitney (W) and Kruskal-Wallis (H) tests assessed significant differences between sizes and TM by sex, diet by sex, and sexual maturity stages, size classes, and years (Daniel, 1991; Celis-de-la-Rosa and Labrada-Martagón, 2014). To compare sex, three categories were considered: indetermined individuals, females, and males. Categories for sexual maturity stages were immature and mature. Immature individuals showed maturity stages 1 and 2, whereas mature ones, from 3 to 5. The years compared were 2013 and 2014. Individuals were classified into four groups according to their size classes: <30 cm TL, 31–45 cm TL, 46–60 cm TL, and 61–78 cm TL.

Size and TM range, mean ($\bar{X}$), and standard deviation (±) were established for each category. Size frequency histograms were elaborated with 5-cm intervals (modified from Holden and Raitt, 1975). Additionally, the length-total mass relation was determined by the potential model in Ricker (1975): $TM = a * TL^b$, in which a = intersection of the ordinate axis and b = slope of the curve. Parameter a is also denominated as the condition factor or coefficient and b, as the allometry factor or coefficient (Pauly, 1983; Espino-Barr et al., 2008). Model adjustment to the length-total mass data, with their respective 95% confidence intervals (IC 95%) and a significance level of $\alpha = 0.05$, was completed with the Minitab v.18 software (Minitab, 2017).

Coincident curve analysis was applied to determine the presence of significant differences between the length-total mass relation curves by sex (Chen et al., 1992):

$$\frac{\frac{SCRp - \sum SCRi}{2(K-1)}}{\frac{\sum SCRi}{N-3K}}$$

In which F = value of the statistic, $SCRp$ = residual sum of squares of all pooled data, $SCRi$ = residual sum of squares of each sex, K = number of curves to compare, and N = total number of length-total mass data pairs. Once the total length-total mass relation coefficients were estimated, a type of growth (isometric or allometric) was determined based on slope values: if $b = 3$, it is isometric; $b > 3$, hyperalometric, and $b < 3$, hypoalometric (Pauly, 1984; Tesch, 1968; Froese et al., 2011). Moreover, growth types were verified as isometric or allometric using the isometry test (Pauly, 1983):

$$tc = \frac{sd(x)}{sd(y)} * \frac{|b-3|}{\sqrt{1-r2}} * \sqrt{(n-2)}$$

in which tc = value of the statistic with a significance level of $\alpha = 0.05$, $sd(x)$ = TL standard deviation of $\log_{10}$ values, $sd(y)$ = total weight standard deviation of $\log_{10}$ values, r^2 = determination coefficient, and $n - 2$ = degrees of freedom.

The number of representative stomachs to adequately describe the diet of *M. gayi* was established by the method in Pileou (Hoffman, 1979). It consists of graphing the number of stomachs with food in the horizontal axis versus the accumulated diversity of the consumed prey. Thus, obtaining the accumulative curve of the latter and the number of stomachs that reach the asymptote indicates the minimum sample size. Likewise, the coefficient of variation for each stomach was obtained and graphed as a secondary axis; such coefficient was obtained as the relation between the standard deviation and the average diversity of Shannon's index (Ferry and Cailliet, 1996; Cortés, 1997). For this, the number of stomachs was calculated using the EstimateS V. 8.0 software (Colwell, 2019). The number of analyzed stomachs was subjected to 100 permutations to eliminate bias with an $\alpha = 0.05$. The variation in selecting the respective number

of stomachs totaled 0.05 (Jiménez-Valverde and Hortal, 2003).

Number (%N), frequency of appearance (%FO$_i$), and gravimetric methods (%M) were used as the ecological indices (Hyslop, 1980). The importance each prey species contributes to the diet of *M. gayi* was evaluated by the Prey-specific index of relative importance (%PSIRI) (Brown et al., 2011):

$$\%PSIRI= \frac{[\%FOi*(\%Ni+\%Mi)]}{2}$$

in which %N$_i$ = percentage of specific abundance for prey and %M$_i$ = percentage of specific mass for prey. These parameters were obtained using the following models: *%Ni = %N/%FOi* and *%Mi = %M/%FOi*. All ecological indices were applied for each factor (by sex, sexual maturity stages, years, and size classes).

The breadth of the predator diet was calculated by the Levin Index (Bi) (Krebs, 1985):

$$Bi= \frac{1}{n-1} *[(\frac{1}{\sum Pij^2})^{-1}]$$

in which Pi_j = proportion of prey *j* in the predator diet *i* and *n* = number of prey species. The values of this index range from 0 to 1, in which values below 0.6 indicate that the diet largely consists of few prey items, making it a specialist predator. Higher values than 0.6 indicate generalist predators (Labropoulou and Eleftheriou, 1997). Also, hakes were categorized as selective and opportunistic. Selective predators use their resources (habitat and food) in different proportions to their availability, whereas opportunistic predators use resources equal to those available (Johnson, 1980; Buskirk and Millspaugh, 2006). Munroe et al. (2014) suggested that resource utilization by predators must be based on their trophic behavior, so it is more appropriate to refer to a low or a high degree of specialization. Therefore, those fish that feed on a broad group of species (from invertebrates to vertebrates) have a low degree, and those that feed on small prey groups must be cataloged with a high degree of specialization.

The trophic overlap analysis (feeding resources repartition degree) was estimated using the Jaccard similarity coefficient (Krebs, 1999):

$$J = \frac{a}{a + b +c}$$

in which *J* = Jaccard index, the same that employs the presence/absence of common prey in predators; *a* = number of common prey species in predators of both sexes, sexual maturity stages, sizes, or time; *b* = the number of exclusive prey species of a predator (females, immature individuals, sizes, and the year 2013); and *c* = number of exclusive prey species of the other predator (males, mature individuals, sizes, and the year 2014). Values close to 0 indicate no overlap, whereas those close to 1 suggest an almost identical use of resources. The software Past V. 4.01 was employed to determine such an index (Hammer, 2020).

The trophic level (*TL*) was obtained by the equation in Cortés (1999):

$$TLk= 1 + (\sum_{j=1}^{n=24} Pjx*TLj)$$

in which TL_k = trophic level of the predator, *n* = the number of prey species, Pj_x = relative proportion of prey items that compose the predator diet, and TL_j = prey trophic levels. The trophic levels of the consumed prey used in the TL_k estimations of *M. gayi* were obtained from Cortés (1999), Cajas-Flores et al. (2022), and Froese and Pauly (2023). Additionally, predators and prey were categorized depending on their trophic level, based on the scale by Odum (1971): 1. Primary producers, 2. Herbivores (fed on level 1), 3. Primary carnivores (consumed level 2), 4. Secondary carnivores (ingested level 3), and 5. Tertiary carnivores (consumed level 4).

RESULTS

DIET COMPOSITION

Characteristics of the sample. This study analyzed 2,993 *M. gayi* individuals with sizes ranging from 23.6 to 78 cm TL, out of which 1807 were females (60%), 1,147 males (39%), and 39 indetermined (1%). Indetermined individuals ranged from 28.4 to 67.5 cm TL ($\bar{x}$ = 49.1 ± 5.1),

females from 25.6 to 77.1 cm TL (x̄ = 48.5 ± 9.3), and males from 23.6 and 78 cm TL (x̄ = 37.0 ± 5.8). Males were 1 cm bigger than females and 11 cm bigger than indetermined individuals. This study found no significant differences between the size of females and indetermined individuals (W = 38,403.50; p > 0.05) but observed them between females and males (W = 34 052.00; p < 0.05) and males and indetermined individuals (W = 34,243.50; p < 0.05). The mode appeared for the 45-49 cm TL class interval for females and 35 -39 cm TL for males (Figure 2). Immature and mature individuals comprised 25 and 75% of the analyzed capture, respectively.
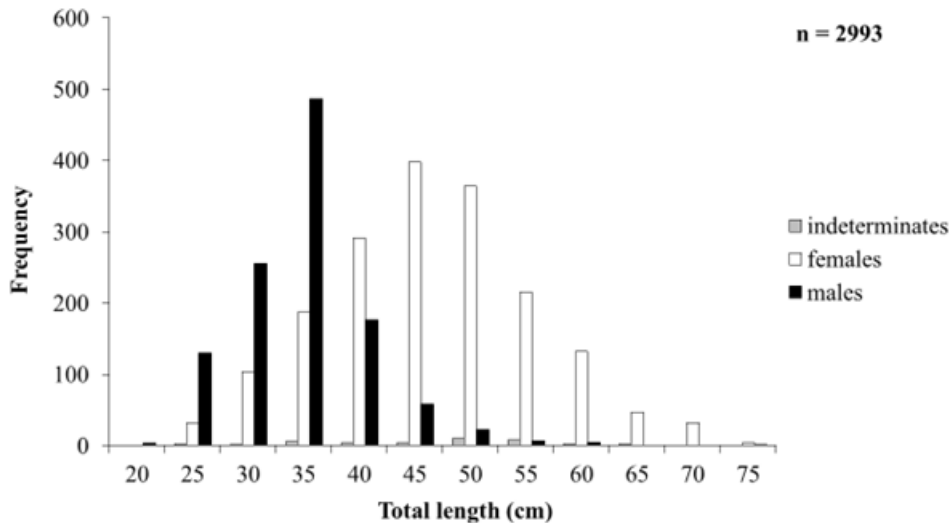

Figure 2. Frequency length distribution of *Merluccius gayi* by sex in the coast of Manabí, Santa Elena, and Guayas provinces, Ecuador. White bars = females, and black bars = males.

The TM of the analyzed hake ranged from 96.4 to 3,730 g: indetermined individuals, from 155 to 2551.5 g (x = 1076.6 ± 617.2); females, from 118.5 to 3,730 g (x = 981.6 ± 613.2); and males, from 96.4 to 2283.6 g (x = 405.9 ± 266.2). Females were heavier than male and indetermined individuals. This study found significant differences between the TM of females and males (W = 36 647.70; p < 0.05) and males and indetermined individuals (W = 37,894; p < 0.05) but not for females and indetermined individuals (W = 39,973.50; p > 0.05).

Merluccius gayi showed a general hyperallometric growth, with an allometry coefficient o f *b* = 3.04 (IC$_{95\%}$ = 3.03-3.05). Indetermined individuals had a *b* = 2.96 (IC$_{95\%}$ = 2.95-2.97), indicating an isometric growth; females, a *b* = 3.08, indicating an hyperallometric growth (IC$_{95\%}$ = 3.07-3.09); and males, a hypoallometric growth with a *b* = 2.52 (IC$_{95\%}$ = 2.51-2.52). Isometry test results confirmed this growth type at the species level (t = 3.12; p < 0.05) in indetermined individuals (t = 0.37; p > 0.05), females (t = 2.51; p < 0.05), and males (t = 10; p < 0.05) (Figure 3).

