Journal of the Marine Biological Association of the United Kingdom, page 1 of 7.
doi:10.1017/S0025315416000175

Diet of common dolphinfish (*Coryphaena hippurus*) in the Pacific coast of Ecuador

JOSÉ LUIS VARELA[1,2,3], CRISTHIAN RONALD LUCAS-PILOZO[1] AND MANUEL MARÍA GONZÁLEZ-DUARTE[4]

[1]Departamento Central de Investigación, Universidad Laica Eloy Alfaro de Manabí, Av. de Circunvalación, Manta, Ecuador, [2]Departamento de Biología, Universidad de Cádiz, Campus de Excelencia Internacional del Mar (CEI·MAR), Av. República Saharaui s/n, 11510 Puerto Real, Cádiz, Spain, [3]Biology Department, Acadia University, 33 Westwood Ave., B4P 2R6 Wolfville, Nova Scotia, Canada, [4]Departamento de Ecología, Center for Marine Conservation, Pontificia Universidad Católica de Chile, Casilla 193, Correo 22, 6513677 Santiago, Chile

The diet and the feeding habits of the common dolphinfish (Coryphaena hippurus*) in the Pacific coast of Ecuador was assessed by examining 320 stomachs of individuals ranging from 51 to 149 cm in total length. Fish was the predominant prey group in the diet (Alimentary Index, %AI = 95.39) followed by cephalopods (%AI = 4.13) and crustaceans (%AI = 0.48). Among the 17 prey items that make up the dolphinfish diet, the Exocoetidae family was the most important prey (%AI = 57.13),* Dosidicus gigas *being the most abundant invertebrate species (%AI = 7.65). Feeding patterns were evaluated using the graphing method of Amundsen, which suggested that this species shows a varying degree of specialization on different prey taxa. Thus, while some species were unimportant and rare (*Hippocampus hippocampus, Lagocephalus lagocephalus, *Gobiidae and* Argonauta *sp.), several dolphinfishes showed a high degree of specialization on Scombridae,* Pleuroncodes planipes, Portunus xantusii *and* Opisthonema libertate. *Size-related and temporal shifts in dietary composition were investigated by PERMANOVA analysis, which showed wide variations among size classes and periods of capture. The results of this study indicate that the common dolphinfish is an opportunistic feeder, which is capable of consuming a wide variety of schooling epipelagic organisms.*

Keywords: Coryphaenidae, trophic biology, stomach content analysis, food items

Submitted 18 November 2015; accepted 19 January 2016

INTRODUCTION

The common dolphinfish (*Coryphaena hippurus*, Linnaeus 1758) is a cosmopolitan species distributed through the tropical and subtropical regions of the Pacific, Indian and Atlantic Oceans (Palko *et al*., 1982). In Ecuador, this species is exploited by artisanal boats and represents one of the most important fishery resources because its flesh is highly appreciated in American markets (Patterson & Martinez, 1991). In spite of the local commercial importance, few studies have been conducted so far to evaluate the feeding habits of the dolphinfish in the Ecuadorian Pacific coast. Trophic ecology studies based on stomach content analysis provide useful information to guide management and conservation efforts of fishery resources within the ecosystem-based fisheries management framework (EBFM) (Ainsworth *et al*., 2010).

The dolphinfish are usually confined to the upper 30 m of the water column, or between the surface and the thermocline (<30 m) (Palko *et al*., 1982; Tripp-Valdez *et al*., 2015). Like other large pelagic fishes, this species plays an important role in epipelagic ecosystems, since it may delineate the structure of the food-webs by top-down controls. Previous trophic biology studies carried out in the Northern Pacific Ocean, Atlantic Ocean and Mediterranean Sea have revealed that *C. hippurus* feeds on a wide variety of fish and invertebrate pelagic organisms (Oxenford & Hunte, 1999; Tripp-Valdez *et al*., 2015), and so has been defined as a non-selective and generalist predator (Massutí *et al*., 1998; Castriota *et al*., 2007). New data regarding the dolphinfish trophic biology in Ecuadorian waters may be useful to understand the pelagic food webs in the Eastern Pacific Ocean (EPO) ecosystem. With this purpose, the present study was undertaken to determine the diet composition, feeding patterns, niche width and consumption rate of the common dolphinfish considering temporal and size-related variations.

MATERIALS AND METHODS

Sampling and stomach-content analysis

Freshly caught common dolphinfish (N = 320), ranging from 51 to 149 cm in total length (TL), were sampled in Playita Mía (Manta, Ecuador) (Figure 1). The fish were captured by artisanal boats during night-time hours off the coast of Ecuador in December–May (2014–2015). The main bait species used in the fishing operations were jumbo squid (*Dosidicus gigas*), longfin salema (*Xenichthys xantii*) and chere-chere grunt (*Haemulon steindachneri*).

