



Foraging ecology of oceanic-stage loggerhead turtles *Caretta caretta*

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ABSTRACT: We examined stomach contents (n = 12) and fecal samples (n = 4) in the first quantitative analysis of diet composition of oceanic-stage loggerhead turtles *Caretta caretta* from the North Atlantic Ocean. We found that loggerheads from the Azores are opportunistic carnivores that feed upon a variety of oceanic and pelagic organisms; our results also show that they exploited novel food resources, such as non-indigenous species. The diversity of prey species was positively correlated with loggerhead body size and volume of stomach contents. Because loggerhead body size was also positively correlated with stomach content volume, we were unable to determine whether increased prey diversity was a result of turtle foraging behavior or simply due to a larger sample volume from larger turtles. Ecological associations among prey species increase the diversity, and possibly the nutritional quality, of prey items, and periodic meteorological events can also increase the diversity of prey items available to loggerhead turtles. Aspects of the life history of some of these prey organisms, such as continued egg brooding, increase the nutritional value of prey items consumed by juvenile turtles.

KEY WORDS: Loggerhead · *Caretta caretta* · Foraging ecology · Diet · Azores · Sea turtle

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INTRODUCTION

Juvenile loggerhead sea turtles *Caretta caretta* in the oceanic habitats of the eastern North Atlantic derive primarily from nesting populations in the western Atlantic (Bolten et al. 1998). During the oceanic stage, loggerheads are commonly associated with convergence zones, upwellings, major gyre systems, and eddies (Carr 1987a, Musick & Limpus 1997, Santos et al. 2007) that provide productive foraging grounds for young loggerheads by concentrating a variety of planktonic and neustonic organisms. Although much has been learned about this oceanic life stage in the eastern Atlantic (Bolten 2003), which lasts from 7 to 12 yr (Bjorndal et al. 2003), the loggerheads' diet remains poorly quantified. A few general reports (reviewed by Bjorndal 1997) have characterized the diet as primarily carnivorous, with a concentration on

sea jellies. Other dietary components from turtles taken in this region include fish, salps, gastropods, and crustaceans. In the only study that examined nematocysts to identify prey species, van Nierop & den Hartog (1984) reported many siphonophores and fewer scyphomedusae and hydromedusae in 5 juvenile loggerheads from the waters around Madeira, Ilhas Selvagens, and the Azores. Diets of loggerheads in oceanic habitats in the central North Pacific (Bolten & Balazs 1995, Parker et al. 2005) and in the Gulf of Mexico (Plotkin 1996) are composed of similar prey.

In the present study, we quantified the prey items in stomach contents from 12 loggerheads and in the feces from 4 loggerheads collected in the Azores, an archipelago of 9 volcanic islands that spans the mid-Atlantic ridge. A very narrow band of coastal, neritic waters surrounds each island before the waters become very deep (>3000 m). The bathymetry of the region is char-

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acterized by a complex of seamounts and areas of high productivity from upwelling. The area is influenced by the Azorean Current, the easternmost arm of the Gulf Stream. Based on satellite telemetry, loggerheads in this region feed in the epipelagic zone of oceanic habitats (Bolten 2003). Here we identify new prey species and evaluate the relationship between prey diversity and body size.

MATERIALS AND METHODS

Stomachs were removed from 12 dead turtles incidentally captured by fishing operations near the Azores ($n = 8$) and from dead specimens stranded on the shore of Faial ($n = 3$) or floating dead near Faial ($n = 1$; Table 1). All turtles had died recently with no apparent decomposition, and no turtles were killed for this study. Fecal samples were collected from 4 live turtles, captured at the ocean surface using a dip net, that defecated while being measured and tagged before release. Stomach and fecal samples were preserved in 70% ethanol and were later identified to the lowest taxonomic level using a dissecting microscope. Fluids associated with each sample were strained through filter

paper to retrieve nematocysts, and the cnidarian species present were determined under light microscopy (up to 1000 \times). Nematocysts were also scraped from whole tissue and tentacles encountered in some samples, following the methods of Frick et al. (2001).