Percentage of stomach fullness and prey digestion states. Regarding the state of stomach repletion, more than half the hake had empty stomachs or were in state 0 (n = 2011; 67%), followed by state 1 (n = 549; 18%), full or state 4 (n = 167; 6%), state 2 (n = 143; 5%), and state 3 (n = 123; 4%). More than half of the prey were wholly digested or in state 4 (67%), followed by partially digested or state 2 (15%), advanced digestion or state 3 (14%), and in a minimum digestive state (4%).

Cumulative curve of prey species. From the 2,993 analyzed stomachs, 1,042 had some content (35%), whereas 1951 were empty, of which, 1,395 were everted. Moreover, 944 stomachs managed to adequately represent the diet or describe the components of this species trophic spectrum (Figure 4).

Trophic spectrum. The species diet comprised 27 food items grouped into four taxonomic groups: foraminifera, cephalopods, crustaceans, and bony fish. Cephalopods generally included squids, whereas crustaceans encompassed copepods, euphausiids, amphipods, and decapods. Bony

fish included anchovies, sardines, codlets, hakes, jacks, and barbels. *M. gayi* consumed 78,453 preys, with a total weight of 13,747 g. According to the %PSIRI, the most important prey species refer to the euphausiid, *Nyctiphanes simplex* (52%), and

the same hake species (*M. gayi*; 31%), making it a cannibal predator. Other less important species include the Peruvian barbel drum (*Ctenosciaena peruviana*), the Pacific thread herring (*Opisthonema libertate*), and other unidentified fish (Table 2).
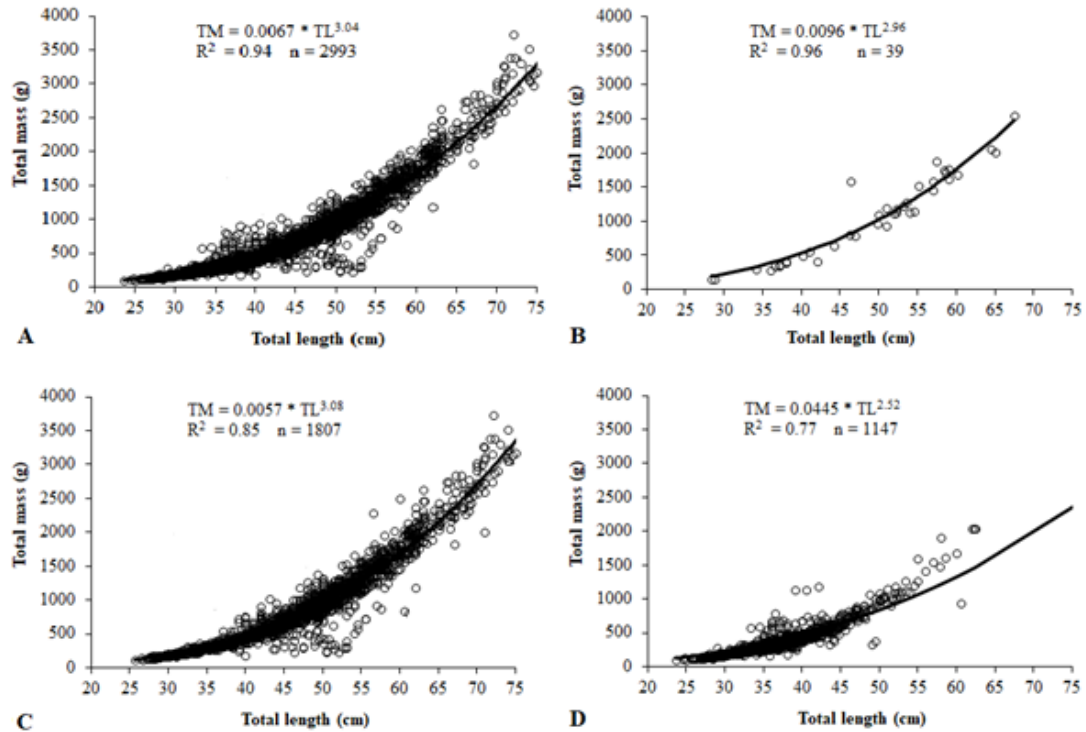

Figure 3. The relation between total length and total body mass of *Merluccius gayi* in the Ecuadorian Pacific Ocean for (a) both sexes, (b) indetermined individuals, (c) females, and (d) males. White circles = observed data, and lines = estimated relationship.
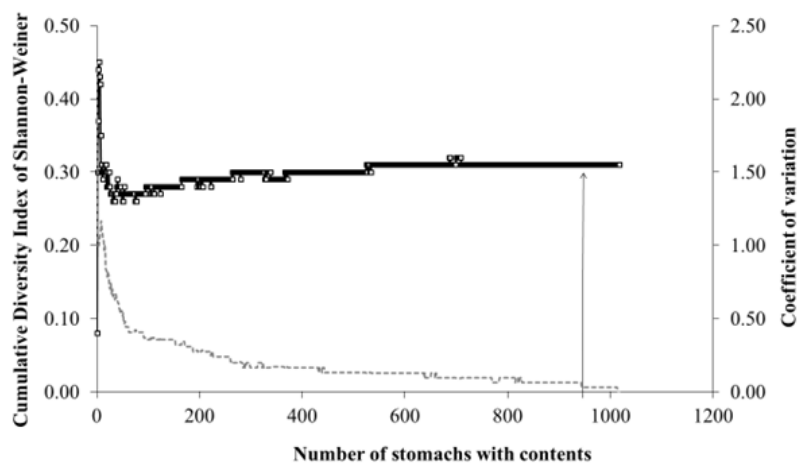

Figure 4. The accumulative curve of prey species in the stomachs of *Merluccius gayi* landed in Santa Rosa, Ecuador, showing the Cumulated Diversity Index of Shannon-Weiner and the Coefficients of Variation against the number of analyzed stomachs. he arrow indicates the number of stomachs whose curve reached the asymptote.

Table 2. Food items *Merluccius gayi* consumed in the Ecuadorian Pacific Ocean and their respective indices: percentage of number (%N), percent of frequency of occurrence (%FOi), percent of total mass (%M), %Ni = percentage of prey-specific abundance, %Mi = percentage of prey-specific mass, and %PSIRI = percentage of prey-specific index of relative importance. The taxonomic order of the prey species is based on Young et al. (2019) for cephalopods; Van der Laan et al. (2023), for fish; and Catalogue of Life (2023), for the remaining prey.

Prey species	%N	%M	%FOi	%Ni	%Mi	%PSIRI
Rhizaria						
Phylum Foraminifera	0.02	0.01	0.38	0.04	0.02	0.01
Cephalopods						
Loligo sp.	0.05	1.72	2.69	0.02	0.64	0.88
Crustaceans						
Euconchoecia chierchiae	0.00	0.00	0.10	0.01	0.00	0.00
Acrocalanus sp.	0.00	0.00	0.19	0.01	0.00	0.00
Calanus sp.	0.03	0.00	1.06	0.02	0.00	0.01
Undinula sp.	0.00	0.00	0.10	0.01	0.00	0.00
Corycaeus sp.	0.00	0.00	0.10	0.01	0.00	0.00
Microsetella rosea	0.00	0.00	0.10	0.01	0.00	0.00
Oncaea clevei	0.00	0.00	0.10	0.03	0.00	0.00
Oncaea venusta	0.00	0.00	0.10	0.01	0.00	0.00
Copepod eggs	0.05	0.00	0.29	0.19	0.00	0.03
Nyctiphanes simplex	96.21	8.27	25.24	3.81	0.33	52.24
Krill eggs	0.93	0.00	0.77	1.21	0.00	0.47
Amphipods	0.02	0.00	0.48	0.03	0.00	0.01
Decapods	1.04	0.00	8.25	0.13	0.00	0.52
Invertebrates						
Invertebrate eggs	0.50	0.00	3.93	0.13	0.00	0.25
Actinopterygii						
Engraulis ringens	0.03	0.77	1.44	0.02	0.53	0.40
Opisthonema libertate	0.05	2.60	2.69	0.02	0.97	1.32
Bregmatoceros bathymaster	0.01	0.03	0.38	0.02	0.09	0.02
Merluccius gayi	0.20	61.78	14.88	0.01	4.15	30.99
Family Bothidae	0.00	0.03	0.10	0.01	0.34	0.02
Symphurus sp.	0.00	0.06	0.19	0.01	0.30	0.03
Chloroscombrus orqueta	0.00	0.31	0.29	0.01	1.08	0.16
Ctenosciaena peruviana	0.03	13.46	2.21	0.01	6.10	6.74
Unidentified fishes	0.23	10.96	17.56	0.01	0.62	5.60
Fish remains (scales)	0.56	0.00	34.84	0.02	0.00	0.28
Fish eggs	0.02	0.00	1.73	0.01	0.00	0.01
Total	100	100				100

Feeding by sex mainly consisted of *N. simplex* and *M. gayi* (78-92%). The trophic spectrum of indetermined individuals showed only five prey species, 681 consumed organisms, and 353 g of ingested mass. The female diet comprised 22 species, 22 714 individuals, and 11 140 g. Males fed on 21 species, 52 209 specimens, and

2301 g. This study found significant differences in diet composition between females and males (W = 742.50; p > 0.05), observing significant differences between females and indetermined individuals (W = 981; p < 0.05) and between males and indetermined individuals (W = 963.50; p < 0.05) (Figure 5).
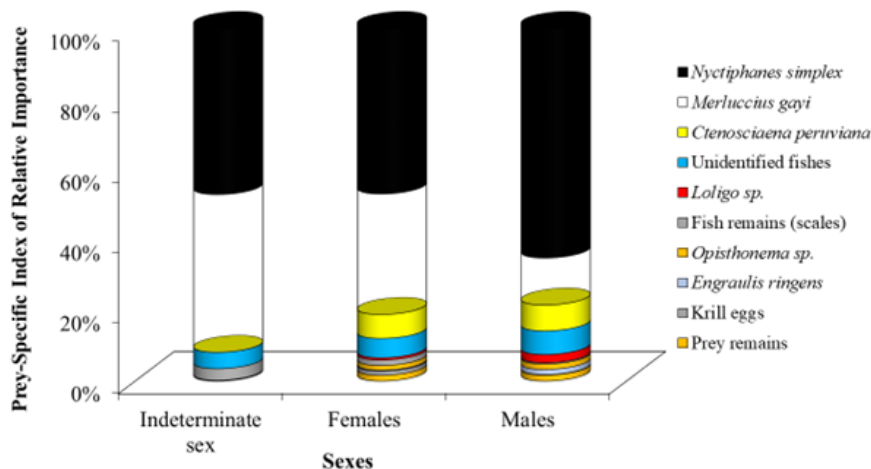

Figure 5. Prey-Specific Index of Relative Importance (%PSIRI) in the diet of *Merluccius gayi* by sex, including indetermined individuals in the Ecuadorian Pacific Ocean.