Whole stomachs (N = 320) were collected from each fish and stored at −20°C until analysis. In the laboratory, they were dissected for prey identification to the lowest possible taxonomic level. Food items considered to be bait were not

Corresponding author:
J.L. Varela
Email: joseluis.varela@uca.es

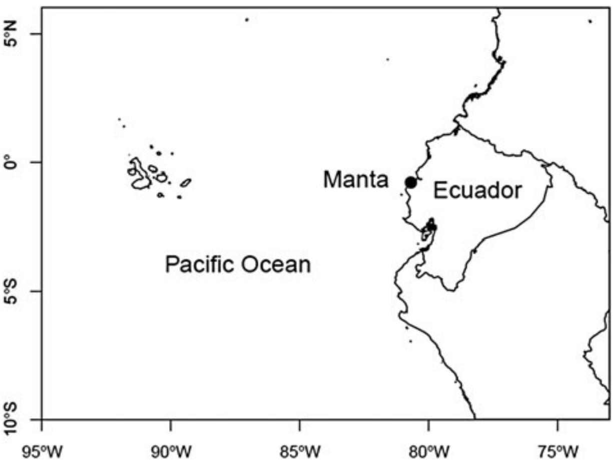

Fig. 1. Common dolphinfish were captured in the Pacific coast of Ecuador. The filled circle represents the sampling location.

taken into consideration for analysis, and the stomachs containing only bait were classified as empty. Hard parts (fish otoliths and cephalopod beaks) were used for identification of partially digested prey using specific taxonomic keys (Clarke, 1986; Harvey *et al.*, 2000; García-Godos Naveda, 2001).

Data analysis

The dietary importance of each prey was assessed by three indices: (1) percentage of wet weight ($\%W_i$), (2) frequency of occurrence ($\%O_i$) and (3) the alimentary index proposed by Kawakami & Vazzoler (1980) expressed as percentage according to the formula: $\%AI_i = [(\%O_i \times \%W_i)/(\Sigma\%W_i \times \%O_i)] \times 100$.

To assess whether the number of stomachs analysed was adequate to describe the diet, the cumulative curve of new prey items was plotted against the cumulative number of stomachs (Ferry & Cailliet, 1996). The cumulative curve was randomly built by resampling the stomachs 500 times by the software R (R Development Core Team, 2015). To determine whether the curve reached an asymptote, the slope of the linear regression estimated from the last four stomachs was compared with 0 (horizontal asymptote) by *t*-test. The cumulative prey curve was constructed grouping the prey categories by family.

The feeding behaviour of *C. hippurus* was evaluated through modification of the graphing method proposed by Costello (1990) (Amundsen *et al.*, 1996). In this procedure, prey-specific abundance is plotted against $\%O_i$ in order to obtain information about prey importance and feeding strategy of the predator. The prey-specific abundance is calculated as follows: $\%P_i = (\Sigma \text{prey } i \text{ weight}/\Sigma \text{ weight of all prey in the stomach containing prey } i) \times 100$. Prey species that only appear in one stomach were not taken into account in the analyses.

The dietary niche breadth was explored by the standardized Levin's index expressed as: $B_i = [1/(n-1)][(\Sigma(1/P_{ij}^2))^{-1}]$, where B_i is the measure of the Levin's niche breadth, n is the number of prey categories and P is the proportion of the AI. The standardized Levin's index ranges between 0 and 1, where low values indicate specialist feeding behaviour and high values indicate generalist feeding behaviour (Krebs, 1989).

Size-related and temporal shifts in diet composition were evaluated by a permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001; McArdle & Anderson, 2001). An experimental design with two fixed factors was considered: 'Size class' (with three levels, <80 cm in TL, 80–110 cm in TL, ≥110 cm in TL) and 'Date of capture' (with three levels, December–January, February–March, April–May). The analysis was based on a Bray–Curtis similarity matrix calculated from the prey weight values, after performing a fourth-root transformation (Bray & Curtis, 1957). Significant terms were investigated using *a posteriori* pair-wise comparisons with the PERMANOVA test. Similarity percentages (SIMPER; Clarke, 1993) were used to identify which dietary categories typified particular groups. Multivariate analyses were performed using the software PRIMER v6.1.11 & PERMANOVA+ v1.0.1 statistical package (Clarke & Gorley, 2006).

The consumption food rate was calculated as proposed by Olson & Mullen (1986), according to the formula: $\hat{r} = \sum_{i=0}^{I} \bar{W}_i/A_i$, 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 is the average time required to evacuate the average proportion of prey i.

Because the dolphinfish feeds during day and night hours (Olson & Galván-Magaña, 2002), daily meal was estimated by multiplying $\hat{r}$ by 24 h. Daily ration (expressed as percentage) was then calculated by dividing the daily meal by the body mass of the dolphinfish. The body mass was estimated from the length using the equation proposed by Lasso & Zapata (1999): $BM = 0.0224 \times (0.8278 \times TL)^{2.78}$, where BM is the body mass (g) and TL is the total length (cm). Size-related shifts in daily ration were investigated by grouping the fish into three size classes: Class I (<80 cm in TL), Class II (80–110 cm in TL) and Class III (≥110 cm in TL).