Stomach and fecal sample contents were analyzed separately because of differences in results between recently consumed diet items (stomach samples) and those that had passed through the digestive tract (fecal samples). Volume of prey items was determined by water displacement in graduated cylinders matched as closely as possible to volume of prey. Frequency of occurrence (F) for each diet taxon was determined by dividing the number of samples containing each diet taxon by the total number of samples examined ($\times 100$). Percent volume by individual (V_{ind}) was calculated by dividing the volume of each diet taxon in a given turtle by the volume of the stomach or fecal sample of that turtle ($\times 100$). Percent total volume (V_t) was calculated for each diet taxon by summing the volume of each diet taxon from all turtles and dividing it by the total volume of all stomach contents collected from all turtles ($\times 100$). V_t is a less useful measure than V_{ind} because information on variance is lost, and differences in sample volumes can bias V_t . We calculated V_t only to allow

Table 1. *Caretta caretta*. Loggerhead turtles from which stomach contents and feces were collected. CCL: curved carapace length; volume: volume of stomach contents or feces; –: data not available

ID number	Date	CCL (cm)	Volume (ml)	Capture method and location
Stomach contents				
86.7.2	2 Jul 1986	–	36.6	Swordfish longline fishery bycatch 80 km North of Faial
P8301	18 Aug 2000	50.5	1151.2	Black scabbard fishery bycatch
P7549	20 Aug 2000	42.7	151.8	Swordfish longline fishery bycatch 38° 3.68' N, 26° 10.10' W
P8475	30 Sep 2000	24.3	43.5	Swordfish longline fishery bycatch 37° 01.13' N, 24° 06.07' W
P8051	23 Sep 2001	32.2	245.0	Swordfish longline fishery bycatch 37° 28.86' N, 24° 38.35' W
P8073	19 Oct 2001	56.0	801.3	Swordfish longline fishery bycatch 37° 47.21' N, 31° 13.62' W
CCA	–	–	789.6	Swordfish longline fishery bycatch
CCB	–	–	1322	Swordfish longline fishery bycatch
CC2	7 Feb 1990	9.3	20.2	Stranded dead, Porto do Alcaide, Faial
CC3	8 Feb 1990	10.5	24.0	Stranded dead, Porto Pim, SE Faial
CC1	25 Jan 1993	10.4	44.8	Stranded dead, Porto Pim, SE Faial
CC4	28 Jun 1992	19.2	11.0	Floating dead, channel between Faial & Pico
Feces				
F6102	12 Jun 1989	13.6	25.7	Dipnetted from research vessel 38° 19.8' N, 28° 59.4' W
F6109	14 Jun 1989	14.6	8.5	Dipnetted from research vessel 38° 4.78' N, 29° 34.89' W
F6110	25 Jun 1989	14.7	10.5	Dipnetted from research vessel 38° 5.8' N, 28° 49' W
BP723	15 Jun 1989	29.8	45.7	Dipnetted from tuna fishing vessel between islands of Faial and Graciosa

comparisons with other studies; we use V_{ind} throughout this paper.

We determined the relative importance of each item in the diets of loggerhead turtles using an index of relative importance (IRI; Bjorndal et al. 1997):

$$IRI = \frac{100(F_i V_i)}{\sum_{i=1}^n (F_i V_i)}$$

where F is the frequency of occurrence of the prey taxon, subscript i refers to the individual sample, V is the mean percent volume in all individual turtles (V_{ind}), and n is the total number of diet taxa.

Relationships between loggerhead body size (curved carapace length, CCL) and number of taxa and volume of stomach contents, as well as between volume of stomach contents and number of taxa, were evaluated with Pearson's product-moment correlations (S-PLUS v. 7.0). Alpha was 0.05.

RESULTS

Twelve stomach samples were collected between July 1986 and October 2001 (Table 1). Nine of the 12 turtles (3 were not measured) ranged in size from 9.3 to 56.0 cm minimum CCL with a mean CCL of 28.3 cm (± 18.0 SD). The volume of stomach samples (Table 1) ranged from 11 to 1322 ml with a mean volume of 386.8 ± 489.2 ml.

Four fecal samples (Table 2) were collected between 12 and 25 June 1989 from turtles ranging in size from 13.6 to 29.8 cm CCL with a mean CCL of 18.2 ± 7.8 cm. The volume of fecal samples (Table 1) ranged from 8.5 to 45.7 ml with a mean of 22.6 ± 17.2 ml.

