

Feeding habits of wahoo (*Acanthocybium solandri*) in the eastern Pacific Ocean

MOLKER MENDOZA-ÁVILA^{1,2}, GABRIELA ZAVALA-ZAMBRANO^{1,2}, FELIPE GALVÁN-MAGAÑA³
AND PEGGY LOOR-ANDRADE¹

¹Facultad de Ciencias del Mar, Universidad Laica Eloy Alfaro de Manabí, Vía San Mateo S/N. Manta, Manabí, Ecuador,

²Viceministerio de Acuicultura y Pesca, Av. 4 Calle 12-13. Manta, Ecuador, ³Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas, Av. IPN S/N, Apdo. Postal 592, La Paz, Baja California Sur, México

*Stomach content analysis was used to assess the feeding habits of *Acanthocybium solandri* based on samples obtained on purse seine fishing trips off the Pacific coasts of Central and South America. A total of 226 samples were obtained; 160 stomachs contained food and 33 prey taxa were identified. Based on the Prey Specific Index of Relative Importance (%PSIRI), cephalopods and fishes were the main prey groups (50.4 and 49.5% PSIRI). *Dosidicus gigas* (23.4% PSIRI), *Stenoteuthis oulaniensis* (9.9% PSIRI) and *Argonauta* spp. (9.4% PSIRI) were the most representative prey. *Acanthocybium solandri* is a generalist predator based on the results of the Amundsen analysis and niche breadth ($B_a = 1$).*

Keywords: cephalopods, ecology, food and feeding, generalist, niche breadth, ontogenetic, predator, prey, Scombridae, stomach content

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INTRODUCTION

The wahoo (*Acanthocybium solandri*) is a highly migratory species distributed in tropical and subtropical waters (Collette & Nauen, 1983; Collette, 2002) that spends most of its time above the thermocline (Sepulveda *et al.*, 2011). Like other scombrids, the species is a fast swimmer with high aerobic performance (Korsmeyer *et al.*, 1996; Katz *et al.*, 2001; Wegner *et al.*, 2006), permitting individuals of the species to travel hundreds of kilometres (Theisen & Baldwin, 2012). This scombrid is captured worldwide mainly as incidental catch in the purse seine, pelagic longline and trolling fisheries, as well as private recreational fishing in the Pacific Ocean (Zischke, 2012). The annual haul in the Pacific Ocean has increased recently, with an estimate of 8279 t in 2013 (FAO, 2016).

Acanthocybium solandri is a high trophic level predator that feeds mainly on fishes and cephalopods (Allain, 2003; Vaske *et al.*, 2003; Baque-Menoscal *et al.*, 2012), consuming a wide variety of prey items (Manooch & Hogarth, 1983; Allain, 2003; Vaske *et al.*, 2003; Franks *et al.*, 2008; Rudershausen *et al.*, 2010; Baque-Menoscal *et al.*, 2012). The species inhabits epipelagic, pelagic, mesopelagic and bathypelagic areas (Allain, 2003). In the Pacific Ocean, fishes are the most important prey (Allain, 2003; Iversen & Yoshida, 1957); however, cephalopods also represent an important part of the wahoo diet (Allain, 2003; Baque-Menoscal *et al.*, 2012).

Studies on *A. solandri* feeding ecology in the Pacific Ocean are scarce. Further studies, including diet description and an assessment of possible regional and interspecific differences

in feeding habits, are necessary to enhance our knowledge of this predator's role in the area. Moreover, considering its economic importance, we also need further research on this species' life history in order to develop effective management programmes. Our goal was to describe the feeding habits of *A. solandri* by identifying the main prey and assessing possible regional, sexual and ontogenetic differences in diet, in addition to evaluating their feeding strategy.

MATERIALS AND METHODS

Sampling and stomach content analysis

Acanthocybium solandri samples were collected by Inter-American Tropical Tuna Commission (IATTC) observers during morning hours on purse seine fishing trips off the Pacific coast of Central and South America (Figure 1) in January, February, March, June and July 2005. Each individual was sexed and the fork length (FL) was measured to the nearest cm; stomach contents were frozen for posterior analysis. Stomach contents were classified and prey were weighed to the nearest 0.01 g and identified to the lowest taxonomic level. Wet weight was used for analysis as wet reconstruction cannot be applied to all prey species. Complete fishes and cephalopods were identified according to Fischer *et al.* (1995a, b), and Jereb & Roper (2010). Fishes were also identified based on the skeleton or otoliths (Clothier, 1950; García-Godos, 2001) and cephalopod species identification was also based on beaks (Clarke, 1962, 1986; Wolff, 1984).