According to sexual maturity stages, results showed the importance of *N. simplex* and *M. gayi* (78-88%) in the diet of this predator. Immature females ingested fewer prey species (13), organisms (4430), and mass (1392 g) than mature females, which had a higher trophic spectrum (22), number of individuals (22 358), and consumed mass (10,104 g, thus evincing significant differences in diet composition

between immature and mature females (W = 612; p < 0.05). Immature males fed on 18 prey species, fewer specimens (14,652), and less mass (745 g) than mature males, which registered 17 species, more than twice the number of individuals (37,557), and a higher mass (1,581 g). However, diet composition between immature and mature males showed no significant differences (W = 736; p > 0.05) (Figure 6).
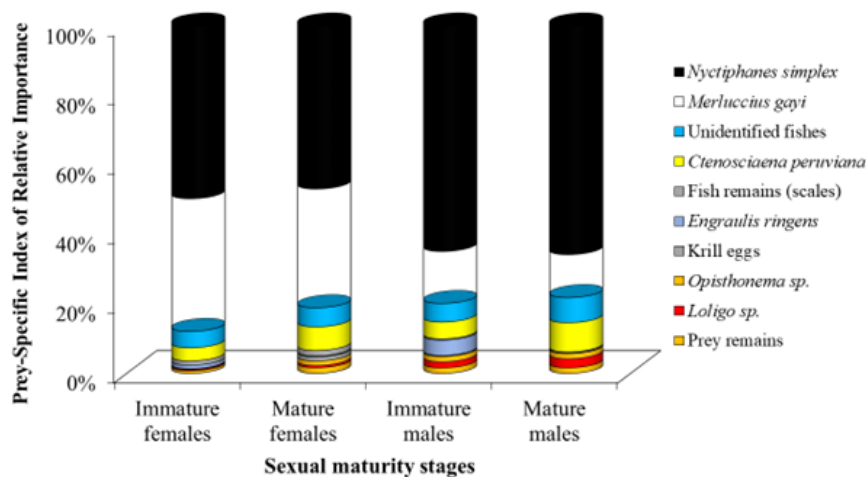

Figure 6. Prey-Specific Index of Relative Importance (%PSIRI) in the diet of *Merluccius gayi* by sexual maturity stages in Ecuador.

Regarding size classes, *N. simplex* and *M. gayi* (58-67%) constituted the most critical components in the trophic spectrum of this species. Hakes <30 cm TL had a diet of 18 species, 12,403 organisms, and 457.35 g. Fish from 31-45 cm TL had many prey species (n = 22), 65,877 organisms, and 2,275 g. Hakes from 46-60 cm TL showed fewer prey species (n = 14), 706 individuals in their diets, and 7,318 g. Fishes from 61-78 cm TL showed the lowest number between analyzed size classes

(n = 10), 387 organisms, and 2194 g. Feeding by size classes showed significant differences (H = 9.48; p < 0.05) (Figure 7).

The trophic spectrum by years also predominantly consisted of *N. Simplex* and *M. gayi* (83-86%). The predators from 2014 consumed a higher quantity of prey (26), specimens (68 859), and mass (12 741 g) than those from 2013. Feeding by years showed significant differences (W = 495.50; p < 0.05) (Figure 8).
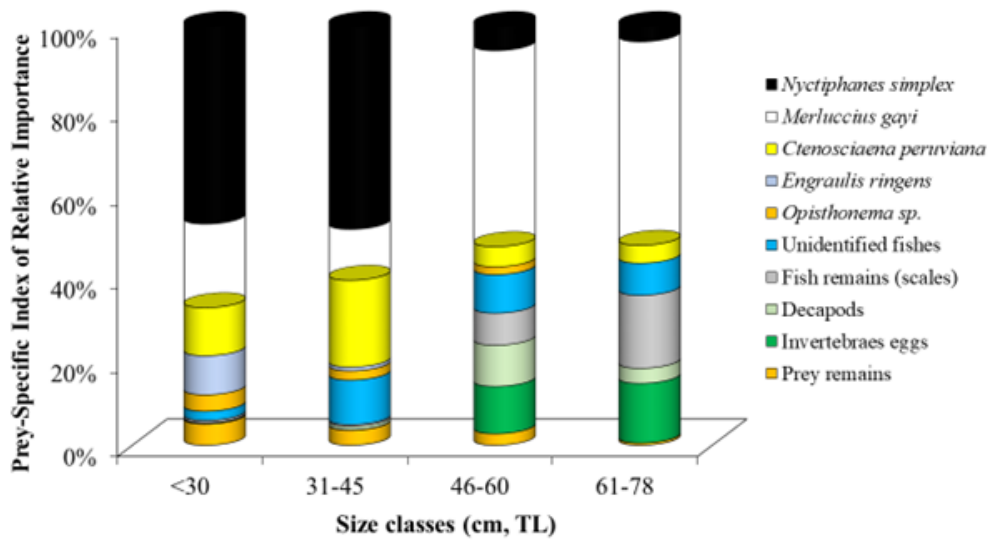

Figure 7. Prey-Specific Index of Relative Importance (%PSIRI) in the diet of *Merluccius gayi* sampled by size classes.
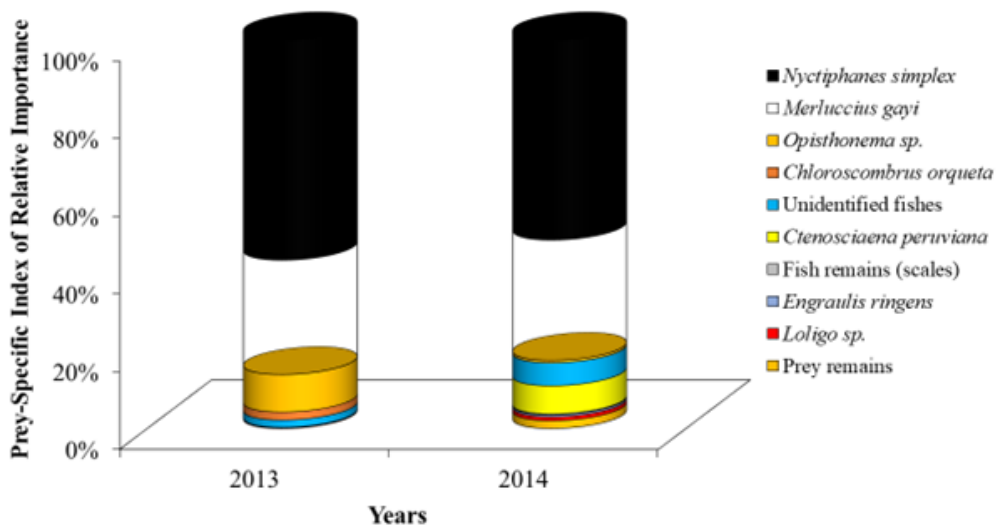

Figure 8. Prey-Specific Index of Relative Importance (%PSIRI) in the diet of *Merluccius gayi* sampled by years.

FEEDING HABITS

Trophic niche breadth. According to Levin's Index, the diet breadth was low (Bi = 0.03) for the general category, indicating that *M. gayi* is a specialist mesopredator due to the preference of two prey species from its diet composed of 27 items. Regarding sex, the three categories showed similar values for indetermined (Bi = 0.05), female, and male individuals (the latter with the same value of Bi = 0.01. This resembled immature and mature females and males, hakes <30 cm TL and 31-45 cm TL, and fish in 2013 and 2014 (Bi = 0.01). However, hakes from 46-60 cm TL (Bi = 0.40) and 61-78 cm TL (Bi = 0.36) showed higher values.

The different proportions of prey species and consumed abundance classified *Merluccius gayi* as a selective predator. Moreover, it shows a high degree of specialization since it preferred to feed on a few prey groups (cephalopods, crustaceans, and Osteichthyes).

Diet overlap. The trophic overlap analysis by sex was low (J = 0.23) for females and indetermined individuals and for indetermined individuals and males (J = 0.24), indicating that they fed on distinct prey in different proportions, i.e., they showed no similarity in their diets. However, females and males had a moderate value (J = 0.59), which suggests a certain degree of similitude in their trophic spectrum and proportions.

Regarding sexual maturity stages, this study found moderate values in the diet of immature and mature females (J = 0.56), immature and mature males (J = 0.67), and mature females and males (J = 0.62). Immature females and males showed a great overlap (J = 0.78), which suggests a feeding similarity; i.e., similar prey species and proportions. For size classes, the diet had moderate values (J = 0.42–0.63), except for hakes from 31-45 and 61-78 cm TL (J = 0.33), which was low. Furthermore, individuals from 2013 and 2014 showed low (J = 0.31) or no similarity.

Trophic level. All *M. gayi* categories showed similar trophic levels. Generally, a TLk = 3.22 indicates a primary carnivore mesopredator. Concerning sex, indetermined individuals (TLk = 3.30) resembled females (TLk = 3.26) and males (TLk = 3.22), as did immature and mature females (TLk = 3.26 for both) and immature and mature males (TLk = 3.22 for both) and hakes <30 cm TL (TLk = 3.25) and

from 31-45 cm TL (TLk = 3.22). However, it was higher for hakes from 46-60 cm TL (TLk = 3.98) and those from 61-78 cm TL (TLk = 4.00). The latter belonged to the category of secondary carnivores. Moreover, hakes from 2013 (TLk = 3.21) and 2014 (TLk = 3.23) resembled each other.

DISCUSSION

DIET COMPOSITION

Percentage of stomach fullness. In this study, 35% of the assessed stomachs had gastric content, whereas 64% of the stomachs of *M. gayi* in Paita, Peruvian Pacific, had gastric content (Orrego and Mendo, 2012). A similar value of 63% has been observed for *M. gayi* in Talcahuano, Chilean Pacific (Cubillos et al., 2003) and 45% for the Panama hake, *M. angustimanus,* in Baja California Sur, Mexico (Balart, 2005). In this study, the low percentage of stomachs with content could stem either from the voracious feeding behavior of hakes (Inada, 1995) or from the passage of time between capture and landing. Overall, twelve hours are sufficient for the gastric juices to break down and digest the food this predator consumes, even after death (Bowen, 1996).

Cumulative curve of prey species. The number of stomachs analyzed to adequately represent the diet of *M. gayi* totaled 944, which included 27 prey species. This quantity of stomachs was higher than those from the same sampling sites for this species; out of the 232 stomachs analyzed, 155 (67%) had content and 77 (33%) were empty. Thus, the latter number of stomachs was insufficient to describe the trophic spectrum (Varela and Pincay-Espinoza, 2019). In this case, the number of prey species totaled 12, and despite being lower than in this, the asymptote remained unreached. Therefore, obtaining a bulk number of stomachs for analysis is necessary regardless of the prey items found. Conversely, the number of stomachs to reach the asymptote for *M. angustimanus* totaled 250, with a diet composed of seven species (Balart, 2005). Hence, a lower prey-specific richness of such species is related to the low number of stomachs analyzed when compared to this study.