RESULTS

The size frequency distribution of the sampled fish is presented in Figure 2. Of the 320 stomachs examined, 188 were considered empty (58.75%) and 132 contained prey (41.25%). The diet comprised of 16 taxa, including 11 fishes, two cephalopods, two crustaceans and one gastropod (Table 1). Fish was the most abundant prey group (%AI = 95.39) followed by cephalopod (%AI = 4.13) and crustacean (%AI = 0.48). The most abundant taxa in terms of %AI were the Exocoetidae family and *Auxis* sp. (57.13 and

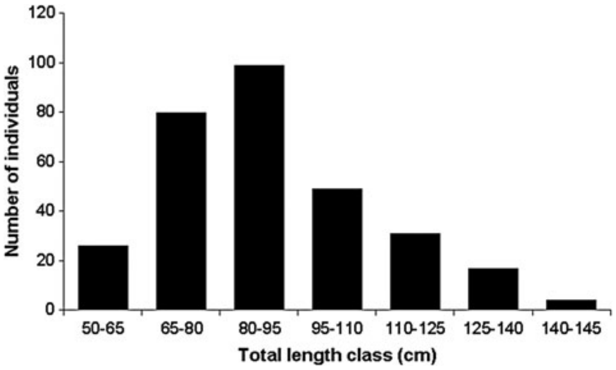

Fig. 2. Length–frequency distribution of the common dolphinfish sampled.

http://dx.doi.org/10.1017/S0025315416000175

25.25%, respectively), whereas the jumbo squid (*Dosidicus gigas*) was the most important invertebrate prey-species (%AI = 7.65) (Table 1).

The cumulative prey curve reached the asymptote for the last four points (Figure 3) (*t*-test, $P > 0.05$) and, therefore, the number of samples was considered adequate to describe the diet.

The Amundsen plot based on prey-specific abundance against occurrence (Figure 4) suggests that in the Ecuadorian Pacific the common dolphinfish has a varying degree of specialization on different prey taxa. Thus, *Hippocampus hippocampus, Lagocephalus lagocephalus*, Gobiidae and *Argonauta* sp. showed low occurrence and low prey-specific abundance (lower left), suggesting that all these species are unimportant and rare prey. Scombridae, *Pleuroncodes planipes, Portunus xantusii* and *Opisthonema libertate* showed low occurrence and high prey-specific abundance (upper left), indicating they are predated by a low number of individuals. Exocoetidae, located in the upper central area of the graph, may be considered the most important prey species, since it was found in a high percentage of stomachs (%O = 39.39). In spite of the fact that some individuals predated on a small proportion of prey, many of them fed on the dominant taxa (Exocoetidae), explaining the narrow niche width observed ($B_i = 0.10$).

The PERMANOVA analysis showed significant differences in the diet of *C. hippurus* among the three levels of 'Size class' and 'Date of capture'. The interactions between both of the factors were also significantly different, indicating that the differences in 'Date of capture' were not homogeneous across the levels of the 'Size class' factor (PERMANOVA, $P = 0.001$) (Table 2). Pair-wise PERMANOVA test revealed significant differences in the dietary composition among the three levels of 'Date of capture' for the smallest and medium specimens (PERMANOVA, $P < 0.01$) (Table 3). Only the largest specimens of *C. hippurus* ($\geq$110 cm in TL) fed on the same prey-species throughout the period of sampling (Table 3).

Table 1. Diet composition of common dolphinfish capture in the Pacific coast of Ecuador. Percentage of weight (%W), occurrence (%O) and alimentary index (%AI).

Prey	%W	%O	%AI
Fish	79.79	83.33	95.39
Exocoetidae	28.24	39.39	57.13
Auxis spp.	23.18	21.21	25.25
Engraulis sp.	8.96	11.36	5.23
Opisthonema libertate	4.49	4.55	1.05
Trachinotus sp.	3.61	1.52	0.28
Scombridae	3.53	2.27	0.41
Merluccius gayi	2.56	0.76	0.10
Lagocephalus lagocephalus	2.22	3.03	0.35
Gobiidae	0.42	1.52	0.03
Hippocampus hippocampus	0.13	1.52	0.01
Myctophum sp.	0.02	0.76	0.00
Unidentifiable fish	2.43	6.82	0.85
Cephalopd	16.50	17.42	4.13
Dosidicus gigas	14.05	10.61	7.65
Argonauta sp.	2.46	6.82	0.86
Crustacean	3.70	9.09	0.48
Pleuroncodes planipes	2.69	3.79	0.52
Portunus xantusii	1.01	5.30	0.27
Gastropoda	0.00	1.52	0.00
Cavolonidae	0.00	1.52	0.00

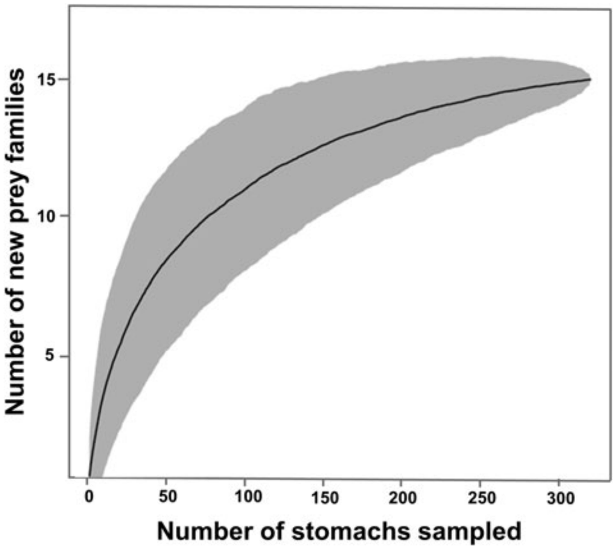

Fig. 3. Cumulative prey curve for common dolphinfish captured in the Pacific coast of Ecuador.