Data analysis

To evaluate whether the sample size was adequate to describe the full diet a randomized cumulative prey curve was

Corresponding author:
F. Galván-Magaña
Email: fgalvan@ipn.mx

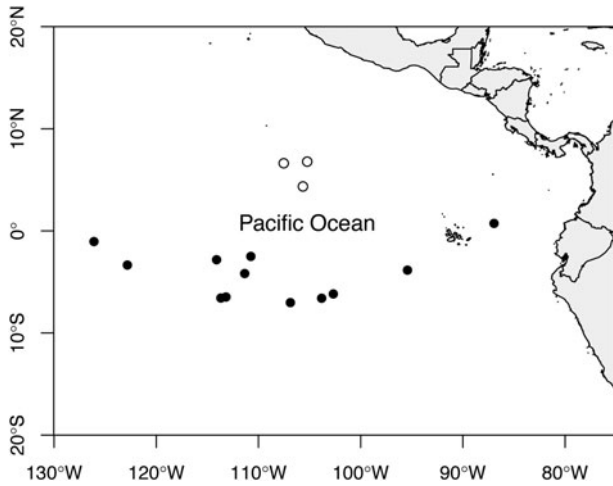


Fig. 1. Map showing the study area. Circles indicate sample sites. Empty circles correspond to the North Pacific Equatorial Countercurrent Province; black circles indicate sites in the Pacific Equatorial Divergence Province (Longhurst, 2007).

generated using the vegan package (Oksanen *et al.*, 2010) in R (R Development Core Team, 2014) including the lowest taxonomic level of each prey (Preti *et al.*, 2012). The mean species accumulation curve (± 2 standard deviations) was plotted from 500 random permutations of the data. When the curve approaches the asymptote, the number of samples is assumed to be sufficient to describe the diet (Hurtubia, 1973). When the asymptote was not evident a straight line to the last 4 points was compared to the slope of the line with a line of slope zero, reaching the asymptote when the lines did not differ significantly (Bizzarro *et al.*, 2007).

To determine the relative importance of each prey to the diet, we calculated the Prey Specific Index of Relative Importance (%PSIRI) (Brown *et al.*, 2012) using the equation: $\%PSIRI = 0.5\%FO_i (\%PN_i + \%PW_i)$, where $\%FO_i$ is the number of stomachs containing prey category i divided by the total number of stomachs, n . Prey-specific abundance was calculated with the equation $\%PA_i = \sum_{j=1}^n \%A_{ij} n_i^{-1}$ where $\%A_{ij}$ is the abundance (by counts, $\%PN_i$ or weight, $\%PW_i$) of prey category i in stomach sample j and n_i is the number of stomachs containing prey i . The %PSIRI is a modification of the Index of Relative Importance (IRI) (Pinkas *et al.*, 1971). The measure accounts for %FO redundancies in the %IRI, and is additive with respect to taxonomic levels; thus, the %PSIRI of a family will be equal to the sum of the %PSIRI of the species in that taxon (Brown *et al.*, 2012).

Individuals were grouped in two size classes based on sexual maturity (Brown-Peterson *et al.*, 2000; Jenkins & McBride, 2009) (juveniles = 66–92 cm, $N = 86$; adults = 93–127 cm, $N = 74$) to identify possible ontogenetic changes in diet. Samples were also classified by geographic area based on Longhurst's (2007) biogeographic provinces (Figure 1) (North Pacific Equatorial Countercurrent Province, $N = 31$; Pacific Equatorial Divergence Province, $N = 129$) in order to assess regional differences.

Sexual, ontogenetic and regional differences in diet were evaluated with multivariate techniques including analysis of similarity (ANOSIM) and non-metric multidimensional scaling (MDS) plots (PRIMER v6.2; www.primer-e.com) using the per cent number (%N) of each prey grouped by

family. Prey items were grouped by family to reduce the number of prey categories in the samples with zero values, increasing the effectiveness of the multivariate analysis (White *et al.*, 2004; Espinoza *et al.*, 2013; Szczepanski & Bengtson, 2014). Data were square-root transformed and a similarity matrix was constructed using the Bray–Curtis similarity coefficient. Data were permuted 999 times for a distribution to determine the P -value of ANOSIM's R statistic ($R = 0$ is identical, $R = -1$ or 1 is most divergent) (Clarke & Gorley, 2001).