Trophic spectrum. The diet of *M. gayi* consisted of 27 preys, including foraminifera, cephalopods, crustaceans, and bony fish. The main prey items referred to *N. simplex* and the same hake species. The trophic spectrum comprised 12 species of similar taxonomic groups, in which *C. peruviana* and *N. simplex* configured the most critical prey (Varela and Pincay-Espinoza, 2019). The particular oceanographic characteristics of each study site could explain the differences in prey number and abundance. The most septentrional regions in Ecuador (Esmeraldas and Manabí province) suffer the influence of the Panama current, with warm waters poor in nutrients. In contrast, southern and central areas (Santa Elena, Guayas, and El Oro provinces) suffer the influence of the coastal Humboldt current, with nutrient-rich cold waters (Sonnenholzner et al., 2013; Martínez-Ortiz et al., 2015).

Changes in phytoplankton communities can reduce the body size and biomass of certain fish communities while favoring other fish species. This has been reported for the Humboldt upwelling system, whose warm water conditions favor phytoplankton communities dominated by picoplankton, which increase sardine biomass. In contrast, cold water conditions favor phytoplankton communities dominated by diatoms, which increase anchovy biomass (Pennington et al., 2006). Similar variations have been observed for specific sites on the Ecuadorian coast, suggesting an essential change in the phytoplankton community between warm and cold months (Torres, 2010; Pesantes, 1983). For example, Puerto Bolivar and the Gulf of Guayaquil seasonally suffer the influence of the Humboldt Current and Humboldt upwelling system (Montecino and Lange, 2009). The influence of these currents explains the higher values of Chlorophyll a (Chl a) in these areas when compared to other sites along a coastal profile of Ecuador (Chinacalle-Martínez et al., 2021). However, Esmeraldas lies farther north, away from the Humboldt upwelling system, suggesting that its high primary production values are associated with nutrient fertilization from river and mangrove discharge (Chinacalle-Martínez et al., 2021). The Gulf of Guayaquil and Esmeraldas receives water discharge from the largest hydrographic systems on the Ecuadorian coast and their estuaries

show high concentrations of nitrates, phosphates, and silicates (Salcedo and Coello, 2018). These nutrients promote the increase in phytoplankton biomass, particularly of diatoms (Naranjo and Tapia, 2002; Prado-España et al., 2017), which have been found as the main contributors to the total marine primary production and particulate carbon exported to depths (Tréguer et al., 2017). In these sites, Chl a concentrations of 1 to 7 mg m^{-3} have been reported (Chinacalle-Martínez et al., 2021), resembling *in situ* studies based on the contribution of nutrients by river discharges (Coello and Prado, 1999; Tapia and Naranjo, 2004). Such studies support the premise that Humboldt upwellings and river discharge systems along the coast of Ecuador can control primary production, thus structuring marine food chains by synthesizing and incorporating matter and energy to feeders at higher trophic levels (Chinacalle-Martínez et al., 2021).

The diet of *M. gayi* in the Peruvian Pacific consisted of 57 species grouped in cephalopods, crustaceans, and Osteichthyes, in which the same hake (41%), *Engraulis ringens* (24%), and the lumptail searobin *Prionotus stephanophrys* (10%) stood out (Orrego and Mendo, 2012). This differed from another study in which the trophic spectrum consisted of 19 species with the same taxonomic groups, including echinoderms with euphausiids (74%) and the same hake (24%) (Castillo, 2018). The latter diet resembles that in this study regarding the most important species.

The diet composition of *M. gayi* failed to differ by sex, showing the prevalence of *N. simplex* and the same hake species. In Argentinian waters in the Southwest Atlantic Ocean, both sexes of the Southern hake, *Merluccius australis,* showed a similar diet (Giussi et al., 2016). In Peru, prey consumed by females included the same hake (*M. gayi*), *C. peruviana*, the shrimp *Pasiphaea americana*, *E. ringens,* and the red squat lobster, *Pleuroncodes monodon*; contrarily, males had different feeding patterns, preferring squid from the Loliginidae family, the same hake (*M. gayi*), *E. ringens*, *P. americana*, and euphausiids (Castillo, 2018). The similarity in the trophic spectrum by sex suggests a certain degree of food competition between females and males. Furthermore, the differences in their diet

composition indicate one selection in feeding due to segregation processes related to habitat use (availability of prey and habitat) and behavior (Wearmouth and Sims, 2008).

The trophic spectrum of *M. gayi* by sexual maturity stages indicated differences in feeding between immature and mature females but not between immature and mature males. This study considered feeding information related to their biological phase cycles due to scarce data regarding its diet composition and feeding habits. Young individuals (<37 cm TL) mostly fed on planktonic crustaceans such as euphausiids, whereas adults (individuals ≥ 37 cm LT) feed on fishes (e.g., anchovy, *Engraulis ringens*, Araucanian herring, *Strangomera bentincki*, and benthic crustaceans (the galatheid *P. monodon*) (Gatica et al., 2015). These feeding differences by sexual maturity stages suggest no intraspecific competition due to the exploitation of food resources in different trophic niches. The ontogenic changes in fish feeding behavior stem from the energetic requirements related to the growth and development of each individual.

The diet of *M. gayi* differed by size classes. The species showed this pattern in its feeding concerning sizes from classes I (< 30 cm de TL), IV (40-45 cm de TL), and V (> 45 cm de TL). Thus, those from class I mainly fed on euphausiids (58%); those from class II (30-35 cm de TL) and III (35-40 cm de TL), on the long-finned butterfish, *Peprilus medius* (56-69%); and class IV and V, on *C. peruviana* (77-88%) (Varela and Pincay-Espinoza, 2019). In the case of *M. angustimanus,* the red crab, *Pleuroncodes planipes*, configured the predominant prey within a trophic spectrum with crustaceans, mollusks, and Osteichthyes. For all size classes (I – IV, <16 – >25 cm TL) in the Mexican Pacific *P. planipes* dominated diets, but in the size class I, the second most important prey refers to *Nyctiphanes simplex*, whereas, in the size classes II, III and IV, the same hake species (Balart, 2005). These feeding differences by size classes indicate that bigger hakes can explore different habitats and capture larger prey. Predators become more successful with size due to various factors, including increased sustained and burst swimming speeds and better visual acuity (Keast and Webb,

1966; Blaxter, 1986; Scharf et al., 2000). For most fish, the sizes of the prey generally increase with predator size (Keast and Webb, 1966; Juanes, 1994; Scharf et al., 2000).

The smallest *M. gayi* individuals also showed distinct feeding preferences, consuming crustaceans and small fish such as *E. ringens* and the South American pilchard, *Sardinops sagax*, whereas the largest individuals ingested bigger fish, such as *P. stephanoprys* and the same hake species (Álamo and Blaskovic 1994; Álamo and Espinoza 1996, 1997). For *M. gayi gayi* in Chile, hakes ranging from 26 to 55 cm TL consumed *P. monodon*, especially those that reached sexual maturity (Arancibia and Fuentealba, 1993).

Bony fish play an essential role in the diet of *M. gayi*, resembling *M. merluccius* from Viscaya Bay and the Celtic Sea, Northeast Atlantic Ocean, in which specimens larger than 23 cm TL preferred to feed on the Atlantic horse mackerel, *Trachurus trachurus*; European pilchard, *Sardina pilchardus*; European anchovy, *Engraulis encrasicolus;* and the blue whiting, *Micromesistius poutassou* (Mahe et al., 2007). These authors sustain that the ontogenic changes in species diet are related to the increased energetic demand for growth. In the stomach contents of *M. merluccius* belonging to different size classes in the Tyrrhenian Sea, south of the Mediterranean, the presence of mesopelagic fish species and euphausiids and mysids highlights the presence of a flow of energy and organic matter from a mesopelagic to epipelagic environment (D'Iglio et al., 2022a). The geomorphic characteristics of this study area, together with the circulation of water masses and upwelling processes (Gasparini et al., 2005; Marullo et al., 2011), promote and increase the vertical migration of mesopelagic fish to shallow waters, increasing contact between this community and demersal predators such as hake (D'Iglio et al., 2022a). This clearly exemplifies reverse energy flow from deep to epipelagic waters, essential for demersal species.

Furthermore, these feeding variations are also associated with morphological growth shifts, which enable them to capture prey of various types and sizes (Castillo, 2018). Similar results have also been reported in this area from 2018 to 2020, in which *M. merluccius* preys on species in

the benthic layer and throughout the water column (D'Iglio et al., 2022b). The trophic spectrum reported for this species ranges from exploited prey in the benthic environment and mesopelagic bioluminescent species and nektobenthic prey species along vertical and horizontal migrations (D'Iglio et al., 2022b). The large spectrum of prey *M. merluccius* exploits makes this species an essential predator, highlighting its crucial role in the energy exchange between different depths and trophic levels (Modica et al., 2015).

Quantitative and qualitative diet shifts could be regulated and synchronized by mouth size (which increases with the size of the individual) and the energetic reward from captured prey when compared to prey availability (Balart, 2005). Notably, a study involving the morphology and histology of the stomachs of *M. australis* in Puerto Montt, Chile, determined this species as a carnivore predator with a digestive system adapted to digest and absorb prey rich in proteins, mainly fish and crustaceans (Serrano et al., 2014).

The diet composition of *M. gayi* individuals collected in 2013 differed from those in 2014. One of the limitations of this study was that sample collection failed to include the whole year of 2013, and 2014 was a year with an El Niño event. This is similar to what was found in Peru, where the same event occurred in 1997 and 1998 and amplified trophic spectrum to 46 prey species, whereas the number of prey items in 1995 and 1996 totaled 15 and 19, respectively (Orrego and Mendo, 2012). The warm water from this event varies habitat temperature, changing prey species or feeding availability in a habitat (Espino, 1990; Guevara-Carrasco and Wosnitza-Mendo, 2009).