Loggerheads consumed a variety of food items (Tables 2 & 3). Nine of the species presented in Table 2 represent new diet records for loggerhead turtles. Percent volume for individual prey items in individual stomach samples ranged from 0 to 89% (Table 2). The 8 diet items most often observed in stomach samples ($F \geq 25\%$) were siphonophores, an unidentified cnidarian, glaucid nudibranchs, pelagic gas-

Table 2. *Caretta caretta*. Stomach contents from 12 oceanic-stage loggerhead turtles collected near the Azores. F : frequency of occurrence; V_i : % of the total volume of stomach contents; V_{ind} : % volume by individual; IRI: index of relative importance. See 'Materials and methods' for calculations

Prey item	F (%)	V_i (%)	V_{ind} (%), mean \pm SD (range)	IRI
Cnidaria				
<i>Apolemia uvaria</i>	16.7	4.3	10.5 \pm 25.3 (0–76.5)	5.9
<i>Aurelia aurita</i>	16.7	4.2	1.4 \pm 3.6 (0–11.9)	0.8
<i>Pelagia noctiluca</i>	16.7	2.1	12.2 \pm 29.3 (0–89.1)	6.8
<i>Physalia physalis</i>	25.0	11.1	4.7 \pm 10.6 (0–32.7)	3.9
<i>Porpita porpita</i>	16.7	5.9	1.9 \pm 5.3 (0–18.0)	1.1
<i>Velella velella</i>	41.7	14.9	9.6 \pm 17.8 (0–57.1)	13.4
Unidentified cnidarian (probably <i>Cyanea</i> sp.)	41.7	2.6	4.6 \pm 9.3 (0–31.7)	6.4
Mollusca				
<i>Argonauta argo</i> ^a	8.3	1.8	0.9 \pm 3.1 (0–10.6)	0.3
<i>Cavolinia tridentata</i>	8.3	0.2	0.1 \pm 0.2 (0–0.7)	0.03
<i>Glaucus atlanticus</i> ^a	41.7	3.7	1.9 \pm 2.7 (0–7.3)	2.7
<i>Janthina janthina</i> ^b	33.3	4.9	1.7 \pm 3.1 (0–9.7)	1.9
<i>Pterotrachea hippocampus</i>	8.3	0.1	0.02 \pm 0.1 (0–0.3)	0.01
Arthropoda				
<i>Alepes pacifica</i> ^a	8.3	0.03	0.1 \pm 0.2 (0–0.8)	0.03
<i>Caprella andreae</i> ^a	16.7	0.5	0.2 \pm 0.6 (0–2.2)	0.1
<i>Dosima fascicularis</i> ^a	8.3	0.1	0.2 \pm 0.7 (0–2.2)	0.1
<i>Halobates micans</i>	25.0	0.8	5.7 \pm 12.0 (0–33.1)	4.8
<i>Idotea metallica</i>	8.3	0.02	0.01 \pm 0.03 (0–0.1)	0.003
<i>Lepas anatifera</i>	16.7	8.3	3.4 \pm 8.7 (0–28.7)	1.9
<i>Lepas anserifera</i> ^a	8.3	7.4	2.5 \pm 8.6 (0–29.8)	0.7
<i>Lepas pectinata</i>	8.3	2.2	0.7 \pm 2.6 (0–8.9)	0.2
<i>Phronima sedentaria</i>	8.3	0.1	1.0 \pm 3.4 (0–11.9)	0.3
<i>Plagusia depressa</i> ^a	25.0	3.3	1.3 \pm 2.8 (0–9.4)	1.1
<i>Planes minutus</i>	25.0	1.6	5.1 \pm 15.8 (0–55.1)	4.3
<i>Schistocerca gregaria</i> ^a	8.3	0.5	4.8 \pm 16.5 (0–57.2)	1.3
Chordata				
<i>Caretta caretta</i>	8.3	0.3		0.1
<i>Exocoetus volitans</i> eggs ^a	8.3	0.3		0.8
<i>Pyrosoma atlanticum</i>	16.7	6.0		1.6
Unidentified salp (barrel)	8.3	0.03	0.5 \pm 1.9 (0–6.4)	0.1
Anthropogenic debris	25.0	0.4	3.4 \pm 7.9 (0–25.7)	2.9
Squid bait	33.3	1.7	5.1 \pm 10.1 (0–31.0)	5.7
Unidentified animal material	91.7	8.9	9.8 \pm 6.6 (0–25.4)	30.2
Unidentified plant material	25.0	1.8	0.8 \pm 1.6 (0–5.0)	0.7

^aNew diet record for *Caretta caretta*
^bIncludes egg capsules and snails

Table 3. *Caretta caretta*. Fecal contents from 4 loggerhead turtles collected near the Azores. Abbreviations as in Table 2. See 'Materials and methods' for calculations

