



Spatial- and size-related shifts in feeding habits of the common dolphinfish (*Coryphaena hippurus*) in the Southeast Pacific Ocean

Jonathan E. Pincay-Espinoza · José L. Varela

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Abstract Feeding habits of common dolphinfish (*Coryphaena hippurus*) were investigated in the Southeast Pacific Ocean using stomach content analysis. Stomachs were collected from 1506 individuals ranging between 18 and 187 cm in fork length. The fish were caught by longliner boats in 2009–2017. Based on percentage of wet weight (%W_i), percentage of number (%N_i), and frequency of occurrence (%O_i), flyingfishes were the predominant prey, followed by the cephalopods jumbo squid (*Dosidicus gigas*) and argonaut (*Argonauta* spp.). Permutational multivariate analysis of variance (PERMANOVA) detected significant differences between zones ($p < 0.001$). PERMANOVA also revealed two size-related shifts in feeding habits to occur at FL ~ 80 cm and FL ~ 110 cm ($p < 0.001$). Cumulative prey curves did not reach an asymptote in any of the zones and size classes, which may be attributed to the fine

taxonomic resolution used. Spatial variations in daily meal ranged between 296.3 and 438.9 g day⁻¹, corresponding to daily ration of 6.1–8.2% body mass BM day⁻¹. Otherwise, size-related variations in both DM and DR were observed. Thus, while daily food intake increased with size from 177.3 for the smallest fish (LF < 80 cm) to 496.7 g day⁻¹ for the largest ones (LF ≥ 110 cm), DR decreased from 13.0 ± 22.1 to 3.7 ± 0.7 BM day⁻¹. The present results contribute to improve the understanding of dolphinfish feeding habits in the Southeast Pacific Ocean.

Keywords Coryphaenidae · Trophic biology · Stomach content analysis · Food items · Daily ration

Introduction

The common dolphinfish (*Coryphaena hippurus*, Linnaeus 1758) is an epipelagic predator occurring in tropical and subtropical regions of the Pacific, Indian, and Atlantic oceans (Palko et al. 1982). This species is caught in open and coastal waters (Briggs 1960), and spends most of its time at the upper 30 m of the water column (Palko et al. 1982; Tripp-Valdez et al. 2015). With a high socio-economic importance, the dolphinfish supports commercial and recreational fisheries in all seas worldwide. Furthermore, it plays an important ecological role delineating pelagic food-webs by “top down” control mechanisms (Olson and Galván-Magaña 2002; Varela et al. 2017a).

J. E. Pincay-Espinoza
Subsecretaría de Recursos Pesqueros, Viceministerio de Acuicultura Y Pesca, Puerto Pesquero Artesanal de San Mateo, Manta, Manabí, Ecuador

J. E. Pincay-Espinoza
Escuela de Acuicultura Y Pesquería, Universidad Técnica de Manabí Extensión Bahía de Caráquez, Sucre, Manabí, Ecuador

J. L. Varela (✉)
Departamento de Biología, Facultad de Ciencias del Mar Y Ambientales, Universidad de Cádiz, Cádiz, Spain
e-mail: joseluis.varela@uca.es

Like other large pelagic fishes inhabiting the southeastern Pacific Ocean, the dolphinfish shows exceptionally high standard metabolic rates (Bennetti et al. 1995; Crossley et al. 2021), which allow fast somatic and gonadal growth (Palko et al. 1982). This, therefore, requires a high consumption of prey, which may significantly impact on the abundance, diversity, or distribution of other species within the food web. In this context, stomach content analysis (SCA) is a powerful tool to understand prey-predator relationships.

Although previous studies carried out in the Southeast Pacific Ocean provide useful data on the feeding habits of dolphinfish, they do not consider spatial-related variations (Lasso and Zapata 1999; Varela et al. 2017a). Thus, while Lasso and Zapata (1999) reported that this species feeds on large number of fishes, mollusks, and crustaceans in the Pacific coast of Colombia and Panama, Varela et al. (2017a) found that the family Exocoetidae was the predominant prey species off Ecuador. The only research conducted to assess spatial-related shifts in the feeding patterns of this top predator was carried out two decades ago by Olson and Galván-Magaña (2002). Therefore, new data on this issue may be useful to better understand the trophic role of this predator in the Southeast Pacific Ocean ecosystem.

The Southeast Pacific coast is characterized by a marked spatial variation in the oceanographic conditions. Thus, the northernmost area is affected by the Panama current (warm and nutrient-poor water), whereas the southernmost area is influenced by the Chile-Peru current (cold and nutrient-rich water) (Sonnenholzner et al. 2013; Martínez-Ortiz et al. 2015). These singular oceanographic features may cause geographic variation in the abundance and distribution of prey between both areas. Moreover, differences in the dietary composition between inshore and offshore waters have been reported for dolphinfish and other large pelagic fishes from the region (Alverson 1963; Olson and Galván-Magaña 2002; Olson et al. 2014). The present study was conducted to assess spatial- and size-related shifts in the dietary composition of the dolphinfish in the southeastern Pacific Ocean considering four regions: North, South, inshore, and offshore (see Fig. 1).

Material and methods

Sampling and stomach content analysis

Stomachs of dolphinfish ($n=1506$) were collected aboard surface longline boats fishing in the Southeast Pacific Ocean in 2009–2017. The main species employed as bait during the fishing operations were jumbo squid (*Dosidicus gigas*) and frigate tuna (*Auxis thazard*).