To determine niche breadth, we calculated the Levin's standardized index (B_a) using the %PSIRI converted to proportions for the different prey species identified (Krebs, 1999). This measure varies between 0 and 1, where values close to 0 express a specialized diet and values close to 1 indicate a generalized diet (Krebs, 1999). To assess feeding patterns, we used the graphical analysis proposed by Amundsen *et al.* (1996), a modification of Costello's (1990) method that provides information regarding prey importance and the predator's feeding strategy in the form of a two-dimensional graph plotting the prey specific abundance ($\%P_i$) vs the $\%FO_i$, with $\%P_i = (\sum \text{prey } i \text{ weight} / \sum \text{weight of all prey in stomachs containing prey } i) \times 100$.

RESULTS

A total of 226 samples were obtained; 160 stomachs contained food representing a total of 33 taxa (Table 1). Sample size was not sufficient to describe the diet ($P < 0.05$) (Figure 2). Of the wahoo with food in their stomachs, 88 were females (69.3–127.0 cm), 70 were males (68.2–126.0 cm), and one was of undetermined sex. Cephalopods and fishes were the main prey groups (50.4 and 49.5% PSIRI, respectively), followed by crustaceans (0.1% PSIRI). *Dosidicus gigas* (23.4% PSIRI), *Senoteuthis oualaniensis* (9.9% PSIRI) and *Argonauta* spp. (9.4% PSIRI) were the most important prey species (Table 1).

ANOSIM did not reveal any significant differences in diet based on sex ($R = 0$, $P = 0.44$), size class ($R = 0$, $P = 0.40$) or regions ($R = 0.039$, $P = 0.22$) and these results are illustrated by MDS plots (Figure 3). Based on the 33 dietary items, the niche breadth was 1.0. Amundsen graphical analysis suggests that *A. solandri* exhibits a generalist feeding pattern, with no clearly dominant prey. Considering their low species abundance and frequency of occurrence, several prey items were

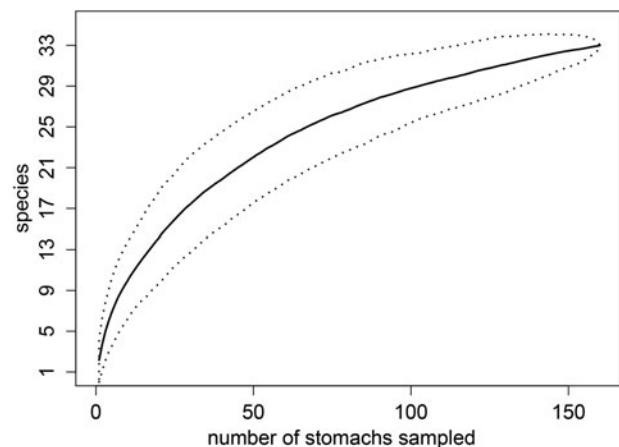


Fig. 2. Cumulative prey curve for *A. solandri*.

Table 1. Diet composition of *Acanthocybium solandri* by per cent frequency of occurrence (%FO), per cent prey-specific number (%PN), per cent number (%N), per cent prey-specific weight (%PW), per cent weight (%W) and prey-specific index of relative importance (%PSIRI).