Prey item	F (%)	V_i (%)	V_{ind} (%), mean \pm SD (range)	IRI
Cnidaria				
<i>Pelagia noctiluca</i>	25	0.4	1.2 \pm 2.4 (0–4.7)	0.4
Arthropoda				
<i>Lepas anatifera</i>	50	26.7	25.1 \pm 30.5 (0–61.9)	18.2
<i>Plagusia depressa</i>	75	34.2	26.2 \pm 22.5 (0–51.4)	28.4
Unidentified animal material	100	22.0	32.9 \pm 20.7 (10.1–58.8)	47.6
Unidentified plant material	25	16.7	14.7 \pm 29.4 (0–58.8)	5.3

tropods (animals and egg capsules), marine insect egg masses (*Halobates micans*), and oceanic crabs. The 'unidentified cnidarian' listed in Table 2 bears nematocysts strongly resembling *Cyanea*, but does not belong to any *Cyanea* species currently reported from the Azores region. The species in question may have been introduced, but this has yet to be determined. Thus, we report this cnidarian simply as 'unidentified,' but distinct from the other cnidarian species encountered from stomach and fecal samples.

Squid was found in the stomachs of 4 turtles (P7549, P8051, P8073, P8475) that were bycaught in the longline fishery for swordfish, which uses squid as bait (Table 1). Because the squid found in stomachs was clearly bait that had been ingested, we do not consider squid to be a natural diet component based on this study.

Unidentified animal and plant material also had high frequencies of occurrence ($F = 91.7$ and 25.0% , respectively; Table 2), but unidentified animal material never represented more than 25% of the volume of any stomach contents. Unidentified plant material made up only 1, 3, and 5% of the volume of the stomach contents in the 3 turtles P8073, P8301 and CCA, respectively.

Anthropogenic debris ($F = 25\%$) was primarily small pieces of hard plastic, but also included corks, white styrofoam pieces, and neon-colored foam similar to that used as recreational fishing floats (bobbers). All items of anthropogenic debris were covered by fragments of *Halobates micans* eggs and, in 1 case, lepadomorph barnacles. Such incrustations may have attracted turtles to consume anthropogenic debris. In the 3 turtles with anthropogenic debris, 1 had stranded dead (CC1), and 2 were found as bycatch (P7549, 86.7.2) in longline fisheries. Debris ingestion did not appear to be the cause of death of CC1.

IRI values provide a more reliable ranking of the importance of diet items because frequency of occurrence and volume are integrated. For example, in Table 2, *Verella verella* and *Glaucus atlanticus* have the same F value (41.7%), but, because mean V_{ind} are so different, the IRI values are very different (13.4 and 2.7 , respectively).

Fecal analyses yielded fewer prey items and higher volumes of unidentified plant and animal material (Table 3), a result of the transit through the digestive tract.

There were significant positive relationships between the CCL of turtles and the volume of stomach contents ($df = 7$, $r = 0.824$, $p = 0.006$; Fig. 1) and between CCL of turtles and the number of diet taxa in the stomach contents ($df = 7$, $r = 0.762$, $p = 0.017$; Fig. 1). In addition, there was a significant positive relationship between volume of stomach contents and number of diet taxa in the stomach contents ($df = 10$, $r = 0.779$, $p = 0.003$).

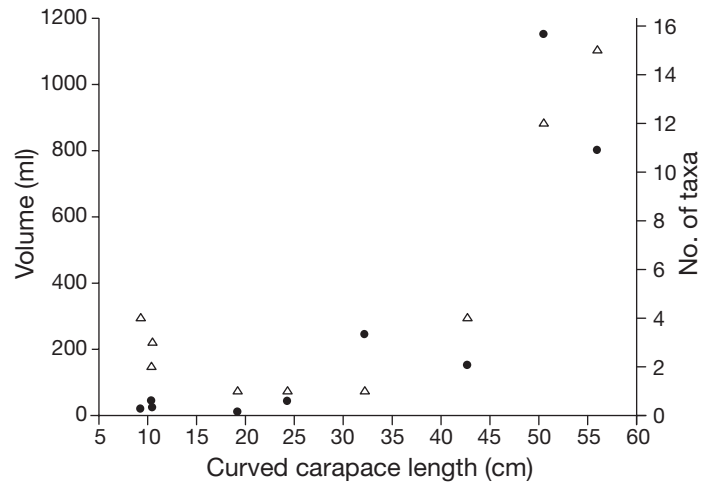


Fig. 1. *Caretta caretta*. Relationship of loggerhead body size (curved carapace length) to volume of stomach contents (●) and number of prey taxa (Δ) in stomach contents