According to the SIMPER analysis (Table 4), the diet of *C. hippurus* was quantitatively characterized by eight prey items (six fish, one cephalopod and 1 crustacean). Exocoetidae was the only prey item that quantitatively characterized the diet in all size classes, whereas *Auxis* spp. and *Dosidicus gigas* were the heaviest contributors to the similarity in two size classes. Thus, *Auxis* spp. was consumed by the medium (contributing to 97.74% of the similarities) and largest specimens (25.29%), and *D. gigas* was consumed by the smallest (27.62%) and biggest ones (20.83%). The other prey species identified by SIMPER analysis exclusively characterized a

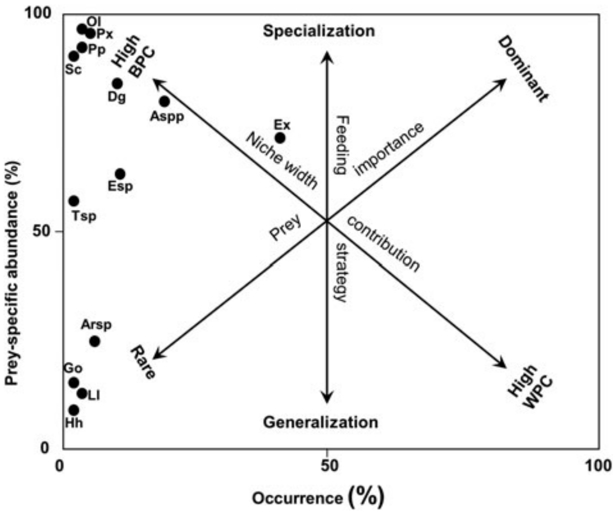

Fig. 4. Prey-specific abundance plotted against frequency of occurrence of prey species for common dolphinfish from the Pacific coast of Ecuador. Explanatory axes for foraging patterns are those of Costello (1990) as modified from Amundsen *et al.* (1996). The two diagonal axes represent the importance of prey (dominant *vs* rare) and the contribution to the niche width (high between-phenotype *vs* high within-phenotype contribution); the vertical axis defines the predator feeding strategy (specialist *vs* generalist). Aspp, *Auxis* spp.; Arsp, *Argonauta* sp.; Dd, *Dosidicus gigas*; Esp, *Engraulis* sp.; Ex, Exocoetidae; Go, Gobiidae; Hh, *Hippocampus hippocampus*; Ll, *Lagocephalus lagocephalus*; Ol, *Opisthonema libertate*; Sc, Scombridae; Tsp, *Trachinotus* sp.; Pp; *Pleuroncodes planipes*; Px, *Portunus xantusii*.

Table 2. Results of PERMANOVA test performed on Bray–Curtis dissimilarity matrix based on biomass of prey per stomach.

Source	Df	SS	MS	Pseudo-F	*P*(perm)
SC	2	20,731	10,366	3.386	0.001*
DC	2	31,933	15,966	5.216	0.001*
SC × DC	4	51,191	12,798	4.117	0.001*
Residual	115	3.52E+09	3061.2		
Total	123	4.73E+09			

Asterisk indicates a significant difference. SC, Size Class; DC, Date of capture.

Table 5. Size-related shifts in daily meal and daily ration (mean ± SD) of *Coryphaena hippurus* in the Pacific coast of Ecuador.

Size class	Daily meal (g)	Daily ration (% BM day^{-1})
Class I (<80 cm)	74.04	4.05 ± 1.34
Class II (80–110 cm)	136.36	3.37 ± 0.79
Class III (≥110 cm)	21.08	2.29 ± 0.44

single size class. Otherwise, for the three levels of the 'Date of capture' factor, a single prey contributed to the diet with more than 40%.

Daily meal and daily ratio were calculated from A_i values reported in earlier studies aimed at determining the consumption rate of the dolphinfish (see Olson & Galván-Magaña, 2002; Varghese *et al.*, 2013). Both daily meal and daily ratio showed variations with size length. Thus, whereas daily meal increased from 74.04 g day^{-1} in the smallest specimens to 210.08 g day^{-1} in the largest ones, the daily ratio decreased from 4.05 ± 1.34 to 2.29 ± 0.44% BM day^{-1} (Table 5).