Prey species	%FO	%PN	%N	%PW	%W	%PSIRI
Cephalopoda						
Ancistrocheiridae						
<i>Ancistrocheirus lesueurii</i>	0.6	20.0	0.1	2.8	<0.1	0.1
Argonautidae						
<i>Argonauta</i> spp.	28.1	44.1	12.4	22.9	6.4	9.4
Bolitaenidae						
<i>Japetella diaphana</i>	0.6	25.0	0.2	<0.1	<0.1	0.1
Enoploteuthidae						
<i>Abraliopsis</i> sp.	0.6	20.0	0.1	2.8	<0.1	0.1
Histioteuthidae						
<i>Histioteuthis</i> spp.	2.5	28.4	0.7	36.7	0.9	0.8
Mastigoteuthidae						
<i>Mastigoteuthis dentata</i>	3.1	33.5	1.0	22.1	0.7	0.9
Ommastrephidae						
<i>Dosidicus gigas</i>	40	53.5	21.4	63.4	25.4	23.4
<i>Stenoteuthis oualaniensis</i>	18.8	48.4	9.1	57.5	10.8	9.9
Thysanoteuthidae						
<i>Thysanoteuthis rhombus</i>	0.6	50.0	0.3	1.1	<0.1	0.2
Unidentified cephalopoda	15.6	31.8	5.0	29.2	4.6	4.8
Crustacean						
Unidentified crustacean	0.6	16.7	0.1	0.7	<0.1	0.1
Osteichthyes						
Clupeidae						
<i>Opisthopterus macrops</i>	0.6	100	0.6	100	0.6	0.6
Coryphaenidae						
<i>Coryphaena hippurus</i>	1.3	66.7	0.8	34.0	0.6	0.9
Engraulidae						
<i>Centengraulis mysticetus</i>	2.5	50.8	1.4	64.7	1.6	1.4
Echeneidae						
Echeneidae	1.3	100.0	1.3	100.0	1.3	1.3
Exocoetidae						
<i>Cheilopogon</i> sp.	1.3	29.2	0.4	44.7	0.6	0.5
<i>Cheilopogon xemopterus</i>	0.6	50.0	0.3	53.0	0.3	0.3
<i>Cypselurus callopterus</i>	1.3	33.3	0.4	24.3	0.3	0.4
Exocoetidae						
<i>Exocoetus monocirrhus</i>	4.4	38.1	1.7	31.3	1.4	1.5
<i>Exocoetus obtusirostris</i>	8.8	47.5	4.2	34.3	3.0	3.6
<i>Exocoetus</i> sp.	0.6	16.7	0.1	32.7	0.2	0.2
<i>Exocoetus</i> sp.	3.8	40.7	1.5	36.5	1.1	1.2
<i>Exocoetus volitans</i>	3.8	40.2	1.5	31.1	1.2	1.3
<i>Fodiator acutus rostratus</i>	2.5	36.5	0.9	25.8	0.6	0.8
<i>Parexocoetus brachypterus</i>	3.1	76.7	2.4	76.5	2.4	2.4
<i>Parexocoetus</i> sp.	0.6	50.0	0.3	7.5	<0.01	0.2
Gempylidae						
<i>Gempylus serpens</i>	5.6	31.4	1.8	50.6	2.8	2.3
Hemiramphidae						
<i>Oxyporhampus micropterus</i>	1.9	38.9	0.7	41.0	0.8	0.7
Scombridae						
<i>Auxis</i> sp.	2.5	38.6	1.0	32.8	0.8	0.9
<i>Auxis thazard</i>	2.5	62.5	1.6	86.2	2.2	1.9
<i>Katsuwonus pelamis</i>	1.3	19.6	0.2	69.7	0.9	0.6
<i>Thunnus</i> spp.	1.9	26.1	0.5	50.3	0.9	0.7
Unidentified teleosts	51.9	50.4	26.2	53.1	27.5	26.8

of little importance (lower left); the squids *Ancistrocheirus lesueurii*, *Abraliopsis* sp., *Japetella diaphana* and *Thysanoteuthis rhombus*; and the dolphinfish *Coryphaena hippurus* (Figure 4).

DISCUSSION

The number of wahoo prey items registered in this study is higher than that reported elsewhere in the Pacific (Iversen &

Yoshida, 1957; Allain, 2003; Baque-Menoscal *et al.*, 2012) and Atlantic Oceans (Franks *et al.*, 2008) probably due to the extensive area and larger sample size considered here. In a long-term study, Manooch & Hogarth (1983) observed more prey items off the Atlantic coast of the USA, in the Gulf of Mexico and around Bimini (Manooch & Hogarth, 1983).