FEEDING HABITS

The trophic niche breadth classified *M. gayi* as a specialist and selective predator with a high degree of specialization since it preferred two species out of 27. This differs from other classifications that cataloged it as an opportunistic predator that feeds on various invertebrates and vertebrates (Varela and Pincay-Espinoza, 2019). It is also categorized as an opportunistic predator because it takes advantage of the feeding resources from various strata in marine environments. For example, the diet of this species in the Peruvian Pacific consisted of 19 prey species (six crustaceans, one cephalopod, one echinoderm, and 11 Osteichthyes). From these, the euphausiids, *M. gayi*, and the glass shrimp, *Pasiphaea americana*, configured the predominant species. Additionally, *M. gayi* inhabiting the Coquimbo and Carrizal bays off northern Chile showed that 22 prey species composed its diet, in which the deep-sea shrimp, *Heterocarpus reedi*; the euphausiid, *Euphausia mucronata;* the yellow squat lobster, *Cervimunida johni;* and *P. monodon* (Vidal et al., 1997) mainly contributed to its trophic spectrum. Hence, it shows a heterogeneous diet and feeds on the most abundant ones, which supports its wide distribution in other areas (Vidal et al., 1997; Castillo, 2018). It is essential to highlight that the categorization of *M. gayi* as a specialist predator is reasonable given that the long-term diet analysis of this species in Chile determined that it has retained its food preferences in the last two decades, focusing on *P. monodon*, the stomatopod, *Pterygosquilla armata*; euphausiids, *E. ringens*; and the hake itself (Arancibia and Fuentealba, 1993).

The trophic level of *M. gayi* indicated it was a mesopredator carnivore (primary and secondary). This is similar to the report for this species in Chilean waters (TL_k = 4.26) (Konchina, 1983), belonging to a high trophic level predator (Meléndez, 1984; Neira and Arancibia, 2004; Neira et al., 2004; Gatica et al., 2015), specifically a secondary carnivore. Moreover, the trophic level of *M. australis* (TL_k = 4.50) indicated that this species is a secondary carnivore whose diet mainly consists of Osteichthyes, cephalopods, crustaceans, and salps (Wöhler et al., 1999; Marí and Sánchez, 2002; Sánchez and Marí, 2002; Giussi et al., 2016). This latter trophic level was similar to the South Pacific hake.

Merluccius gayi is an important mesopredator in the coastal and marine ecosystems of the Ecuadorian Pacific. It comprises the diet of higher trophic level species, such as the pelagic thresher, *Alopias pelagicus*; the crocodile shark, *Pseudocarcharias kamoharai*; the shortfin mako, *Isurus oxyrinchus*; the scalloped hammerhead, *Sphyrna lewini;* the Atlantic blue

marlin, *Makaira nigricans*; the striped marlin, *Kajikia audax;* the Indo-Pacific sailfish, *Istiophorus platypterus*; and the swordfish, *Xiphias gladius* (Estupiñán-Montaño et al., 2009; Rosas-Luis et al., 2016; Loor-Andrade et al., 2017; Calle-Morán and Galván-Magaña, 2020; Calle-Morán et al., 2022), among others. It is also an essential part of the feeding spectrum of the South American sea lion, *Otaria flavescens,* in marine ecosystems from the Chilean Pacific (George-Nascimento et al., 1985). The hake fulfills a fundamental role in such ecosystems because it is a mesopredator that allows nutrient and energy flow in the trophic chains it participates in.

The diet of *M. gayi* included the same hake species, which indicated cannibalism (13-45%). This has also been observed for the species in the Peruvian and Ecuadorian oceans (Hermosilla, 1959; Meléndez, 1984; Cubillos et al., 2003; Orrego and Mendo, 2012; Castillo, 2018). Such behavior is typical in most hake species, such as *M. angustimanus*, *M. merluccius*, the shallow-water Cape hake, *M. capensis*, and the deep-water Cape hake, *M. paradoxus* (Punt et al., 1992; Balart, 2005; Carpentieri et al., 2005; Mahe et al., 2007). The hypotheses that attempts to explain cannibalism indicate that (a) it is a self-regulation population mechanism given that hakes form large shoals in which small and large individuals coexist and the biggest consume the smallest (Lleonart et al., 1983, 1985); (b) this behavior occurs during autumn and winter, seasons in which its energy increases due to growth (Fuentes et al., 1989); and (c) the lower availability of *E. ringens* increases cannibalism as individuals can take advantage of their species (Álamo and Espinoza, 1997).

The hunting behavior of *M. gayi* indicates that it remains close to the bottom of the ocean during the day, forming more or less dense shoals and performing vertical migrations to the surface during sunset and night (Avilés et al., 1979). These movements enable the species to feed on organisms with different habitats. Hence, its diet is predominantly pelagic, followed by benthic and demersal species (Meléndez, 1984; Cubillos et al., 2003).

CONCLUSION

The feeding strategy of *Merluccius gayi* involved a diet composed of 27 feeding items, including foraminifera, squid, crustaceans, and bony fish. The species highly preferred two prey species: the euphausiid, *Nyctiphanes simplex,* and the same hake species, *M. gayi*, evincing cannibalism in its trophic behavior. Its diet differed during its first life stages (individuals with indetermined sex), remaining similar in females and males. Immature and mature males showed a similar feeding spectrum. However, mature and immature females ingested different prey at a temporal scale. This species is a selective specialist mesopredator with a high specialization degree that exploits the trophic niche resources of its environment. Its estimated trophic level classifies it as a first-order carnivore predator.

Feeding studies based on stomach contents precisely describe the prey species that individuals consume on a recent time scale. However, carbon and nitrogen stable isotope analysis is recommended to investigate feeding patterns over extended periods. Knowing what an individual consumes helps to understand a species role within an ecosystem and how it relates to its environment.

AUTHOR CONTRIBUTIONS

A.R.H.T: Conceptualization; Investigation; Formal Analysis; Writing – original draft; Writing – review & editing.

J.M.C.F.: Methodology; Software; Formal Analysis; Investigation; Writing – review & editing.

A.O.F: Conceptualization; Investigation; Writing – original draft; Writing – review & editing;

M.D.C.M.: Methodology; Software; Formal Analysis; Investigation; Writing – original draft; Writing – review & editing.

R.J.B.O.: Conceptualization; Investigation; Writing – original draft; Writing – review & editing.

REFERENCES

Aguayo-Hernández, M. 1995. *Biology and fisheries of Chilean hakes (M. gayi and M. australis)*. In: Alheit, J. & Pitcher, T.J. (eds.). *Hakes: biology, fisheries, and markets* (pp. 305–338). London: Chapman & Hall.

Ahlstrom, E. H. 1972. Kinds and abundance of fish larvae in the Easter Tropical Pacific on the second multivessel EASTROPAC survey, and observations on the annual cycle of larval abundance. *Fishery Bulletin*, 70(4), 1153–1242.

Álamo, A. & Espinoza, P. 1996. Comportamiento alimenticio de la merluza durante el invierno de 1996. Crucero BIC SNP-1 9607-08. *Informe Instituto del Mar del Perú*, 124, 79–85.

Álamo, A. & Espinoza, P. 1997. Espectro alimentario de la merluza durante el otoño de 1997. Crucero BIC Humboldt 9705-06. *Informe Instituto del Mar del Perú*, 128, 47–55.

Álamo, A. & Blaskovic, V. 1994. Espectro alimentario y ración de alimentación de *Merluccius gayi peruanus* durante el invierno de 1994. Lima, Instituto del Mar del Perú.

Allan, J. D. & Castillo, M. M. 2007. *Stream Ecology: structure and function of running waters*. (2nd ed). New York, Springer.

Amezaga Herrán, R. 1988. Análisis de contenidos estomacales en peces. Revisión bibliográfica de los objetivos y la metodología. *Informes técnicos*, 63, 1–74.

Arana, P. & Williams, S. 1970. Contribución al conocimiento del régimen alimentario de la merluza (*Merluccius gayi gayi*). *Investigaciones Marinas*, 1(7), 139–154.

Arancibia, H. & Fuentealba, M. 1993. Análisis de la alimentación de *Merluccius gayi* de Chile Central, en el largo plazo. *Biología Pesquera*, 6, 45-52.

Avilés, S., Aguayo, M., Inostroza, F. & Canon, J. 1979. *Merluza común, Merluccius gayi (Guichenot)*. *In*: Instituto del Fomento Pesquero *Estado actual de las principales pesquerías nacionales. Bases para un desarrollo pesquero*. Chile: IFOP.

Bahamonde, N. & Carcamo, M. 1959. Observaciones sobre la alimentación de la merluza (*Merluccius gayi*) en Talcahuano. *Investigaciones Zoológicas Chilenas*, 5, 211–216.

Balart, E. 2005. *Biología y ecología de la merluza bajacaliforniana, Merluccius angustimanus, Garman 1899, en la costa occidental de Baja California Sur, México* [Phd thesis]. San Nicolás de los Garza: Universidad Autónoma de Nuevo Léon.

Beltrán-León, B. & Ríos, R. 2000. *Estadios tempranos de peces del Pacífico colombiano*. Tomo 2. Buenaventura: Instituto Nacional de Pesca y Acuacultura.

Blaskovic, V. & Espinoza, P. 2011. Dieta de la merluza peruana en el verano 2004. Crucero Bic Olaya 0401-02 Informe. *Informe Instituto del Mar del Perú*, 38(3), 311–319.

Blaxter, J. H. S. 1986. Development of sense organs and behavior of teleost larvae with special reference to feeding and predator avoidance. *Transactions of the American Fisheries Society,* 115, 98–114.

Boltovskoy, D. 1981. *Atlas del Zooplancton del Atlántico Sudoccidental y métodos de trabajo para el zooplancton marino*. Mar del Plata, Instituto Nacional de Investigación Pesquera.

Bowen, S. H. 1996. Quantitative description of the diet. In: Murphy, B.R. & Willis, D. W. (eds). *Fisheries Techniques*. (2nd ed, pp. 513–532). Bethesda: American Fisheries Society.

Brown, S. C., Bizzarro, J. J., Cailliet, G. M. & Ebert, D. A. 2011. Breaking with tradition: redefining measures for diet description with a case study of the Aleutian skate *Bathyraja aleutica* (Gilbert, 1896). *Environmental Biology of Fishes*, 95, 3–20. DOI: https://doi.org/10.1007/s10641-011-9959-z.

Buskirk, S. W. & Millspaugh, J. J. 2006. Metrics for studies of resource selection. *Journal of Wildlife Management*, 70, 358–366.

Cahu, C. 2004. Domestication et fonction nutrition chez les poissons. *INRA Production Animals*, 17(3), 205–210.

Cajas-Flores, J. M., Coello, D. & Domínguez, C. 1998. Comunidades del fitoplancton y zooplancton en el Estuario Interior del Golfo de Guayaquil. *In*: Instituto nacional de pesca. *Comportamiento temporal y espacial de las características físicas, químicas y biológicas del Golfo de Guayaquil y sus afluentes Daule y Babahoyo entre 1994-1996* (pp. 261–284). Guayaquil: Instituto Nacional de Pesca.

Cajas-Flores, J. M., Prado-España, D. M., Bucheli-Quiñónez, R. J., Calle-Morán, M. D. & Hernández-Téllez, A. R. 2022. Ecología trófica del machuelo hebra pinchagua, Opisthonema libertate, en el océano Pacífico ecuatoriano. *Acta Oceanográfica del Pacífico*, 4(2), 91–117.