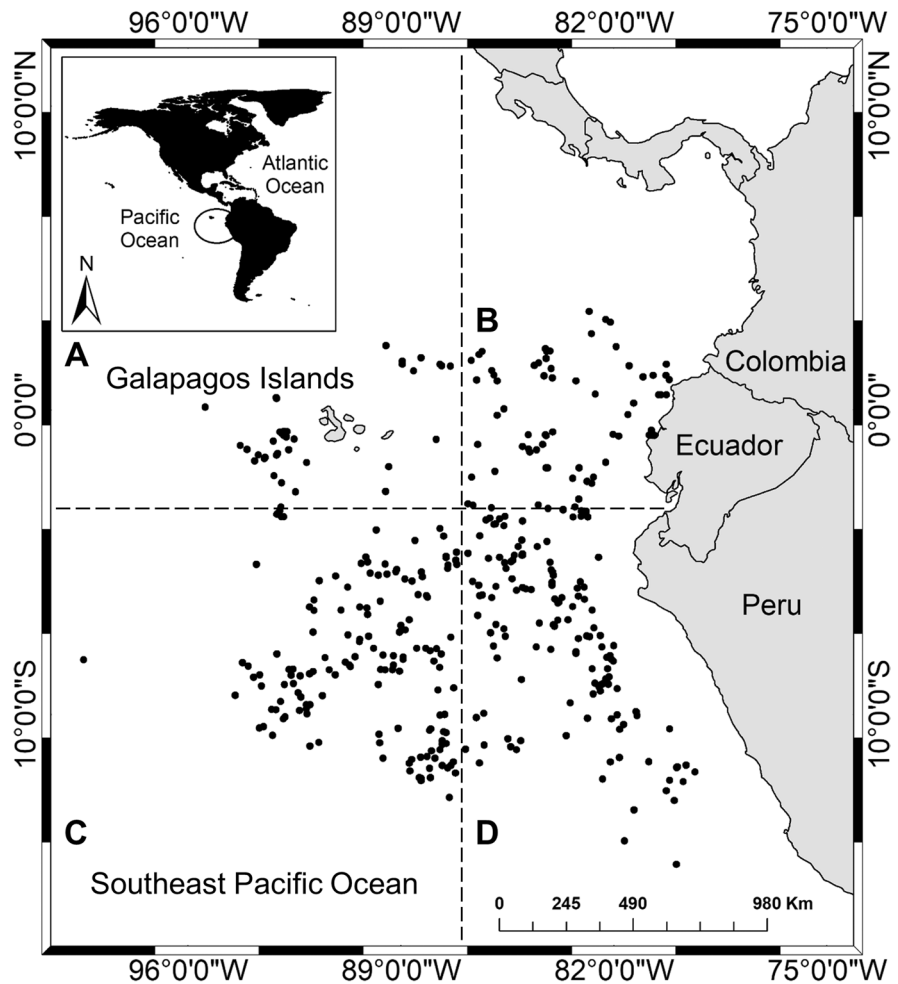
Most fish were measured to the nearest centimeters (fork length, FL) and the stomachs were stored at $-20\text{ }^{\circ}\text{C}$ until analysis. In the laboratory, they were thawed and opened and prey species were weighed, counted, and identified to the lowest possible taxonomic level using a stereoscopic microscope. Food items considered as bait were not taken into consideration for analysis, and the stomachs containing only these species were treated as empty. Fish and cephalopod species were identified from otoliths and lower beaks, respectively, using available guides (Clarke 1986; Harvey et al. 2000; García-Godos Naveda 2001).

Data analysis

The contribution of each prey to the diet was evaluated by three indices: (1) percentage of wet weight (%W_i), (2) percentage of number (%N_i), and (3) frequency of occurrence (%O_i).

Spatial- and size-related shifts in dietary composition were tested by a permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001; McArdle and Anderson 2001; Anderson et al. 2008). The analytical design considered “zone” as fixed factor with four levels. As in Varela et al. (2017a), we also considered the factor “size class” with 3 levels (<80 cm in FL, 80–110 cm in FL, ≥ 110 cm in FL). The analysis was based on a Bray–Curtis similarity matrix calculated from the prey weight values, after performing a fourth-root transformation (Van Ginderdeuren et al 2014; Kvaavik et al. 2019; Valls et al. 2022). Significant terms were investigated using a posteriori pair-wise comparisons with PERMANOVA test. Multivariate dispersion among zones was tested by PERMDISP (Anderson 2006). Both PERMANOVA and PERMDISP were performed using the software PRIMER v6.1.13 and

Fig. 1 Map showing sampling locations



the PERMANOVA+ v1.0.3 statistical package (PRIMER-E Ltd., Plymouth, UK).

Cumulative prey curves (CPCs) were used to evaluate if the sample size was sufficient to describe the food habits of dolphinfish in each zone, size class, and in the whole area (Ferry and Cailliet 1996). CPCs were built using the vegan package (Oksanen et al., 2010) in R (R Core Team, 2020). To determine whether the curve reached an asymptote, the slope of the linear regression estimated from the last four stomachs was compared with a horizontal asymptote by *t* test.

The food consumption rate was estimated from the formula $\hat{r} = \sum_{i=0}^I \bar{W}_i / A_i$ (Olson and Mullen 1986), where \hat{r} is the feeding rate measured in grams per hour, \bar{W}_i is the weight of prey *i* divided by the total number of stomachs, and A_i represents the average time required to evacuate the average proportion of

prey *i*. As in Olson and Galván-Magaña (2002), we applied A_i values estimated for yellowfin tuna (*Thunnus albacares*) (Olson and Boggs 1986). Considering that the dolphinfish feeds during both day and night hours (Olson and Galván-Magaña 2002), daily meal (DM) was estimated by multiplying \hat{r} by 24 h. Daily ration (DR) is equivalent to the daily meal expressed as percent of the dolphinfish body mass (BM). BM was estimated from the length using the equation proposed by Lasso and Zapata (1999).