The cephalopods *D. gigas*, *S. oualaniensis* and *Argonauta* spp. were the main prey species in this study. Around the Galapagos Islands, *D. gigas* was also one of the most

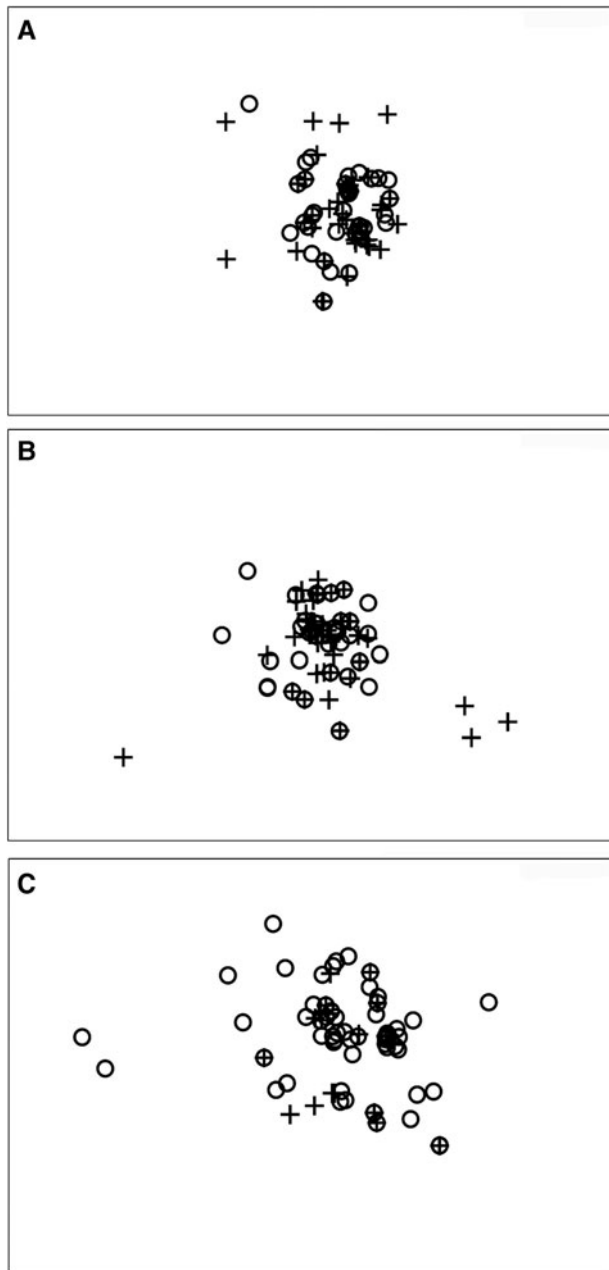


Fig. 3. (A) MDS plots comparing wahoo males (+) vs females (o); (B) juveniles (+) vs adults (o); and North Pacific Equatorial Countercurrent Province (+) vs Pacific Equatorial Divergence Province (o). The stress level for the 2-D ordination was 0.01.

representative prey items based on the per cent number (%N) (Baque-Menoscal *et al.*, 2012). Fishes were the most important prey group registered in the Western and Central Pacific in terms of number, frequency of occurrence and weight (Allain, 2003) and were also the most frequent prey in the Line Islands (Iversen & Yoshida, 1957). For the Western and Central Pacific not considering unidentified fish, the most frequent prey items were squids, *Alepisaurus* sp. (lancetfish) and Chiasmodontidae fishes; based on number, the most common prey items were squids, and Siganidae and Chiasmodontidae fishes (Allain, 2003).

Squids make up an important component of the wahoo diet. Based on a decadal study of the *Thunnus albacares*