Calderón, G. 2011. *Catálogo de huevos y larvas de peces colectadas en aguas ecuatorianas*. Boletín Especial. Guayaquil, Instituto nacional de Pesca.

Calle-Morán, M. D. & Galván-Magaña, F. 2020. Diet composition and feeding habits of the pelagic thresher shark, *Alopias pelagicus*, in Eastern Central Pacific Ocean, Ecuadorian waters. *Journal of the Marine Biological Association of the United Kingdom*, 100(5), 1–9. DOI: https://doi.org/10.1017/S0025315420000569.

Calle-Morán, M. D., Hernández-Téllez, A. R., Tibán-Vivar, E. R., Intriago-Vera, Y. E., Del Valle-Coello, I. G., Loor-Jama, B. C. & Ganchozo-López, A. R. 2022. Diet composition and feeding habits of the crocodile shark, *Pseudocarcharias kamoharai*. *Environmental Biology of Fishes*, 105(6), 685–697. DOI: https://doi.org/10.1007/s10641-022-01277-x.

Carpentieri, P. Colloca, F., Cardinale, M., Belluscio, A., Ardizzone, G. D. 2005. Feeding habits of European hake (*Merluccius merluccius*) in the central Mediterranean Sea. *Fishery Bulletin*, 103(2), 411–416.

Carrozzi, V., Di Lorenzo, M., Massia, D., Titonea, A., Ardizzoneb, G., & Collocaac, F. 2019. Prey preferences and ontogenetic diet shift of European hake, *Merluccius* (Linnaeus, 1758) in the central Mediterranean Sea. *Regional Studies in Marine Science*, 25, 100440. DOI: https://doi.org/10.1013/j.rsma.2018.100440.

Castillo, R., Juárez, L. & Aldana, L. 1995. Composición y consumo de alimento de la merluza peruana con especial énfasis en la ración diaria total. *Informe Instituto del Mar del Perú*, (71), 3–13.

Castillo, R., Juárez, L. & Aldana, L. 1997. Composición y consumo del alimento de la merluza peruana *Meiuccius gayi peruanus* (Guitchenot) com especial énfasis en la ración diaria total. *Informe Instituto del Mar del Perú*, (112), 5–18.

Castillo, D. 2018. Dieta de la merluza peruana (*Merluccius gayi peruanus*, Ginsburg) durante el otoño 2015. *Informe Instituto del Mar del Perú*, 45(1), 82–90.

Castillo, D. 2019. Dieta de la merluza peruana (*Merluccius gayi peruanus*, Ginsburg, 1954) en otoño 2012. *Informe Instituto del Mar del Perú*, 34(2), 355–368.

Castillo, R., Juárez, L. & Higginson, L. 1989. Depredación y canibalismo en la población de la merluza peruana en el área de Paita- Perú. Memorias del Simposio Internacional de los Recursos Vivos y las Pesquerías en el Pacífico Sudeste de 1988. *Comisión Permanente del Pacífico Sur (CPPS)*, (Número Especial).

Celis-de-la-Rosa, A.J. & Labrada-Martagón, V. 2014. *Bioestadística*. Ciudad de México, El Manual Moderno.

Chen, Y., Jackson, D. A. & Harvey, H. H. 1992. A comparison of von Bertalanffy and polynomial function in modeling fish growth data. *Canadian Journal of Fisheries and Aquatic Sciences*, 49(6), 1228–1235. DOI: https://doi.org/10.1139/f92-138.

Chinacalle-Martínez, N., García-Rada, E., López-Macías, J., Pinoargote, S., Loor, G., Zevallos-Rosado, J., Cruz, P., Pablo, D., Andrade, B., Robalino-Mejía, C., Añazco, S., Guerrero, J., Intriago, A., Veelenturf, C. & Peñaherrera-Palma, C. 2021. Oceanic primary production trend patterns along coast of Ecuador. *Neotropical Biodiversity*, 7(1), 379–391.

Christensen, V. & Pauly, D. 1995. Fish production, catches and the carrying capacity of the world oceans. *Naga, The ICLARM Quarterly*, 18(3), 34-40.

Clarke, M. 1986. *A handbook for the identification of cephalopod beaks*. Oxford, Clarendon Press.

Clothier, C. 1950. *A key to some southern California fishes based on vertebral characters*. Fishery Bulletin no. 79. California, Bureau of Marine Fisheries.

Clothier, C. & Baxter, J. 1969. *Vertebral characters of some Californian fishes with notes on other Eastern Pacific species*. Sacramento, Marine Resources Operations.

Coello, D. & Prado, M. 1999. Variabilidad del fitoplancton y microzooplancton frente a la costa ecuatoriana durante 1995-1999. *Boletín especial Instituto Nacional de Pesca*, 72–108.

Colwell, R. K. 2019. *Statistical estimation of species richness and shared species from samples. EstimateS* version 9.1.0. Storrs, University of Connecticut.

Cortés, E. 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, 54(3), 726–738. DOI: https://doi.org/10.1139/f96-316.

Cortés, E. 1999. Standardized diet composition and trophic level in sharks. *ICES Journal of Marine Science,* 56(5), 707–717. DOI: https://doi.org/10.1006/jmsc.1999.0489.

Cubillos, L. A., Alarcón, C. & Arancibia, H. 2007. Selectividad por tamaño de las presas en merluza común (*Merluccius gayi gayi*), zona centro-sur de Chile (1992–1997). *Investigaciones Marinas*, 35(1), 55–69. DOI: https://doi.org/10.4067/S0717-71782007000100005.

Cubillos, L.A., Rebolledo, H. P. & Hernández, A. F. 2003. Prey composition and estimation of Q/B for the Chilean hake, *Merluccius gayi* (Gadiformes, Merluccidae), in the central-south area off Chile (34°-40°S). *Archive of Fishery and Marine Research*, 50(3), 271–286.

Daniel, W. W. 1991. *Bioestadística, base para el análisis de las Ciencias de la Salud*. 4a ed. Ciudad de México, Limusa.

De Silva, S.; Turchini, G. & Francis, D. 2012. Nutrition. *In*: Lucas, J. S. & Southgate, P. C. (Eds.). *Aquaculture-farming aquatic animals and plants* (2nd ed, pp. 164–187). Oxford: Wiley-Blackwell.

D'Iglio, C., Porcino, N., Savoca, S., Profeta, A., Perdichizzi, A., Armeli Minicante, E., Salvati, D., Soraci, F., Rinelli, P. & Giordano, D. 2022a. Ontogenetic shift and feeding habits of the European hake (*Merluccius merluccius* L., 1758) in Central and Southern Tyrrhenian Sea (Western Mediterranean Sea): A comparison between past and present data. *Ecology and Evolution*, 12(3), e8634. DOI: https://doi.org/10.1002/ece3.8634.

D'Iglio, C., Famulari, S., Albano, M., Giordano, D., Rinelli, P., Capillo, G., Spano, N. & Savoca, S. 2022b. Time-scale analysis of prey preferences and ontogenetic shift in the diet of European hake, *Merluccius merluccius* (Linnaeus, 1758) in southern and central Tyrrhenia Sea. *Fishes*, 7(4), 167. DOI: https://doi.org/10.3390/fishes7040167.

Espino, M. 1990. "El Niño": su impacto sobre los peces demersales del Perú. *Boletín Instituto del Mar del Perú*, 14(2), 3–27.

Espino-Barr, E., González-Vega, A., Santana-Hernández, H. & González-Vega, H. 2008. *Manual de Biología pesquera*. Nayarit: Instituto Nacional de la Pesca y Acuicultura: Universidad Autónoma de Nayarit.

Espinoza, P. 2000. Interacción trófica merluza-anchoveta, ¿existe realmente impacto por depredación? *Boletín Instituto del Mar del Perú*, 19(1–2), 15–20.

Espinoza, P. 2001. Alimentación de la merluza (*Merluccius gayi peruanus*) y sus fluctuaciones en el tiempo. *In*: Espino, M., Samamé, M. & Castillo, R. (eds.). *La merluza peruana (Merluccius gayi peruanus) biología y pesquería* (pp. 50–54). Lima: IMARPE.

Estupiñán-Montaño, C., Cedeño-Figueroa, L. G. & Galván-Magaña, F. 2009. Hábitos alimentarios del tiburón martillo, *Sphyrna lewini* (Griffith & Smith 1834) (Chondrichthyes) en el Pacífico ecuatoriano. *Revista de Biología Marina y Oceanografía*, 44(2), 379–386. DOI: doi.org/10.4067/S0718-19572009000200011.

Ferry, L.A. & Cailliet, G. M. 1996. *Sample size and data analysis: are we characterizing and comparing diet properly? In*: Mackinlay, D. & Shearer, K. (eds.). *Feeding ecology and nutrition in fish. International Congress of the Biology of Fishes* (pp. 71–80). Bethesda: AFS.

Fischer, W., Krupp, F., Schneider, W., Sommer, C., Carpenter, K. & Niem, V. 1995. *Guía FAO para la identificación de especies para los fines de la pesca. Pacífico Centro Oriental*. Roma: FAO.

Froese, R., Tsikliras, A. C. & Stergiou, K. I. 2011. Editorial note on weight–length relations of fishes. *Acta Ichthyologica et Piscatoria*, 41(4), 261–263. DOI https://doi.org/10.3750/AIP2011.41.4.01.

Froese, R. & Pauly, D. 2023. FishBase. Available from: https://www.fishbase.org. Access date: 2024 Mar 13.

Fuentealba, M. 1993. *Relaciones tróficas intraespecíficas de la merluza común, Merluccius gayi (Guichenot, 1848); de Chile Central* [Thesis]. Concepción: Universidad de Concepción.

Fuentes, H. 1983. Algunas consideraciones sobre la relación predador-presa en la merluza peruana (*Merluccius gayi peruanus*) del área de Paita. *In: IX Congreso Latinoamérica de Zoología*, Arequipa.

Fuentes, H., Antonietti, E. & Muck, P. 1989. Alimentación de la merluza (*Merluccius gayi peruanus*) de la zona de Paita. *In*: Jordán, H., Kelly, R., Mora, O., De Vildoso, A. C. & Enríquez, N. (eds.). *Memorias del Simposio Internacional de los recursos vivos y las pesquerías en el Pacífico sudeste* (pp. 279-286). Guayaquil: Comisión Permanente del Pacífico Sur.

Garcia, S., Rice, J. & Charles, A. 2014. Governance of Marine Fisheries and Biodiversity Conservation: Convergence or Coevolution? *In*: Garcia, S., Rice, J. & Charles, A. (eds.) *Governance of Marine Fisheries and Biodiversity Conservation: Interaction and Coevolution* (pp. 18–36). Chichester: John Wiley & Sons.