DISCUSSION

The high importance of fish in the diet of *C. hippurus* captured in the Pacific coast of Ecuador is in accordance with previous dietary studies carried out on this species (Aguilar-Palomino *et al.*, 1998; Olson & Galván-Magaña, 2002; Tripp-Valdez *et al.*, 2010). Within the fish group, flyingfish (Exocotidae) was the most important prey category, as has also been reported in all seas worldwide (Massutí *et al.*, 1998; Oxenford & Hunte, 1999; Sakamoto & Kojima, 1999; Olson & Galván-Magaña, 2002; Malone *et al.*, 2011; Varghese *et al.*, 2013). This family represents a good source of amino acids and lipids (Harewood *et al.*, 1993), showing a high caloric content in comparison with the invertebrate prey species found in the stomachs (Robertson & Chivers, 1997; Tripp-Valdez *et al.*, 2010).

Because *C. hippurus* were captured during night-time hours, the presence of *Myctophum* sp., *Merluccius gayi* and *D. gigas* at an early stage of digestion suggests nocturnal foraging events. Nevertheless, the great number of empty stomachs found (58.75%) indicates that this species feeds mainly in the daytime. This fact was also suggested in similar studies carried out in the Mediterranean, Caribbean and Arabian Seas (Masutti *et al.*, 1998; Oxenford & Hunte, 1999; Varghese *et al.*, 2014). Yet, this hypothesis should be addressed in further studies, since previous observations made in the Gulf of Mexico stream indicated that dolphinfish do not feed during the night (Gibbs & Collette, 1959). The jumbo squid (*D. gigas*) was the most abundant invertebrate

Table 3. *A posteriori* pair-wise permutational multivariate analysis of variance comparison for the significant 'Size Class' and 'Data of capture' interaction.

Data of capture	Class I (<80 cm)		Class II (80–110 cm)		Class III (≥110 cm)	
	T	*P*(perm)	*T*	*P*(perm)	*t*	*P*(perm)
Dec–Jan/Feb–Mar	1.81	0.006*	3.38	0.001*	1.41	0.122
Dec–Jan/Apr–May	3.07	0.001*	2.52	0.001*	1.33	0.141
Feb–Mar/Apr–May	2.11	0.004*	3.97	0.001*	0.82	0.640

Asterisk indicates a significant difference. Dec–Jan, December 2014–January 2015; Feb–Mar, February–March 2015; Apr–May; April–May 2015.

Table 4. Contribution of main prey types (expressed as percentage) to diet of *Coryphaena hippurus* identified by similarity percentage (SIMPER) analysis.

Prey	<80 cm			80–110 cm			≥110 cm
	Dec–Jan	Feb–Mar	Apr–May	Dec–Jan	Feb–Mar	Apr–May	Dec–May
Auxis spp.	–	–	–	–	97.74	–	25.29
Dosidicus gigas	–	27.62	–	–	–	–	20.83
Engraulis sp.	–	–	–	64.19	–	–	–
Exocoetidae	–	58.81	99.33	23.41	–	96.94	41.27
Loagocephalus lagocephalus	–	–	–	–	–	–	6.89
Opisthonema libertate	85.38	–	–	–	–	–	–
Portunus xantusii	–	–	–	8.03	–	–	–
Unidentifiable fish	8.69	8.22	–	–	–	–	–

Dec–Jan, December 2014–January 2015; Feb–Mar, February–March 2015; Apr–May, April–May 2015; Dec–May, December 2014–May 2015.

http://dx.doi.org/10.1017/S0025315416000175

found, although its contribution may be overestimated because this species is a common bait used in fishing operations. This squid serves as a trophic link between small mesopelagic organisms and top predators (Gilly *et al.*, 2006) and represents an important component in the diet of sharks, tunas and billfishes in the Ecuadorian Pacific coast (Galván-Magaña *et al.*, 2013; Olson *et al.*, 2014; Rosas-Luis *et al.*, 2016). For instance, Galván-Magaña *et al.* (2013) reported that *D. gigas* was the predominant prey in the diet of two pelagic sharks, while Olson *et al.* (2014) and Rosas-Luis *et al.* (2016) observed that this species is frequent in the diet of yellowfin tuna (*Thunnus albacares*) and swordfish (*Xiphias gladius*). In South Baja California, Aguilar-Palomino *et al.* (1998) and Tripp-Valdez *et al.* (2015) reported that the jumbo squid was the most important species in the diet of dolphinfish, while no individual was identified by Tripp-Valdez *et al.* (2010) in the same area. These marked discrepancies are probably associated with environmental changes, which may cause variation in the abundance of this ommastrephid (Nevárez-Martínez *et al.*, 2010).

The presence of the squat lobster (*Pleuroncodes planipes*) in the diet of dolphinfish was also reported in earlier studies carried out in the eastern Pacific coast (Aguilar-Palomino *et al.*, 1998; Olson & Galvan-Magaña, 2002; Torres-Rojas *et al.*, 2014). In terms of energy budget, this crustacean is of little importance for top predator fishes, since galaterids only contain 0.94 kcal g^{-1} dry weight (Abitia-Cardenas *et al.*, 1997). Nevertheless, this anomuran can appear in a vast abundance in association with El Niño Southern Oscillation (ENSO) events (Thompson *et al.*, 1993; Gutiérrez *et al.*, 2008), as the one that occurred in 2015 (NOAA, 2015).