DISCUSSION

Our data indicate that oceanic-stage loggerheads are opportunistic predators, feeding upon a variety of planktonic and neustonic organisms, as well as animals commonly occurring 100 m or more below the surface. IRI values indicate that 4 cnidarians (*Verella verella*, *Pelagia noctiluca*, the unidentified cnidarian, and *Apolemia uvaria*) are the most important dietary resources for the oceanic-stage loggerhead turtles in this study. However, if energy or nutrient concentration are considered, the large quantity of dilute cnidarians may be of less importance in energy and nutrient balance than the smaller quantities of more dense prey (e.g. *Glaucus atlanticus*).

Nine new diet items for loggerhead turtles were encountered in this study. *Glaucus atlanticus* (average length ~25 mm) is a common inhabitant of oceanic habitats in the eastern North Atlantic. It swims upside-down searching for cnidarian prey, particularly *Physalia physalis* and *Verella verella*, but other sea jellies are also consumed (Lalli & Gilmer 1989). The nematocysts of its prey are ingested whole and incorporated into the nudibranch for its defense. Therefore, when nematocysts are used to identify the cnidarians consumed by sea turtles, cnidarian species fed on by *G. atlanticus* may be over-represented in the diet. We were able to identify *G. atlanticus* in the diet of loggerheads because whole or nearly intact specimens were present.

All stomachs containing *Glaucus atlanticus* or *Janthina janthina* (average diameter ~40 mm) also contained sea jellies (nematocysts and associated tissue). Thus, these sea jelly predators may have been con-

sumed incidentally by loggerheads targeting sea jelly species.

Alepas pacifica, an exclusively epizoic lepadomorph barnacle, is also associated with sea jellies. This tiny stalked barnacle is highly modified for pelagic life attached to sea jellies, and it feeds on the tissue of its hosts (Pages 2000). We found *A. pacifica* attached to a scyphozoan, *Pelagia noctiluca*, in the stomach of 1 turtle (P7549). Ingestion of *A. pacifica* was almost certainly incidental to the ingestion of its host.

Another pelagic lepadomorph barnacle previously unknown from the diet of loggerheads is *Dosima fascicularis*. The only cnidarian species to which *D. fascicularis* can attach are those with chitinous floats, such as *Velella* and *Porpita* (Pages 2000). However, this barnacle will also settle upon a variety of other floating objects such as seaweed, snails, and anthropogenic debris. In our study, *D. fascicularis* was attached to a fragment of a wine bottle cork that was also covered with eggs of *Halobates micans*.

Other lepadomorph barnacles consumed were *Lepas anatifera*, *L. anserifera*, and *L. pectinata*. *Lepas* spp. attach to a variety of floating objects and could easily be gleaned from flotsam by loggerheads. Three smaller specimens of *L. anserifera* that had been swallowed whole were ovigerous. Ovigerous prey items provide enhanced nutrition to sea turtles, particularly those like *Lepas* that can begin to reproduce 2 wk after settling (Anderson 1994) and produce multiple broods, year-round, for the life span of the barnacle (Zann & Harker 1978). Thus, a high proportion of *Lepas* consumed by oceanic loggerheads is probably ovigerous. Egg matter may account for some unidentified animal material found in stomachs also containing *Lepas* or any other ovigerous invertebrates.

Also associated with flotsam, and representing new diet records, are the amphipods *Caprella andreae* and the grapsid crab *Plagusia depressa* (megalopa and adults). Both species were always found in stomachs also containing *Lepas* spp. barnacles and pelagic siphonophores (*Physalia*, *Velella*, or *Porpita*), and both have been reported to utilize *Lepas* and siphonophores as clinging substratum (Williams 1984, Foster et al. 2004). Thus, *C. andreae* and *P. depressa* were probably consumed incidentally. The relatively high frequency of occurrence of *P. depressa* (25%) is interesting because *P. depressa* is a non-indigenous species in the Azores (first reported in 1901; Cardigos et al. 2006).