García-Domínguez, M., Gilces, I., Lavayen-Zapata, F., Daza-Bermeo, C., Bermúdez, C., Ávila-Zambrano, E. & Cevallos-García, A. 2014. *Pesquería del recurso merluza (Merluccius gayi) en el Ecuador Continental 2013*. Manta: Ministerio de Agricultura, Ganadería, Acuacultura y Pesca.

García-Godos, I. 2001. *Patrones morfológicos del otolito sagitta de algunos peces óseos del mar peruano* (Vol. 20). Callao: IMARPE.

Gática, C., Neira, S., Arancibia, H. & Vásquez, S. 2015. The biology, fishery and market of Chilean hake (Merluccius gayi gayi) in the Southeastern Pacific Ocean. *In*: Arancibia, H. (ed.). *Hakes: Biology and Exploitation* (pp. 126-153). Chichester: John Wiley & Sons.

Gasparini, G. P., Ortona, A., Budillon, G., Astraldi, M. & Sansone, E. 2005. The effect of the Eastern Mediterranean Transient on the hydrographic characteristics in the Strait of Sicily and in the Tyrrhenian Sea. *Deep Sea Research Part I: Oceanographic Research Papers*, 52(6), 915–935. DOI: https://doi.org/10.1016/j.dsr.2005.01.001.

George-Nascimento, M., Bustamente, R. & Oyarzún, C. 1985. Feeding ecology of the South American sea lion, *Otaria flavescens*: food contents and food selectivity. *Marine Ecology Progress Series*, 21(1/2), 135–143. DOI: https://doi.org/10.3354/MEPS021135.

Giussi, A. R., Gorini, F. L., Di Marco, E. J., Zavatteri, A. & Marí, N. 2016. Biology and fishery of the Southern hake (*Merluccius australis*) in the Southwest Atlantic Ocean. *Revista de Investigación y Desarrollo Pesquero*, 28, 37-53.

Global Marine Commodities. 2018. *Informe de cambio de pesquería objetivo para el proyecto cadenas mundiales sostenibles de suministro de productos del mar–Ecuador*. Justificación del cambio de merluza a peces pelágicos pequeños. Guayaquil: Global Marine Commodities.

Guevara-Carrasco, R. & Wosnitza-Mendo, C. 2009. Cambios en la productividad de la merluza peruana (*Merluccius gayi peruannus* Ginsburg). *Boletin Instituto del Mar del Perú*, 24(1-2), 15–20.

Guevara-Carrasco, R. & Lleonart, J. 2008. Dynamics and fishery of the Peruvian hake: between nature and man. *Journal of Marine Systems*, 71, 249–259. DOI: https://doi.org/10.1016/j.jmarsys.2007.02.030.

Hendrickx, M. 1995. *Cangrejos*. In: Fischer, W., Krupp, F., Schneider, W., Sommer, C., Carpenter, K. E. & Niem, V.H. (eds). Guía FAO para la identificación de especies para los fines de la pesca. Pacifico Centro-Oriental (Vol. 1: Plantas e Invertebrados, pp. 565–636). Roma: FAO.

Hermosilla, I. 1959. *Contribución al estudio del régimen alimentario de Merluccius gayi (Guichenot) frente a la zona de Concepción*. Concepción: Universidad de Concepción.

Hoffman, M. 1979. The use of Pielou's method to determine simple size in food studies. *In*: Lipovsky, S. J. & Simenstad, C. A. (eds.). *Gutshop '78: Fish food habits studies. Proceedings of the second Pacific Northwest Technical Workshop* (pp. 56-61). Seattle: University of Washington.

Holden, M. J. & Raitt, D. F. S. 1975. *Manual de Ciencia Pesquera*. Parte 2 - *métodos para investigar los recursos y su aplicación.* Roma: FAO.

Hyslop, E. 1980. Stomach contents analysis, a review of methods and their application. *Journal of Fish Biology*, 17(4), 411–429. DOI: https://doi.org/10.1111/j.1095-8649.1980.tb02775.x.

Inada, T. 1995. *Merluccidae, Merluzas*. *In*: Fischer, W., Krupp, F., Schneider, W., Sommer, C., Carpenter, K. E. & Niem, V. H. (eds). *Guía FAO para la identificación de especies para los fines de la pesca. Pacífico Centro-Oriental.* (Vol. 3: Vertebrados parte 2, pp. 1272–1274). Roma: FAO.

Iverson, K. & Pinkas, L. 1971. A pictorial guide to beaks of certain Eastern Pacific cephalopods. *Fishery Bulletin*, 152, 7–35.

Iwamoto, T., Eschmeyer, W., Alvarado, J. & Bussing, W. 2010. *Merluccius gayi*. The IUCN Red List of Threatened Species. https://www.iucnredlist.org/species/183527/8128809. Access date: 4 Sept. 2023.

Jereb, P. & Roper, C. F. E. 2010. *Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date.* (Vol. 2: Myopsid and Oegopsid Squids). Rome, FAO.

Jereb, P., Roper, C. F. E., Norman, M. D. & Finn, J. K. 2014. *FAO Species Catalogue for Fishery Purposes. Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date*. (Vol. 3: Octopods and Vampire Squids). Rome: FAO.

Jiménez-Prado, P. & Béarez, P. 2004. *Peces marinos del Ecuador continental/Marine fishes of continental Ecuador*. Quito: SIMBIOE.

Jiménez-Valverde, A. & Hortal, J. 2003. Las curvas de acumulación de especies y la necesidad de evaluar la calidad de los inventarios biológicos. *Revista Ibérica de Aracnología*, 8, 151–161.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 61, 65–71. DOI: https://doi.org/10.2307/1937156.

Juanes, F. 1994. What determines prey size selectivity in piscivorous fishes? *In*: Stouder, D. J., Fresh, K. L., Feller, R. J. (eds.) *Theory and application in fish feeding ecology* (pp. 79–100). Columbia: Carolina University.

Keast, A. & Webb, D. 1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. *Journal of the Fisheries Board of Canada,* 23, 1845–1874. DOI: https://doi.org/10.1139/f66-175.

Konchina, Y. V. 1983. The feeding niche of the hake, *Merluccius gayi* (Merluccidae), and the jack mackerel, *Trachurus symmetricus* (Carangidae), in the trophic system of the Peruvian coastal upwelling. *Journal of Ichthyology*. 23(2), 87–98.

Krebs, C. J. 1985. *Ecología: estudio de la distribución y la abundancia* (2nd ed). Ciudad de México: Harla.

Labropoulou, M. & Eleftheriou, A. 1997. The foraging ecology of two pairs of congeneric demersal fish species: importance of morphological characteristics in prey selection. *Journal of Fish Biology*, 50(2), 324–340. DOI: https://doi.org/10.1111/j.1095-8649.1997.tb01361.x.

Lleonart, J., Salat, J. & Macpherson, E. 1983. Efecto del canibalismo en la población de *Merluccius capensis* en la división 1.5. *Collection of Scientific Papers ICSEAF*, 10(1), 111–128.

Lleonart, J., Salat, J. & Macpherson, E. 1985. CVPA, an expanded VPA with cannibalism. Aplications to a hake population. *Fishery Research*, 3, 61–79. DOI: https://doi.org/10.1016/0165-7836(85)90008-6.

Lloris, D., Matallanas, J. & Oliver, P. 2005. *Hakes of the world (Family Merlucciidae). An annotated and illustrated catalogue of hake species known to date*. Rome: FAO.

Loor-Andrade, P., Pincay-Espinoza, J., Carrera-Fernández, M. & Rosas-Luis, R. 2017. Feeding habits of billfishes (Carangaria: Istiophoriformes) in the Ecuadorian Pacific Ocean. *Neotropical Ichthyology*. 15(3), e160162. DOI: doi.org/10.1590/1982-0224-20160162.

Mahe, K., Amara, R., Bryckaert, T., Kacher, M. & Brylinski, J. M. 2007. Ontogenetic and spatial variation in the diet of hake (*Merluccius merluccius*) in the Bay of Biscay and the Celtic Sea. ICES Journal of Marine Science, 64(6), 1210–1219.

Marí, N. E. & Sánchez F. 2002. *Espectros tróficos específicos de varias especies de peces demersales de la región austral y sus variaciones anuales entre 1994 y 2000*. Informe técnico. Buenos Aires, INIDEP.

Martínez-Ortiz, J., Aires-Da-Silva, A. M., Lennert-Cody, C. E. & Maunder, M. N. 2015. The Ecuadorian artisanal fishery for large pelagics: species composition and spatio-temporal dynamics. *Plos One*, 10, e0135136. DOI: https://doi.org/10.1371/journal.pone.0135136.

Marullo, S., Santoleri, R., & Bignami, F. 2011. The surface characteristics of the Tyrrhenian Sea: Historical satellite data analysis. *In*: La Violette, P. E. (ed.). *Seasonal and interannual variability of the Western Mediterranean Sea* (pp. 135-154). Washington: AGU American Geophysical Union.

Meléndez, R. 1984. Alimentación de *Merluccius gayi* (Guichenot) frente a Chile central (32°05'S-36°50'S). *Boletín Museo Nacional de Historia Natural de Chile*, 40, 145–151.

Minitab, Inc. 2017. Minitab V. 17. Available on https://www.minitab.com.

Modica, L., Cartes, J. E., Velasco, F. & Bozzano, A. 2015. Juvenile hake predation on myctophidae and sternoptychidae: quantifying an energy transfer between mesopelagic and neritic communities. Journal of Sea Research. 95, 217-225. DOI: https://ui.adsabs.harvard.edu/link_gateway/2015JSR....95..217M/doi:10.1016/j.seares.2014.05.004

Montecino, V. & Lange, C. 2009. The Humboldt Current System: ecosystem components and processes, fisheries, and sediments studies. *Progress in Oceanography*, 83(1-4), 65-79.

Muck, P., Espino, M., Fuentes, H., Wosnitza-Mendo, C. & Esquerre, M. 1988. Predación de la merluza peruana (*Merluccius gayi peruanus*) sobre la anchoveta *(Engraulis ringens)*. *In*: Salzwedel, H. & Landa, A. (eds.). *Recursos y dinámica del ecosistema de afloramiento peruano* (pp. 249–253). Lima: IMARPE.

Munroe, S. E. M., Simpfendorfer, C. A. & Heupel, M. R. 2014. Defining shark ecological specialization: concepts, context, and examples. *Reviews in Fish Biology and Fisheries*, 24, 317–331. DOI: https://doi.org/10.1007/s11160-013-9333-7.

Muñoz, H. 2012. *Características de los otolitos sagitales de peces pelágicos pequeños de interés comercial en las costas de Santa Elena, Pacífico ecuatoriano, julio 2011 - enero 2012* [Thesis]. La Libertad: Universidad Península de Santa Elena.

Naranjo, C. & Tapia, M. 2002. Composición, distribución y abundancia del plancton en el estuario de San Lorenzo, Esmeraldas-Ecuador. *Acta Oceanográfica del Pacífico,* 11(1), 113–128.