The size-related and temporal shifts observed in the dietary composition of the common dolphinfish are probably related to the availability of its potential preys. It is known that oscillations in physical (e.g. temperature or salinity) or chemical (e.g. oxygen) factors influence on the abundance of marine organisms (Chavez *et al.*, 2008). Thus, the 2015 El Niño, which increased the water temperature in the coast of Ecuador (NOAA, 2015), may cause not only the proliferation of squat lobster but also sporadic increases in squid (i.e. *D. gigas*) and small fishes (i.e. Myctophidae or *Engraulis* sp.) (Chavez *et al.*, 2008).

The daily food intake (74.04–210.08 g) suggests that *C. hippurus* plays an important trophic role in pelagic ecosystems, consuming an estimated 27.03–76.68 kg of prey per individual per year in the Pacific coast of Ecuador. In the eastern Arabian Sea, a higher daily food consumption was found for this species (332.63 g) (Varghese *et al.*, 2013). In comparison with scombrid species, the daily meal estimated in the present study was higher than that reported for tuna mackerel (*Euthynnus affinis*) in eastern Australia (26–108 g) (Griffiths *et al.*, 2009) and lower than that found for yellowfin tuna in the Equatorial Atlantic Ocean (363.2–1530.9 g) (Ménard *et al.*, 2000). Otherwise, the daily prey consumption rate (2.29–4.05% BM day^{-1}) was lower than those previously reported for dolphinfish in the Eastern Pacific Ocean (5.6 ± 0.56 BM day^{-1}) (Olson & Galván-Magaña, 2002) and in the eastern Arabian Sea (5.23% BM day^{-1}) (Varghese *et al.*, 2013). In contrast, Young *et al.* (1997) and Griffiths *et al.* (2007) estimated values of 0.73–12.69 and 1.30–2.36% BM day^{-1} for tunas captured in Australian waters. The marked differences in the consumption rate among locations and taxa may be caused by several factors, including temperature, prey availability, prey biomass and prey type (Buckel & Conover, 1997).

In agreement with an earlier study (Olson & Galván-Magaña, 2002), the dolphinfish daily consumption rate decreased with size length. This finding can be explained by the fact that young fish have faster metabolic rates and thus require more feed relative to their body mass than do larger fish (NRC, 1978). Similarly, Maldeniya (1996) and Griffiths *et al.* (2009) found that in scombrids the daily ration decreases with increasing body size.

The results of this study indicate that the common dolphinfish is an opportunistic feeder, which is able to ingest a wide variety of schooling epipelagic organisms. In order to complement the available information obtained from stomach content analysis, stable isotope analyses, which provide information at larger time-scales, should be undertaken in further investigations aimed at increasing our knowledge on the trophic biology of this species.

FINANCIAL SUPPORT

The present work has been funded by the Andalucía Talent Hub Program launched by the Andalusian Knowledge Agency, co-funded by the European Union's Seventh Framework Program, Marie Skłodowska-Curie actions (COFUND – Grant Agreement no. 291780) and the Ministry of Economy, Innovation, Science and Employment of the Junta de Andalucía. J.L.V. benefitted from a grant under the Prometeo Project programme (SENESCYT, Ecuador). This is CEIMAR contribution #114.

REFERENCES

Abitia-Cardenas L.A., Galván-Magaña F. and Rodriguez-Romero J. (1997) Food habits and energy values of prey of striped marlin, *Tetrapturus audax*, off the coast of Mexico. *Fishery Bulletin* 95, 360–368.

Aguilar-Palomino B., Galván-Magaña F., Abitia-Cardenas L.A., Muhlia-Melo A.F. and Rodriguez-Romero J. (1998) Aspectos alimentarios del dorado *Coryphaena hippurus* Linnaeus, 1758 en Cabo San Lucas, Baja California Sur, México. *Ciencias Marinas* 24, 253–265.

Ainsworth C.H., Kaplan I.C., Levin P.S. and Mangel M. (2010) A statistical approach for estimating fish diet compositions from multiple data sources: Gulf of California case study. *Ecological Applications* 20, 2188–2202.

Amundsen P.A., Gabler H.M. and Staldvik F.J. (1996) A new approach to graphical analysis of feeding strategy from stomach contents data – modification of the Costello (1990) method. *Journal of Fish Biology* 48, 607–614.

Anderson M.J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26, 32–46.

Bray J.R. and Curtis J.T. (1957) An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs* 27, 325–349.

Buckel J.A. and Conover D.O. (1997) Movements, feeding periods, and daily ration of piscivorous young-of-the-year bluefish, *Pomatomus saltatrix*, in the Hudson River estuary. *Fishery Bulletin* 95, 665–679.

Castriota L., Pipitone C., Campagnuolo S., Romanelli M., Potoschi A. and Andaloro F. (2007) Diet of *Coryphaena hippurus*

(Coryphaenidae) associated with FADs in the Ionian and Southern Tyrrhenian Seas. *Cybium* 31, 435–441.