One turtle (86.7.2) contained eggs of the 2-winged flying fish *Exocoetus volitans*, an oceanic species that spawns in areas of upwelling (Grudtsev et al. 1987). The buoyant eggs of this species passively drift within the pelagic environment. Accumulations of these eggs in convergence zones may attract foraging loggerheads; it seems unlikely that single, floating eggs

(diameter ~3 mm) would attract foraging turtles. A total of 28 eggs was found in a single sample, although unidentified material within the same stomach may represent masticated eggs. The same stomach contained eggs of *Halobates micans*, some attached to a 1 × 0.5 cm piece of styrofoam, suggesting that the turtle was foraging upon larger items in an area of convergence where these drifting prey items were concentrated.

The stomach contents from the largest turtle examined in this study (P8073) contained 2 interesting items. One of these was the remains of a small, juvenile loggerhead sea turtle, approximately 10 cm long. To our knowledge, there is only 1 other report of cannibalism in loggerheads: an adult turtle that had consumed a hatchling in South Africa (Dodd 1988).

The other was the remains of a paper nautilus *Argonauta argo*. Shell fragments within the stomach and imbedded into the masticated specimen indicate that the paper nautilus was a mature female. *A. argo* is not a true nautilus but rather a pelagic octopus; females form a paper-thin shell, or egg case, that coils around the octopus (David 1965, Clarke 1986). Argonauts feed upon pelagic mollusks and sea jellies to which they attach themselves while feeding (Heeger et al. 1992). Both prey types were also present within the same stomach sample. Thus, the loggerhead may have intentionally ingested the *A. argo* (85 ml volume) or ingested it by consuming a cnidarian being eaten by the *A. argo*.

One turtle (P8475) contained desert locusts *Schistocerca gregaria*, which represented 57% of the stomach content volume for this individual. Although most specimens were disarticulated, the presence of 7 hind legs (3 left and 4 right) indicates that at least 4 locusts were eaten by this turtle. The desert locust is native to Africa, the Middle East, and southwest Asia (Rosenberg & Burt 1999). Swarms of these insects are occasionally displaced off-shore into the eastern Atlantic by trade-winds, tropical waves, or hurricanes. In 1988, a swarm was reported to have utilized persistent trade-winds to invade areas as far west as the Caribbean and South America (Rosenberg & Burt 1999). Northward invasions into Europe are not uncommon, so it is not surprising that some individuals are displaced into the waters surrounding the Azores. Terrestrial insects have been reported in the stomachs of post-hatchling loggerheads off the coast of the southeast USA (Dodd 1988, Richardson & McGillivray 1991, Witherington 2002), indicating that windborne displacement is also a likely mechanism contributing to the diversity of prey items consumed by loggerheads in the western North Atlantic.

The significant, positive relationships of CCL to stomach content volume and prey diversity and of

stomach content volume to prey diversity raise the question of whether larger turtles actually have a more diverse diet, or whether the greater diversity in large turtles was simply a result of the larger volume of stomach contents from larger turtles. The former may well be true because larger turtles can consume larger prey items and may forage over a greater range of water depths. However, smaller turtles may feed on prey species smaller than the prey range of larger turtles. The possibility that greater diet diversity in large turtles was simply a result of the larger volume of stomach contents cannot be discounted; more stomach content analyses from a wide size range of turtles are needed.

The presence of marine debris in 3 of the 12 stomachs that we examined confirms the threat of debris to oceanic loggerheads that was first addressed by Carr (1987b). Ingestion of marine debris is a widespread and continuing problem (see review by Tomás et al. 2002).

Our conclusions are limited by the small sample size. Attempts to increase the sample size through esophageal lavage were not successful. Lavage is a difficult technique to employ with sea jelly consumers. The water stream can disintegrate the sea jelly prey, and retrieving nematocysts from the fairly large quantities of water required to flush the esophagus is challenging. Greater effort should be made to obtain stomachs from turtles killed as bycatch in fisheries.

Our study indicates that oceanic-stage loggerheads are opportunistic carnivores that feed upon a variety of oceanic and pelagic organisms. Ecological associations among prey species increase the diversity, and possibly the nutritional quality, of prey items. Additionally, periodic meteorological events are also responsible for increasing the diversity of prey items available to loggerheads. Aspects of the life history of some of these organisms, such as nearly continual egg-brooding, may increase the nutritional value of prey items consumed by juvenile turtles. Loggerheads from the Azores region exploit novel food resources, such as non-indigenous species. Some of the species reported here as prey are also known to be epibionts on loggerheads in these habitats (Frick et al. 2003, 2004). The complexities of these inter-species interactions should be further explored.

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