Stomach content data from unmeasured fish were not considered in the analysis involving FL.

Results

FL of the sampled dolphinfish ranged between 18 and 187 (mean ± SD = 96.7 ± 20.1 cm). A total

of 1506 stomachs were analyzed, of which 1270 (84.3%) contained at least one prey (Table 1). The diet was made up of 57 prey items, including 35 fishes, 19 cephalopods, and 3 crustaceans. Fishes were the most important prey group (%W=60.9, %N=54.5, and %O=67.9), followed by cephalopods (%W=39.1, %N=54.5, and %O=50.9) and crustaceans (%W<0.1, %N=0.1, and %O=0.2). Among all the prey species, flyingfishes were the most abundant (%W=30.7, %N=34.8, and %O=39.8), followed by the cephalopods jumbo squid (*Dosidicus gigas*) (%W=34.9, %N=13.0, and %O=21.0) and argonaut (*Argonauta* spp.) (%W=1.2%, N=24.9, and %O=24.4) (Table 2).

The dolphinfish caught in zone A ranged from 36.0 to 187.0 cm in FL (mean SD: 94.0 ± 20.6 cm), whereas the size range of the individuals sampled in zone B was 36–187 in FL (85.8 ± 28.7 cm). The dolphinfish from the zone C ranged between 26 and 154 cm in FL (98.9 ± 16.2), and the fish caught in zone D sized from 37 to 187 in FL (96.7 ± 20.1). Although fishes were the most representative prey group in all zones, spatial variations in dietary composition were found. In zone A, flyingfishes were the most abundant prey species (%W=50.1, %N=40.6, and %O=8.1%), followed by jumbo squid (%W=26.3, %N=15.7, and %O=7.5) and frigate tuna (*Auxis* spp.) (%W=15.6, %N=6.5, and %O=5.9). Dolphinfish caught in zone B mainly consumed flyingfishes (%W=40.6, %N=47.4, and %O=19.2), frigate tuna (%W=11.4, %N=5.6, and %O=10.5), and argonauts (%W=0.8, %N=13.7, and %O=11.0). In zone C, flyingfishes (%W=27.7, %N=32.8, and %O=38.6), jumbo squid (%W=33.6, %N=16.5, %O=49.8), and frigate

tuna (%W=26.4, %N=12.1, %O=53.4%) were the most representative prey food. The diet of the specimens from zone D was mainly composed of flyingfishes (%W=27.5, %N=29.8, and %O=34.0), argonauts (%W=1.4, %N=35.6, and %O=53.2), and jumbo squid (%W=42.1, %N=11.0, and %O=33.0) (Table 2). Fishes were also the predominant prey group in the three size classes, but dietary composition changed with body size. Class I fish (<80 cm) fed mainly on flyingfishes (%W=43.1, %N=29.4, and %O=30.9), argonauts (%W=2.9, %N=30.4, and %O=19.1), and jumbo squid (%W=19.7, %N=9.5, and %O=14.9) (Table 3). The medium-sized fish (80–110 cm, FL) mainly consumed flyingfishes (%W=29.8, %N=37.0, and %O=31.0), frigate tuna (%W=23.6, %N=11.4, and %O=20.9), and argonauts (%W=0.9, %N=19.6, and %O=24.8). The largest fish (≥ 110 cm) preyed fed mainly on flyingfishes (%W=25.2, %N=32.3, and %O=27.7), jumbo squid (%W=35.9, %N=14.4, and %O=28.5), and frigate tuna (%W=14.2, %N=8.1, and %O=16.4) (Table 2). Despite the large number of stomachs analyzed ($n=1506$), CPCs did not reach an asymptote in any of the zones, size classes, or in the whole stomach sample (t test, $p < 0.05$).

The PERMANOVA analysis detected significant spatial- and size-related differences in the dietary composition ($p < 0.05$) (Table 4). The interactions between both factors were also significantly different, indicating that the differences in “zone” were not homogeneous across the levels of the “size classes” factor (PERMANOVA, $p < 0.05$) (Table 4). Pair-wise PERMANOVA comparisons indicated significant differences between the four zones or between the three size classes ($p < 0.05$). Overall, significant dietary differences between size classes were found by zone ($p < 0.05$), except in zone C ($p > 0.05$) (Table 5). The PERMDISP analysis showed no significant differences ($p > 0.05$), suggesting that the differences detected by PERMANOVA were not due to multivariate dispersion.