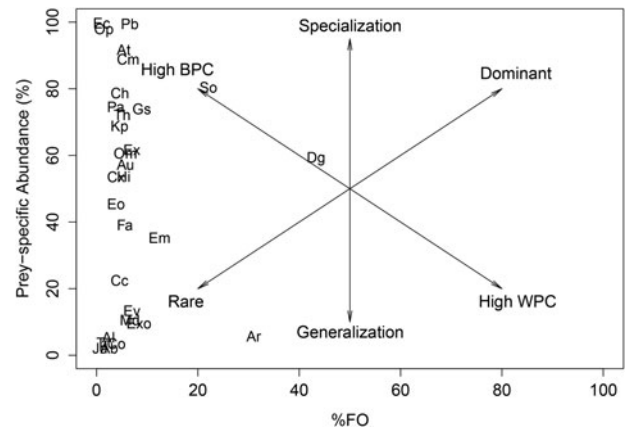


Fig. 4. Prey-specific abundance (% P_i) plotted against the frequency of occurrence for *A. solandri* prey species. The explanatory axes for foraging patterns are those used by Costello (1990) as modified by Amundsen *et al.* (1996). The two diagonal axes represent the importance of prey (dominant vs rare) and the contribution to niche width (high between-phenotype vs high within-phenotype contribution); the vertical axis defines the predator feeding strategy (specialist vs generalist). Ab, *Abraliopsis* sp.; Al, *Ancistrocheirus lesueurii*; Ar, *Argonauta* spp.; At, *Auxis thazard*; Au, *Auxis* sp.; Cc, *Cypselurus callopterus*; Ch, *Cheilopogon* sp.; Cm, *Centegraulis mysticetus*; Co, *Coryphaena hippurus*; Cx, *Cheilopogon xemopterus*; Dg, *Dosidicus gigas*; Ec, Echineidae; Em, *Exocoetus monocirrhus*; Eo, *Exocoetus obtusirostris*; Ex, *Exocoetus* sp.; Ev, *Exocoetus volitans*; Exo, Exocoetidae; Fa, *Fodiator acutus rostratus*; Gs, *Gempylus serpens*; Hi, *Histioteuthis* spp.; Jd, *Japetella diaphana*; Kp, *Katsuwonus pelamis*; Md, *Mastigoteuthis dentata*; Om, *Oxyporhumpus micropterus*; Op, *Opisthopterus macrops*; Pa, *Paraexocoetus* sp.; Pb, *Paraexocoetus brachypterus*; So, *Stenoteuthis oualaniensis*; Th, *Thunnus* spp.; Tr, *Thysanoteuthis rhombus*.

diet, Olson *et al.* (2014) argued for broad-scale changes in the pelagic food web in the Eastern Tropical Pacific, with squids and crustaceans predominating. The abundance of squids as *D. gigas* in this area (Nigmatullin *et al.*, 2001) may contribute to the high rate of consumption as they are also an important prey item for other oceanic predators in the eastern Pacific, including sharks (Galván-Magaña *et al.*, 2013) and tunas (Olson *et al.*, 2014). The high site fidelity displayed by this predator may be related to the abundance of prey in particular areas, as previously suggested for this species off Baja California Sur, Mexico (Sepulveda *et al.*, 2011).

Crustaceans do not make a significant contribution to the *A. solandri* diet in the eastern Pacific Ocean. In this study, only one hard part in one stomach was observed; a low frequency of occurrence also had been reported for this prey group around the Galapagos Islands (Baque-Menoscal *et al.*, 2012). However, in the western and central Pacific, wahoo feed on a wide variety of crustaceans, including shrimp, Amphipoda and Hyperiidea (Allain, 2003). The importance of crustaceans in the wahoo diet varies by geographic area rather than availability in the marine environment; in the Pacific Ocean, Olson *et al.* (2014) observed that cephalopods and crustaceans were more prevalent in the *Thunnus albacares* diet in the 2000s than in the 1990s. To date, no studies have been conducted on temporal changes in the wahoo diet in the Pacific Ocean; however, Rudershausen *et al.* (2010) mentioned that the wahoo diet exhibited low interannual variability in the North Atlantic Ocean.

We observed high trophic overlap and no regional differences in diet between males and females. Ontogenetic shifts in diet have been observed in scombrids (Graham *et al.*, 2007; Shimose *et al.*, 2013). However, our study also reports

high trophic overlap between size classes, likely related to the narrow size range of the wahoo sampled.

Acanthocybium solandri is a generalist consumer in the study area with a wide niche breadth. An opportunistic feeding strategy had been suggested for *A. solandri* (Zischke, 2012) and observed for other scombrids, like *Thunnus albacares*, *Thunnus obesus* (Ménard *et al.*, 2006) and *Thunnus orientalis* during the early stages of life (Shimose *et al.*, 2013). Epipelagic and mesopelagic cephalopods and epipelagic fishes are the most representative prey in the wahoo diet in this area; this is in contrast to the western and central Pacific, where deeper fish species like *Alepisaurus* sp. and Chiasmodontidae have been registered (Allain, 2003). Few data are available on *A. solandri* and this study presents new information on the importance of cephalopods to the wahoo diet. Due to their economic importance and role as generalist predators, studies involving longer study periods and larger sample sizes are needed to evaluate possible temporal and interspecific differences in wahoo feeding habits.

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Correspondence should be addressed to:

F. Galván-Magaña
 Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas, Av. IPN S/N, Apdo. Postal 592, La Paz, Baja California Sur, México
 email: fgalvan@ipn.mx