Naranjo, C. & Tapia, M. 2013. Variabilidad estacional del plancton en la Bahía de Manta en la costa ecuatoriana, durante el 2011. *Acta Oceanográfica del Pacífico*, 18(1), 40–46.

Neira, S. & Arancibia, H. 2004. Trophic interactions and community structure in the Central Chile marine ecosystem (33◦S–39◦S). *Journal of Experimental Marine Biology and Ecology*, 312(2), 349–366. DOI: http://dx.doi.org/10.1016/j.jembe.2004.07.011

Neira, S., Arancibia, H. & Cubillos, L. 2004. Comparative analysis of trophic structure of commercial fishery species off Central Chile in 1992 and 1998. *Ecological Modeling*, 172 (2–4), 233–248. DOI: https://doi.org/10.1016/j.ecolmodel.2003.09.009.

Orrego, H. & Mendo, J. 2012. Variación interanual de la dieta de la merluza, *Merluccius gayi peruanus* (Guitchenot, 1848) en la costa peruana. *Ecología aplicada*, 11(2), 103–116.

Odum, E. P. 1971. *Fundamentals of Ecology*. (3rd ed). Philadelphia, Saunders.

Olson, J. & Galván-Magaña, F. 2002. Food habits and consumption rates of dolphinfish (*Coryphaena hippurus*)

in the Eastern Pacific Ocean. *Fishery Bulletin*, 100(2), 279–298.

Pauly, D. 1983. *Algunos métodos simples para la evaluación de recursos pesqueros tropicales*. FAO Documento Técnico de Pesca 234. Roma: FAO.

Pauly, D. 1984. *Fish population dynamics in tropical waters: A manual for use with programmable calculators*. Studies and Reviews 8. Manila: ICLRM.

Pennington, J. T., Mahoney, K. L., Kuwahara, V. S., Kolber, D. D., Calienes, R. & Chávez, F. P. 2006. Primary production in the eastern tropical Pacific: a review. *Progress in Oceanography*, 69(2-4), 285–317. DOI: https://doi.org/10.1016/j.pocean.2006.03.012.

Perea, A., Sánchez, J. & Buitrón, B. 2015. Escala de madurez gonadal de merluza peruana *Merluccius gayi peruanus* (Ginsburg, 1954). *Boletín Instituto del Mar del Perú*, 30(1-2), 20–28.

Pesantes, F. 1983. Los dinoflagelados como indicadores de "El Niño" en el mar ecuatoriano. *Acta Oceanográfica del Pacífico*, 2(1), 84–117.

Prado-España, M. & Cajas-Flores, J. 2010. Variabilidad del plancton en estaciones fijas frente a la costa ecuatoriana durante 2007. *Revista de Ciencias del Mar y Limnología*, 4(3), 59–69.

Prado-España, M., Troccoli-Ghinaglia, L. & Cajas J. 2017. Análisis del estado trófico y microfitoplancton de la zona costera de la provincia del Guayas, Ecuador. *Boletin de Investigaciones Marinas y Costeras,* 46(2), 91–114.

Proulx, S. R., Promislow, D. E. L. & Phillips, P. C. 2005. Network thinking in ecology and evolution. *Trends in Ecology and Evolution*, 20(6), 345–353.

Punt, A. E., Leslie, R. W. & Du Plessis, S. E. 1992. Estimation of the annual consumption of food by Cape hake, *Merluccius capensis* and *M. paradoxus* off the South African west coast. *South African Journal of Marine Sciences*, 12(1), 611–634. DOI: https://doi.org/10.2989/02577619209504728.

Riccioni, G., Stagioni, M., Piccinetti, C. & Libralato, S. 2018. A metabarcoding approach for the feeding habits of European hake in the Adriatic Sea. *Ecology and Evolution*, 8(21), 10435–10447. DOI: https://doi.org/10.1002/ece3.4500.

Ricker, W. E. 1975. *Computation and interpretation of biological statistics of fish populations*. Ottawa, Department of Environment, Fisheries and Marine Service.

Robertson, D. R. & Allen, G. R. 2015. *Peces costeros del Pacífico Oriental Tropical: sistema de Información en línea*. Versión 2.0. Balboa, Instituto Smithsoniano de Investigaciones Tropicales.

Roper, C. F. E., Sweeney, M. J. & Hochberg, F. G. 1995. *Cefalópodos*. In: FISCHER, W., KRUPP, F., SCHNEIDER, W., SOMMER, C., CARPENTER, K. & NIEM V. (eds.). *Guía FAO para la identificación de especies para los fines de la pesca, Pacífico centro oriental, Vol. 1. Plantas e invertebrados*. Roma: FAO, pp. 305–354.

Rosas-Luis, R., Pincay-Espinoza, J. E., Loor-Andrade, P. & Carrera-Fernández, M. 2016. Trophic ecology of the shortfin mako, Isurus oxyrinchus (*Lamniformes: Lamnidae*) in the Eastern Pacific Ocean. In: Kovács,

A. & Nagy, P. (eds.). *Advances in Marine Biology* (pp. 147–182). New York: Nova Science Publishers.

Salcedo, J. & Coello, D. 2018. Dinámica del plancton en la primera milla náutica frente a la provincia de El Oro, Ecuador. *Revista de Biología Tropical*, 66(2), 836–847. DOI: http://dx.doi.org/10.15517/rbt.v66i2.33417

Sagar, M. V., Gop, A. M. & Nair, R. J. 2018. Stomach content analysis techniques in fishes. *In*: Nair, R. J. (ed.). *Recent advances in fishery biology techniques for biodiversity evaluation and conservation* (pp. 104-115). New Delhi: Indian Agricultural Statistics Research Institute.

Saikia, S. K. 2015. Food and feeding of fishes. What do we need to know? *Transylvanian Review of Systematical and Ecological Research*, 17(1), 71-84. DOI: https://doi.org/10.1515/trser-2015-0049.

Sánchez, F. & Marí, N. R. 2005. *Interacciones tróficas entre especies demersales en la región austral entre 45° S y 54°S*. Informe técnico. Buenos Aires, INIDEP.

Shackell, N. L., Frank, K. T., Fisher, J. A. D., Petrie, B. & Leggett, W. C. 2010. Decline in top predator body size and changing climate alter trophic structure in an oceanic ecosystem. *Proceedings of the Royal Society B: Biological Science*, 277(1686), 1353–1360. DOI: https://doi.org/10.1098/rspb.2009.1020.

Scharf, F. S., Juanes, F. & Rountree, R. A. 2000. Predator size-prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Marine Ecology Progress Series*, 208, 229–248. DOI: https://dx.doi.org/10.3354/meps208229

Serrano, E, Leiva, C., Lonza, C., Sánchez, J. C., Wacyk, J., Zegers, T. & Godoy, M. 2014. Caracterización histológica y morfológica del tracto digestivo de la merluza austral (*Merluccius australis*). *International Journal of Morphology*, 32(3), 1079-1084. DOI: http://dx.org/10.4067/S0717-95022014000300054.

Stillwell, C. & Kohler, N. 1982. Food, feeding habits, and estimates of daily ration of the shortfin mako (*Isurus oxyrinchus*) in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*, 39(3), 407–414. DOI: https://doi.org/10.1139/f82-058.

Sonnenholzner, J., Brandt, M., Francisco, V., Hearn, A., Luzuriaga, M., Guarderas, P. & Navarro, J. C. 2013. *Echinoderms of Ecuador*. *In*: Alvarado, J. J. & Solís-Marín, F. (eds.). *Echinoderm Research and Diversity in Latin America* (pp. 183–233). Berlin: Springer.

Stobberup, K. A. 1992. Food composition and consumption of Chilean hake (*Merluccius gayi gayi*) with special reference to cannibalism. *ICES Demersal Fish Committee*, 43, 1–34.

Tapia, M. & Naranjo, C. 2004. Diversidad del plancton en el estuario interior de Puerto Bolívar, Ecuador durante julio de 2002. *Acta Oceanográfica del Pacífico*, 12(1), 29-49.

Tesch, F.W. 1968. Age and growth. *In:* Ricker, W.E. (ed). *Methods for assessment of fish production in fresh waters* (pp. 93–123). Oxford, Blackwell Scientific Publications.

Torres, G. 2010. *Composición y distribución del fitoplancton en aguas costeras ecuatorianas durante La Niña*

(septiembre 2001). [thesis]. Guayaquil: Universidad de Guayaquil.

Tréguer, P., Bowler, C., Moriceau, B., Dutkiewicz, S., Gehlen, M., Aumont, O., Bittner, L., Dugdale, R., Finkel, Z., Iudicone, D., Jahn, O., Guidi, L., Lasbleiz, M., Leblanc, K., Levy, M. & Pondaven, P. 2017. Influence of diatom diversity on the ocean biological carbon pump. *Nature Geoscience*, 11(1), 27–37. DOI: https://doi.org/10.1038/s41561-017-0028-x.

Varela, J. L. & Pincay-Espinoza, J. E. 2019. Food habits of South Pacific hake (*Merluccius gayi*) in Ecuadorian waters. *Journal of the Marine Biological Association of the United Kingdom*, 99(8), 1851–1856. DOI: doi. org/10.1017/S0025315419000936.

Vidal, R., Acuña, R. & Méndez, R. M. 1997. Dieta de la merluza, *Merluccius gayi* (Guichenot, 1848) del norte de Chile. *Boletín Instituto Español de Oceanografía*, 13(1-2), 37–45.

Vinueza, E. 2015. *Catálogo de otolitos sagitta de especies comerciales en los cantones de Sucre y San Vicente,* *Manabí, Pacífico ecuatoriano*. [dissertation]. Portoviejo: Pontificia Universidad Católica del Ecuador.

Wearmouth, V. J. & Sims, D. W. 2008. Chapter 2, Sexual segregation in marine fish, reptiles, birds and mammals: behaviour patterns, mechanisms and conservation implications. *Advances in Marine Biology*, 54, 107–170. DOI: https://doi.org/10.1016/S0065-2881(08)00002-3

Wöhler, O. C., Giussi, A. R., García De La Rosa, S. B., Sánchez, M.F., Hansen, J.E., Cordo, H. D., Alvarez-Colombo, G. L., Incorvaia, I. S., Reta, R. & Abachián, V.E. 1999. Resultados de la campaña de evaluación de peces demersales australes efectuada en el verano de 1997. *INIDEP Informe Técnico*, 24, 1–70.

Wolff, G. 1982. A beak key for eight Eastern Tropical Pacific cephalopod species, with relationship between their beak dimension and size. *Fishery Bulletin*, 80(2), 357–370.

Wolff, G. 1984. *Identification and estimation of size from beaks of eighteen species of cephalopods from the Pacific Ocean.* NOAA Technical Report NMFS no. 17. USA: NOAA.