DM showed similar values in zones A, B, and C, whereas highest values were found in zone C. DR estimates were comparable in all zones, except in zone B where they were highest (Table 2). Otherwise, size-related variations in both DM and DR were observed. Thus, while daily food intake increased with size from 177.3 for the smallest fish

Table 1 Data summary of sampled dolphinfish by zone and size class

	Fork length (cm)		<i>n</i>	Percentage of stomachs containing prey
	Range	mean \pm SD		
Zone A	36–187	94.0 ± 20.6	105	81.9% ($n=86$)
Zone B	18–147	85.8 ± 28.7	234	83.8% ($n=196$)
Zone C	26–154	98.9 ± 16.2	630	84.3% ($n=531$)
Zone D	37–150	99.0 ± 18.5	537	85.1% ($n=457$)
Size class I	<80		191	84.8% ($n=162$)
Size class II	80–110		797	84.6% ($n=674$)
Size class III	≥ 110		320	85.6% ($n=274$)

Table 2 Results of the stomach content analysis (SCA) by zone. %W, percentage weight; %N, percentage of number; %O, frequency of occurrence; DM, daily meal; DR, daily ration; BM, body mass

Preys	Whole sample			Zone A			Zone B			Zone C			Zone D		
	%W	%N	%O	%W	%N	%O	%W	%N	%O	%W	%N	%O	%W	%N	%O
Fishes															
Family Balistidae															
<i>Balistes polylepis</i>	<0.1	<0.1	0.1										0.1	0.1	0.2
Family Belontiidae															
<i>Ablennes hians</i>	<0.1	<0.1	0.1							<0.1	0.1	0.2			
Family Carangidae															
Carangidae	0.1	<0.1	0.1				0.6	0.2	0.5						
<i>Naucrates ductor</i>	0.5	0.2	0.4							0.9	0.4	0.8	0.3	0.1	0.2
Family Cottidae															
<i>Leptocottus armatus</i>	<0.1	<0.1	0.1												
<i>Oligocottus rubellio</i>	<0.1	<0.1	0.1	0.4	0.5	1.2							<0.1	0.1	0.2
Family Coryphaenidae															
<i>Coryphaena hippurus</i>	2.5	0.3	0.6				1.5	0.2	0.5	1.7	0.3	0.4	4.5	0.4	0.9
Family Clupeidae															
<i>Opishonema libertate</i>	0.2	0.2	0.2				0.9	0.5	1.0				0.1	0.3	0.2
Family Echeineidae															
<i>Remora remora</i>	0.1	0.1	0.2				0.2	0.2	0.5				0.3	0.1	0.2
Family Exocoetidae															
<i>Cheilopogon arrisignis</i>	0.1	0.1	0.2										0.4	0.3	0.7
<i>Cheilopogon cyanopterus</i>	0.1	0.1	0.2							0.2	0.1	0.2	0.1	0.1	0.2
<i>Cheilopogon exsilens</i>	0.9	0.6	0.9	1.7	1.4	3.5	0.6	1.0	1.0	0.2	0.1	0.2	2.0	0.7	1.3
<i>Cheilopogon furcatus</i>	1.2	1.1	1.6				3.5	2.7	3.6	1.3	1.2	1.3	0.4	0.7	1.3
<i>Cheilopogon heterurus</i>	0.1	0.1	0.2										0.3	0.2	0.4
<i>Cheilopogon papilio</i>	0.1	0.1	0.2										0.1	0.3	0.7
<i>Cheilopogon spilomopteris</i>	1.0	0.7	0.9	5.0	1.4	3.5	2.1	1.0	1.0	0.1	0.2	0.2	1.2	0.9	1.1
<i>Cheilopogon unicolor</i>	0.3	0.2	0.3							0.2	0.2	0.4	0.6	0.3	0.4
<i>Cypselurus callopterus</i>	1.4	0.7	1.1				0.2	0.2	0.5	2.4	1.4	1.9	0.7	0.3	0.7
Exocoetidae	<0.1	<0.1	0.1							0.1	0.1	0.2			
<i>Exocoetus</i> spp.	0.9	0.7	0.9	2.9	1.4	2.3	1.2	1.2	1.0	1.1	0.8	1.1	0.2	0.2	0.4
<i>Exocoetus monocirrhus</i>	7.4	10.2	14.2				9.7	12.2	18.9	6.2	9.2	12.1	9.4	12.9	17.3
<i>Exocoetus volitans</i>	8.7	8.6	10.1	15.8	14.8	16.3	7.7	8.8	9.2	9.6	10.4	12.6	6.5	5.2	6.4
<i>Fodiator acutus</i>	0.1	0.1	0.2				0.2	0.2	0.5				0.1	0.1	0.2

Table 2 (continued)

Preys	Whole sample			Zone A			Zone B			Zone C			Zone D		
	%W	%N	%O	%W	%N	%O	%W	%N	%O	%W	%N	%O	%W	%N	%O
<i>Hirundichthys marginatus</i>	0.1	0.1	0.2	1.6	0.5	1.2				0.1	0.2	0.2			
<i>Parexocoetus brachypterus</i>	0.2	0.1	0.2	1.0	0.5	1.2				0.2	0.2	0.4			
<i>Prognichthys sealei</i>	0.9	0.6	0.9				0.4	0.5	1.0	1.5	1.0	1.3	0.5	0.2	0.4
Family Hemiramphidae															
<i>Oxyporhamphus micropterus</i>	7.2	10.6	12.1	22.3	20.7	20.9	15.1	19.6	22.5	4.6	7.8	8.9	5.1	7.4	9.9
Family Myctophidae															
Myctophidae	<0.1	<0.1	0.1	0.1	0.5	1.2									
Family Scombridae															
<i>Axaxis thazard</i>	19.6	9.0	17.2	15.6	6.5	15.1	11.4	5.6	11.7	26.4	12.1	22.0	13.4	7.6	14.4
Familia Stromateidae															
<i>Peprilus similimus</i>	0.1	0.6	0.7				0.7	3.2	3.6				<0.1	0.2	0.4
Family Syngnathidae															
<i>Hippocampus ingens</i>	0.1	0.6	1.0				0.1	0.4	0.6				0.2	1.3	2.2
Family Tetraodontidae															
<i>Lagocephalus lagocephalus</i>	2.3	1.4	2.5	0.7	0.5	1.2	6.3	4.2	7.1	1.07	0.7	1.3	2.9	1.1	2.2
<i>Sphoeroides trichocephalus</i>	0.7	0.5	0.6	1.6	0.5	1.2	3.8	2.2	2.6	0.1	0.2	0.4			
Family Trichiuridae															
<i>Trichiurus lepturus</i>	0.1	0.2	0.2				0.6	1.0	1.0	<0.1	0.1	0.2			
Fish remains	4.0	6.5	12.1	2.1	4.6	11.6	3.1	76	12.8	4.9	8.5	15.1	3.2	4.3	8.3
Cephalopods															
Family Ancistrocheiridae															
<i>Ancistrocheirus lesueurii</i>	0.3	1.1	2.0	<0.1	0.5	1.2	1.9	1.0	1.0	<0.1	1.5	2.6	0.1	1.0	1.8
Family Argonautidae															
<i>Argonauta</i> sp.	1.1	23.6	23.1				0.8	13.5	16.8	1.1	20.2	17.3	1.4	32.9	33.7
<i>Argonauta nouri</i>	0.1	1.3	1.3	0.2	1.4	3.5	<0.1	0.2	0.5	0.1	0.5	0.4	<0.1	2.8	2.4