Chavez F.P., Bertrand A., Guevara-Carrasco R., Soler P. and Csierke J. (2008) The northern Humboldt Current System: brief history, present status and a view towards the future. *Progress in Oceanography* 95, 95–105.

Clarke M.R. (1986) *A handbook for the identification of cephalopod beaks.* Oxford: Clarendon Press.

Clarke K.R. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18, 117–143.

Clarke K.R. and Gorley R.N. (2006) *PRIMER-E v6: user manual/tutorial.* Plymouth: PRIMER-E.

Costello M.J. (1990) Predator feeding strategy and prey importance: a new graphical analysis. *Journal of Fish Biology* 36, 261–263.

Ferry L.A. and Cailliet G.M. (1996) Sample size and data: are we characterizing and comparing diet properly? In Makinlay D. and Shearer K. (eds) *Feeding ecology and nutrition in fish; proceedings of the symposium on feeding ecology and nutrition in fish.* San Francisco, CAA: American Fisheries Society, pp. 70–81.

Galván-Magaña F., Polo-Silva C., Hernández-Aguilar S.B., Sandoval-Londoño A., Ochoa-Díaz R.M., Aguilar-Castro N., Castañeda-Suárez D., Cabrera Chavez-Costa A., Baigorrí-Santacruz A., Torres-Rojas Y.E. and Abitia-Cárdenas L.A. (2013) Shark predation on cephalopods in the Mexican and Ecuadorian Pacific Ocean. *Deep-Sea Research Part II – Tropical Studies in Oceanography* 95, 52–62.

García-Godos Naveda I. (2001) Patrones morfológicos del otolito sagitta de algunos peces óseos del mar Peruano. *Boletín del Instituto del Mar de Perú* 20(1–2), 1–83.

Gibbs R.H. Jr. and Collette B.B. (1959) On the identification, distribution, and biology of the dolphins *Coryphaena hippurus* and *C. equiselis. Bulletin of Marine Science of the Gulf and Caribbean* 1, 117–152.

Gilly W.F., Markaida U., Baxter C.H., Block B.A., Boustany A., Zeidberg L., Reisenbichler K., Robison B., Bazzino G. and Salinas C. (2006) Vertical and horizontal migrations by the jumbo squid *Dosidicus gigas* revealed by electronic tagging. *Marine Ecology Progress Series* 324, 1–17.

Griffiths S.P., Fry G.C., Manson F.J. and Pillans R.D. (2007) Feeding dynamics, consumption rates and daily ration of longtail tuna (*Thunnus tonggol*) in Australian waters, with emphasis on the consumption of commercially important prawns. *Marine and Freshwater Research* 58, 376–397.

Griffiths S.P., Kuhnert P.M., Fry G.F. and Manson F.J. (2009) Temporal and size-related variation in the diet, consumption rate, and daily ration of mackerel tuna (*Euthynnus affinis*) in neritic waters of eastern Australia. *ICES Journal of Marine Science* 66, 720–733.

Gutiérrez M., Ramirez A., Bertrand S., Morón O. and Bertrand A. (2008) Ecological niches and areas of overlap of the squat lobster 'munida' (*Pleuroncodes monodon*) and anchoveta (*Engraulis ringens*) off Peru. *Progress in Oceanography* 79, 256–263.

Harewood P.M., Wood N.P. and Constantinides S.M. (1993) Quality characteristics of flyingfish (Exocoetidae spp.). *Journal of Food Protection* 56, 986–987.

Harvey J.T., Loughlin T.R., Perez M.A. and Oxman D.S. (2000) Relationship between fish size and otolith length for 63 species of fishes from the eastern North Pacific Ocean. *NOAA Technical Report NMFS* 150, 1–35 pp.

Kawakami E. and Vazzoler G. (1980) Método gráfico e estimativa de Índice Alimentar aplicado no estudo de alimentação de peixes. *Boletim do Instituto de Oceanografia* 29, 205–207.

Krebs C.J. (1989) *Ecological methodology.* New York, NY: Harper Collins.

Lasso J. and Zapata L. (1999) Fisheries and biology of *Coryphaena hippurus* (Pisces: Coryphaenidae) in the Pacific coast of Colombia and Panama. *Scientia Marina* 63, 387–399.

Maldeniya R. (1996) Food consumption of yellowfin tuna, *Thunnus albacares*, in Sri Lankan waters. *Environmental Biology of Fishes* 47, 101–107.

Malone M.A., Buck K.M., Moreno G. and Sancho G. (2011) Diet of three large pelagic fishes associated with drifting fish aggregating devices (DFADs) in the western equatorial Indian Ocean. *Animal Biodiversity and Conservation* 34, 287–294.

Massutí E., Deudero S., Sanchez P. and Morales-Nin B. (1998) Diet feeding of dolphin (*Coryphaena hippurus*) in Western Mediterranean waters. *Bulletin of Marine Science* 63, 329–341.

McArdle B.H. and Anderson M.J. (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82, 290–297.

Ménard F., Stéquert B., Rubin A., Herrera M. and Marchal E. (2000) Food consumption of tuna in the Equatorial Atlantic ocean: FAD-associated versus unassociated schools. *Aquatic Living Resources* 13, 233–240.