Table 2 (continued)

Preys	Whole sample			Zone A			Zone B			Zone C			Zone D			
	%W	%N	%O	%W	%N	%O	%W	%N	%O	%W	%N	%O	%W	%N	%O	
Family Cranchiidae																
<i>Cranchia scabra</i>	<0.1	<0.1	0.1													
<i>Helicocranchia pfefferi</i>	<0.1	<0.1	0.1	0.1	0.5	1.2										
Family Enoploteuthidae																
<i>Abraliopsis felis</i>	<0.1	0.2	0.4													
Family Gonatidae																
<i>Gonatus</i> sp.	<0.1	0.2	0.5													
<i>Gonatus anonychus</i>	0.1	0.2	0.4	<0.1	0.5	1.2	<0.1	0.2	0.5	0.3	0.3	0.6	<0.1	0.3	0.3	0.7
Family Histioeuthidae																
<i>Stigmatoteuthis dofleini</i>	<0.1	0.7	1.3	<0.1	0.9	2.3	<0.1	0.7	1.5	0.1	0.5	0.9	<0.1	0.8	1.3	1.3
Family Loliginidae																
<i>Loligo</i> sp.	<0.1	<0.1	0.1													
Family Mastigoteuthidae																
<i>Mastigoteuthis dentata</i>	<0.1	0.6	1.3	<0.1	0.5	1.2	<0.1	0.5	1.0	<0.1	0.7	1.3	<0.1	0.7	1.3	1.3
Family Octopoteuthidae																
<i>Octopoteuthis sicula</i>	0.2	0.8	1.6	<0.1	0.9	2.3	<0.1	1.2	2.0	0.3	0.9	1.7	0.2	0.6	1.1	1.1
Family Ocythoidae																
<i>Ocythoe tuberculata</i>	<0.1	<0.1	0.1													
Family Ommastrephidae																
<i>Dosidicus gigas</i>	34.9	13.0	21.0	26.3	15.7	23.3	26.6	7.3	13.3	33.6	16.5	25.1	42.1	11.0	19.3	19.3
<i>Sthenoteuthis oulantiensis</i>	0.6	0.2	0.3													
Family Onychoteuthidae																
<i>Onychoteuthis borealijaponica</i>	0.1	1.0	1.4	2.2	4.2	3.5	<0.1	1.7	3.1	<0.1	0.1	0.2	<0.1	1.0	1.8	1.8
Family Pholidoteuthidae																
<i>Pholidoteuthis boschmai</i>	<0.1	0.3	0.6	<0.1	1.4	3.5										

Table 2 (continued)

Preys	Whole sample			Zone A			Zone B			Zone C			Zone D		
	%W	%N	%O	%W	%N	%O	%W	%N	%O	%W	%N	%O	%W	%N	%O
Family Vampyroteuthidae															
<i>Vampyroteuthis infernalis</i>	<0.1	0.2	0.4	<0.1	0.5	1.2							<0.1	0.4	0.9
Cephalopod remains	1.5	1.8	3.5	0.3	0.5	1.2	1.0	1.2	2.6	1.2	1.7	3.2	2.6	2.4	4.8
Crustaceans															
Infraorder Caridea															
Unidentified Caridea	<0.1	<0.1	0.1							<0.1	0.1	0.2			
Family Xanthidae															
Xanthidae	<0.1	<0.1	0.1										<0.1	0.1	0.2
Crustacean remains	<0.1	<0.1	0.1										<0.1	0.1	0.2
DM (g day ⁻¹)	382.6			296.3			329.3			438.9			350.8		
DR (%BM day ⁻¹)	8.2±20.0			6.1±7.2			17.6±41.0			6.8±9.9			5.7±5.4		

(LF < 80 cm) to 496.7 g day⁻¹ for the largest ones (LF ≥ 110 cm), DR decreased from 13.0 ± 22.1 to 3.7 ± 0.7 BM day⁻¹ (Table 3).

Discussion

SCA data showed that the diet of dolphinfish from the Southeast Pacific Ocean is mainly composed of epipelagic fishes and cephalopods (flyingfishes, frigate tuna, jumbo squid, and argonauts). This finding is consistent with earlier studies carried out in the region (Lasso and Zapata 1999; Olson and Galván-Magaña 2002; Varela et al. 2017a). Lasso and Zapata (1999) and Varela et al. (2017a, b) reported that family Exocoetidae was the most important prey in the diet of dolphinfish caught in the Pacific coast of Colombia, Panama, and Ecuador, whereas Olson and Galván-Magaña (2002) found that flyingfishes and epipelagic cephalopods were the predominant prey species in the coast of Ecuador and Peru. Similarly, Campos et al. (1993) reported that the dolphinfish preyed mainly on exocoetids and squids off Costa Rica. In the southeastern Gulf of California, Tripp-Valdez et al. (2010) and Bergés-Tiznado et al. (2019), however, observed that the dolphinfish fed primarily on the fishes longfin halfbeak (*Hemiramphus saltator*) and finescale triggerfish (*Balistes polylepis*), respectively. Torres-Rojas et al. (2014) and Tripp-Valdez et al. (2015) found that crustaceans (*Pleuroncodes planipes* and *Hemisquilla californiensis*) were the dominant prey group in the southern Gulf of California. These marked spatial variations indicate that dolphinfish show high feeding plasticity, adjusting their diet to local prey availability.

Comparing dolphinfish diet with that of other large pelagic fishes co-occurring in the region may be useful to infer trophic relationships. Assuming that interspecific food competition occurs when the presence of a food item is more than 25% in two or more predators (Johnson 1977), we found that niche partitioning occurs between dolphinfish and yellowfin tuna, swordfish (*Xiphias gladius*), and striped marlin (*Kajikia audax*) in the southeastern Pacific Ocean (see previous studies for yellowfin tuna, striped marlin and swordfish; Alverson 1963; Baque-Menoscal et al. 2012; Rosas-Luis et al. 2016; Varela et al. 2017b; Loor-Andrade et al. 2017; Zambrano-Zambrano et al., 2019). Off eastern Australia, Young et al. (2010) reported that these predators feed on different

Table 3 Results of the stomach content analysis (SCA) by size class. *FL*, fork length; %*W*, percentage weight; %*N*, percentage of number; %*O*, frequency of occurrence; *DM*, daily meal; *DR*, daily ration; *BM*, body mass

Preys	FL < 80 cm			80 cm ≤ FL < 110 cm			FL ≥ 110 cm		
	%W	%N	%O	%W	%N	%O	%W	%N	%O
Fishes									
<i>Balistes polylepis</i>				0.1	0.1	0.1			
Family Belonidae									
<i>Ablennes hians</i>				<0.1	0.1	0.1			
Family Carangidae									
Carangidae							0.3	0.2	0.4
<i>Naucrates ductor</i>				<0.1	0.2	0.4	1.6	0.2	0.4
Family Cottidae									
<i>Oligocottus rubellio</i>				<0.1	0.1	0.1			
Family Coryphaenidae									
<i>Coryphaena hippurus</i>				11.1	0.2	0.3	7.1	1.0	2.0
Family Clupeidae									
<i>Opisthonema libertate</i>	0.8	0.3	0.6				0.2	0.5	0.4
Family Echeneidae									
<i>Remora remora</i>				0.1	0.1	0.1			
Family Exoetidae									
<i>Cheilopogon atrisignis</i>				0.2	0.2	0.3			
<i>Cheilopogon cyanopterus</i>				<0.1	0.1	0.1	0.4	0.2	0.4
<i>Cheilopogon exsiliens</i>				1.3	0.7	1.3	0.3	0.7	0.8
<i>Cheilopogon furcatus</i>				1.1	1.1	1.4	1.9	2.2	3.5
<i>Cheilopogon heterurus</i>				<0.1	0.1	0.1			
<i>Cheilopogon papilio</i>				<0.1	0.2	0.3			
<i>Cheilopogon spilonotus</i>	1.7	0.3	0.6	1.5	1.1	1.3			
<i>Cheilopogon unicolor</i>	1.0	0.3	0.6	0.3	0.2	0.3			
<i>Cypselurus callopterus</i>	0.8	1.3	1.9	2.0	0.8	1.2	0.4	0.3	0.4
Exocoetidae				<0.1	0.1	0.1			
<i>Exocoetus</i> spp.	0.2	0.3	0.6	1.0	1.1	1.3	1.4	0.5	0.8
<i>Exocoetus monocirrhus</i>	21.9	15.7	20.4	5.5	8.1	10.8	5.7	8.8	13.3
<i>Exocoetus volitans</i>	8.0	3.3	5.6	9.6	11.1	11.4	9.0	9.3	12.9
<i>Fodiator acutus</i>				0.1	0.1	0.1			
<i>Hirundichthys marginatus</i>	1.4	0.3	0.6						
<i>Parexocoetus brachypterus</i>				0.2	0.2	0.3			
<i>Prognichthys sealei</i>	1.0	0.7	1.2	1.3	0.8	1.2			
Family Hemiramphidae									
<i>Oxyporhamphus micropterus</i>	7.3	7.2	10.5	7.0	11.3	11.8	6.1	10.3	10.6
Family Myctophidae									
Myctophidae	0.1	0.3	0.6						
Family Scombridae									
<i>Auxis thazard</i>	20.1	6.5	12.4	23.6	11.4	20.9	14.2	8.1	16.9
Familia Stromateidae									
<i>Peprilus simillimus</i>	1.9	4.9	5.6						
Family Syngnathidae									
<i>Hippocampus ingens</i>	0.1	0.3	0.6	0.1	0.8	1.2	0.1	0.3	0.8