National Research Council (1978) Nutrient requirements of fishes. In National Academy of Sciences (ed) *Nutrient requirements of laboratory animals.* Washington, DC: National Academy Press, pp. 84–96.

Nevárez-Martínez M.O., Morales-Bojórquez E., Cervantes-Valle C., Santos Molina J.P. and López-Martínez J. (2010) Population dynamics of the jumbo squid (*Dosidicus gigas*) in the 2002–2008 fishing seasons off Guaymas, Mexico. *Fisheries Research* 106, 132–140.

NOAA (2015) http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/enso_update/sstanim.shtml.

Olson R.J., Duffy L.M., Kuhnert P.M., Galván-Magaña F., Bocanegra-Castillo N. and Alatorre-Ramirez V. (2014) Decadal diet shift in yellowfin tuna (*Thunnus albacares*) suggests broad-scale food web changes in the eastern tropical Pacific Ocean. *Marine Ecology Progress Series* 497, 157–178.

Olson R.J. and Galván-Magaña F. (2002) Food habits and consumption rates of common dolphinfish (*Coryphaena hippurus*) in the eastern Pacific Ocean. *Fishery Bulletin* 100, 279–298.

Olson R.J. and Mullen C.H. (1986) Recent developments for making gastric evacuation and daily ration determinations. *Environmental Biology of Fishes* 16, 183–191.

Oxenford H.A. and Hunte W. (1999) Feeding habits of the dolphinfish (*Coryphaena hippurus*) in the eastern Caribbean. *Scientia Marina* 63, 303–315.

Palko B.J., Beardsley G.L. and Richards W.J. (1982) Synopsis of the biological data on dolphin-fishes, *Coryphaena hippurus* Linnaeus and *Coryphaena equiselis* Linnaeus. *NOAA, Technical Report, NMFS Circular* 443, 1–28.

Patterson K.R. and Martinez J. (1991) Exploitation of the dolphin-fish *Coryphaena hippurus* L. off Ecuador: analysis by length-based virtual population analysis. *Fishbyte* 9, 21–23.

R Core Team (2015) *R: a language and environment for statistical computing.* Vienna: R Foundation for Statistical Computing. www.r-project.org.

Robertson K.M. and Chivers S.J. (1997) Prey occurrence in pantropical spotted dolphins, *Stenella attenuata*, from the eastern tropical Pacific. *Fishery Bulletin* 95, 334–348.

Rosas-Luis R., Loor-Andrade P., Carrera-Fernández M., Pincay-Espinoza J.E., Vinces-Ortega C. and Chompoy-Salazar L. (2016) Cephalopod species in the diet of large pelagic fish (sharks and billfishes) in Ecuadorian waters. *Fisheries Research* Part 2 173, 159–168.

Sakamoto R. and Kojima S. (1999) Review of dolphinfish biological and fishing data in Japanese waters. *Scientia Marina* 63, 375–385.

Thompson B., Tsukada D. and Laughlin J. (1993) Megabenthic assemblages of coastal shelves, slopes and basins off Southern California. *Bulletin of the Southern California Academy of Sciences* 92, 25–42.

Torres-Rojas Y.E., Hernández-Herrera A., Ortega-García S. and Soto-Jiménez M.F. (2014) Feeding habits variability and trophic position of dolphinfish in waters south of the Baja California Peninsula, Mexico. *Transactions of the American Fisheries Society* 143, 528–542.

Tripp-Valdez A., Galván-Magaña F. and Ortega-García S. (2010) Feeding habits of dolphinfish (*Coryphaena hippurus*) in the southeastern Gulf of California, Mexico. *Journal of Applied Ichthyology* 26, 578–582.

Tripp-Valdez A., Galván-Magaña F. and Ortega-García S. (2015) Food sources of common dolphinfish (*Coryphaena hippurus*) based on stomach content and stable isotopes analyses. *Journal of the Marine Biological Association of the United Kingdom* 95, 579–591.

Varghese S.P., Somvanshi V.S., John M.E. and Dalvi R.S. (2013) Diet and consumption rates of common dolphinfish, *Coryphaena hippurus*, in the eastern Arabian Sea. *Journal of Applied Ichthyology* 9, 1022–1029.

Varghese S.P., Somvanshi V.S., John M.E. and Dalvi R.S. (2014) Diet composition, feeding niche partitioning and trophic organisation of large pelagic predatory fishes in the eastern Arabian Sea. *Hydrobiologia* 736, 99–114.

and

Young J.W., Lamb T.D., Le D., Bradford R. and Whitelaw A.W. (1997) Feeding ecology and interannual variations in diet of southern bluefin tuna, *Thunnus maccoyii*, in relation to coastal and oceanic waters off eastern Tasmania, Australia. *Environmental Biology of Fishes* 50, 275–291.

Correspondence should be addressed to:

J.L. Varela
Departamento de Biología, Universidad de Cádiz, Campus de Excelencia Internacional del Mar (CEI·MAR), Av. República Saharaui s/n, 11510 Puerto Real, Cádiz, Spain
email: joseluis.varela@uca.es