Table 3 (continued)

Preys	FL < 80 cm			80 cm ≤ FL < 110 cm			FL ≥ 110 cm		
	%W	%N	%O	%W	%N	%O	%W	%N	%O
Family Tetraodontidae									
<i>Lagocephalus lagocephalus</i>	0.1	0.3	0.6	1.7	1.6	2.7	5.1	2.1	4.3
<i>Spherooides trichocephalus</i>	0.5	0.7	1.2	0.1	0.2	0.3	0.4	0.2	0.4
Family Trichiuridae									
<i>Trichiurus lepturus</i>	1.5	1.3	1.2	<0.1	0.1	0.1			
Fish remains	5.0	8.8	15.4	4.1	8.0	14.0	4.5	3.6	8.2
Cephalopods									
Family Ancistrocheiridae									
<i>Ancistrocheirus lesueurii</i>	0.3	0.7	1.2	<0.1	1.3	2.3	1.1	1.7	2.8
Family Argonautidae									
<i>Argonauta</i> sp.	2.8	29.7	19.1	0.8	18.7	23.6	1.5	28.0	19.6
<i>Argonauta nouri</i>	<0.1	0.7	1.2	0.1	0.9	0.9	<0.1	0.3	0.8
Family Cranchiidae									
<i>Helicocranchia pfefferi</i>							<0.1	0.2	0.4
Family Enoploteuthidae									
<i>Abraliopsis felis</i>	<0.1	1.3	1.9	<0.1	0.1	0.1	<0.1	0.2	0.4
Family Gonatidae									
<i>Gonatus</i> sp.				<0.1	0.3	0.6	<0.1	0.2	0.4
<i>Gonatus anonychus</i>	<0.1	0.3	0.6	0.1	0.2	0.4			
Family Histioteuthidae									
<i>Stigmatoteuthis dofleini</i>				0.1	0.7	1.2	<0.1	0.7	1.6
Family Loliginidae									
<i>Loligo</i> sp.							0.1	0.2	0.4
Family Mastigoteuthidae									
<i>Mastigoteuthis dentata</i>	<0.1	1.0	1.9	<0.1	0.7	1.3	<0.1	0.3	0.8
Family Octopoteuthidae									
<i>Octopoteuthis sicula</i>	<0.1	0.3	0.6	0.3	1.1	1.9	0.3	1.0	2.4
Family Ommastrephidae									
<i>Dosidicus gigas</i>	19.7	9.5	14.8	35.0	13.2	21.0	35.9	14.4	27.8
<i>Sthenoteuthis oualaniensis</i>	0.9	0.7	0.6	0.6	0.2	0.3	0.7	0.2	0.4
Family Onychoteuthidae									
<i>Onychoteuthis borealijaponica</i>	2.0	0.7	1.2	<0.1	1.1	1.2	<0.1	0.9	1.6
Family Pholidoteuthidae									
<i>Pholidoteuthis boschmai</i>				<0.1	0.3	0.6	<0.1	0.5	1.2
Family Vampyroteuthidae									
<i>Vampyroteuthis infernalis</i>				<0.1	0.2	0.3	<0.1	0.5	1.2
Cephalopod remains	1.1	2.0	3.7	1.0	1.4	2.6	1.9	2.2	5.1
Crustaceans									
Infraorder Caridea									
Unidentified Caridea				<0.1	0.1	0.1			
Crustacean remains	0.1	0.3	0.6						
DM (g day ⁻¹)	177.3			386.2			496.7		
DR (%BM day ⁻¹)	13.0 ± 22.1			5.7 ± 1.4			3.7 ± 0.7		

Table 4 Results of PERMANOVA test performed on Bray–Curtis dissimilarity matrix based on prey biomass

Source	df	SS	MS	Pseudo- <i>F</i>	<i>P</i>
Zo	3	59,922	19,974	4.73	0.01
Si	2	25,126	12,563	2.97	0.01
Zo × Si	6	57,049	9508.2	2.95	0.01
Residual	1098	4.64E+09	4224.2		
Total	1109	4.81E+09			

Zo, zone; Si, size class

prey sizes, depths, and/or times, which would allow them to reduce their trophic competition. These authors, however, stated that this pattern may be not consistent across all oceans. Moteki et al. (2001), in fact, reported that dolphinfish and yellowfin tuna may compete for exocoetids in the eastern tropical Pacific Ocean, whereas Oxenford and Hunte (1999) suggested that these two predators may compete for flying gurnards (*Dactylopterus volitans*) and for filefish (Monacanthidae) in Barbados waters (see Lewis and Axelsen 1967). Conversely, Kojadinovic et al. (2008), based on stable isotope analysis, observed trophic segregation between common dolphinfish and tuna species in Reunion Islands waters.

Although flyingfishes were the dominant prey in all zones, interspecific variations in their abundance were observed. Thus, while smallwing flyingfish (*Oxyporhamphus micropterus*) was the main prey species in the North region, barbel flyingfish (*Exocoetus monocirrhus*) was the most abundant prey species in the South region (see Table 2). These differences may be related to variations in the oceanographic features. Lewallen et al. (2018), in fact, reported that surface temperature and salinity are key parameters defining flyingfish habitats. Otherwise, spatial variations between inshore and offshore waters were also found, epipelagic

cephalopods such as argonauts being more prevalent in inshore caught fish. Similarly, Olson and Galván-Magaña (2002) found that epipelagic cephalopods were more abundant in fish caught nearshore. Multivariate analysis also suggested two size-related shifts in feeding habits. The first shift in the feeding habits was detected between the small- and the medium-sized fish, and was caused by a decrease in the consumption of barbel flyingfish along with an increased proportion of frigate tuna. The second shift was found around 110 cm, where the cephalopods jumbo squid and argonauts showed a higher contribution to the diet than flyingfishes. This finding is consistent with previous studies carried out in Brazilian waters and EPO area (Zavala-Camin 1986; Olson and Galván-Magaña, 2002), where large-sized dolphinfish also show greater predation on cephalopods than on flyingfishes.

Similar to what was observed by Varela et al. (2017a) in dolphinfish caught in Ecuadorian waters, DR decrease with body size. Benetti et al. (1995) stated that the dolphinfish mass-specific standard metabolic rate (SMR) diminishes with increasing body weight. This fact, therefore, suggests that smaller fish may need to consume proportionally larger amount of food to meet their SMR, and that DR decreases with increasing size has also been reported in others top predators. For instance, Ménard et al. (2000) found that DR of yellowfin tuna in the equatorial Atlantic Ocean decreased from 16.0% BM day⁻¹ for > 90 cm fish to 2.6% BM day⁻¹ for > 90 cm fish. Similarly, Griffiths et al. (2007) found that DR values of longtail tuna (*Thunnus tonggol*) in Australian waters decreased from 2.2% BM day⁻¹ for < 60 cm fish to 1% BM day⁻¹ for > 130 cm fish. The highest DR values (17.6% BM day⁻¹) in zone B may be attributed to the smaller fish size in this region (FL = 85.8 ± 28.7 cm). This result is consistent with the findings of Olson

Table 5 Results of a posteriori pair-wise PERMANOVA for the interaction between “zone” and “size class” factors

Size	Zone							
	A		B		C		D	
	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>
FL < 80 cm / 80 cm ≤ FL < 110 cm	1.31	>0.05	2.21	<0.01	0.84	>0.05	1.53	<0.05
FL < 80 cm / FL ≥ 110 cm	1.43	<0.01	2.05	<0.01	0.90	>0.05	2.01	<0.01
80 CM ≤ FL < 110 cm / FL ≥ 110 cm	1.97	<0.01	1.19	>0.05	1.24	>0.05	1.87	<0.01

FL, fork length

and Galván-Magaña (2002) who reported DR values $\sim 20\%$ BM day⁻¹ for individuals ranging between 65 and 80 cm in FL.

In comparison with other large pelagic fishes inhabiting the study area, our DR estimates were greater than those reported for yellowfin tuna (3.9% BM day⁻¹; Olson and Boggs 1986) and swordfish (1.6–8.2% BM day⁻¹; Zambrano-Zambrano et al. 2019). Such differences may be attributed to species-specific factors that may affect prey evacuation rates, such as metabolic rates or gut morphology (Griffiths et al., 2007; Perelman et al., 2017). Another factor explaining DR differences among these species may be related to the consumed prey type (Buckel and Conover 1997). Thus, Olson and Boggs (1986) reported that scombrids were the main prey species in the diet of yellowfin tuna, whereas Zambrano-Zambrano et al. (2019) found that the diet of swordfish was mainly composed of squids, which are more easily digested and evacuated (Varghese and Somvanshi, 2016).

The presence of conspecifics in the stomachs was not unexpected, since dolphinfish cannibalism has been widely reported in all seas worldwide (Oxenford and Hunte 1999; Olson and Galván-Magaña 2002; Castriota et al. 2007; Rudershausen et al. 2010; Brewton et al. 2016; Luckhurst 2017). The cannibalism rate found in the present study (0.6 based on %O) was similar to that previously reported in the eastern Pacific Ocean. Thus, Olson and Galván-Magaña (2002) reported %O=0.4, whereas Torres-Rojas et al. (2014) found %O values of 2.2. However, Moteki et al. (2001) based on a low sampled size ($n=38$) reported higher cannibalism rates (%O=10.5). According to Torres-Rojas et al. (2014), dolphinfish cannibalism may be sporadic as this species shows spatial stratification by size.

The present study provides new information on the feeding habits and consumption rate of common dolphinfish in the Southeast Pacific Ocean. Our findings indicate that this species is an epipelagic carnivorous predator that shows two size-related dietary changes to occur at a FL ~ 80 cm and FL ~ 110 cm. Although flyingfishes seem to be the main prey species in the whole sampling area, interspecific variations among zones were found. Considering that surface temperature and salinity are factors that define flyingfish habitats, this spatial variation may be related to the oceanographic features of each zone. For instance,

the northern area is affected by the Panama current (warm water), whereas the southern area is influenced by the Chile-Peru current (cold water). Otherwise, our estimates of daily ration suggest that this species play an important trophic role structuring pelagic ecosystems. However, the lack of information on specific gastric evacuation rates for dolphinfish may bias our estimates. Therefore, further investigations should be addressed to determine accurate rates of gastric evacuation for this predator.

Author contribution All authors contributed to study conception, design, laboratory work, data analysis, and manuscript writing.

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Data availability Datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

Code availability No applicable.

Declarations

Ethics approval The present research involved no animal experimentation or harm. Samples were collected from fish harvested for commercial purposes, and permits for animal collections were not required.

Consent to participate Not applicable as this research did not involve human participants.

Consent for publication The authors all agree with the content of the manuscript.

Conflict of interest The authors declare no competing interests.

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