JELLYFISH BLOOMS

Effects of El Niño-driven environmental variability on black turtle migration to Peruvian foraging grounds

Javier Quiñones · Victoria González Carman ·
Jorge Zeballos · Sara Purca · Hermes Mianzan

Abstract We analyzed sea temperature as an environmental factor, in association with ENSO, affecting the migration of East Pacific black turtle, *Chelonia mydas* (=*Chelonia agassizii* Bocourt), to its foraging areas and its feeding ecology at San Andrés, Peru. A 19-year sea turtle landing database (1970–1988) was constructed to associate landing fluctuations with environmental variability represented by the Peruvian Oscillation Index. A positive correlation between them ($r = 0.75$, $P < 0.05$) indicated that exceptionally large black turtle landings occurred in San Andrés port during El Niño episodes. Warmer waters (SST 22–28°C) approached near the Peruvian coast during El Niño episodes, thus facilitating black turtle access to this area. Furthermore, during El Niño 1987, large juvenile and adult black turtles, known to be primarily herbivorous, fed mainly on the scyphozoan jellyfish *Chrysaora plocamia* Péron & Lesueur, which was very abundant during this event. It is likely that black turtles exploited this resource opportunistically. Inter-annual environmental variability, driven by El Niño Southern Oscillation, has profound consequences for the ecology of the endangered black turtle, which should be considered when evaluating the effects of anthropogenic activities on its population dynamics.

Keywords *Chelonia mydas* (=*Chelonia agassizii*) · ENSO · Trophic migration · Jellyfish · Sea turtle landings · Peru

J. Quiñones · J. Zeballos
Laboratorio Costero de Pisco, Instituto del Mar del Perú
(IMARPE), Av. Los Libertadores A-12, Urb. El Golf,
Paracas, Ica, Peru
e-mail: javierantonioquinones@gmail.com

V. González Carman · H. Mianzan (✉)
CONICET-Instituto Nacional de Investigación y
Desarrollo Pesquero (INIDEP), Paseo Victoria Ocampo
n°1, B7602HSA Mar del Plata, Argentina
e-mail: hermes@inidep.edu.ar

S. Purca
Centro de Investigaciones en Modelaje Oceanográfico y
Biológico-Pesquero (CIMOBP), Instituto del Mar del Perú
(IMARPE), Esquina Gamarra y General Valle s/n
Chucuito, Callao, Peru

Introduction

The coastal ecosystem off Peru and Chile is characterized by strong, persistent wind-driven upwelling of nutrient-rich waters. This upwelling sustains high biological productivity and supports one of the world's largest single-species fisheries (Chavez et al., 1999, 2008; Pennington et al., 2006). Oceanographic and atmospheric conditions fluctuate on seasonal to inter-decadal scales (Wyrtki, 1975; Tourre et al., 2005). Among such variations, inter-annual variability due to the El Niño Southern Oscillation (ENSO) is known to affect physical, chemical, and

nutritional conditions of the ocean (Fiedler et al., 1991; Chavez et al., 1999; Ayón et al., 2004). During an ENSO, the equatorial zonal winds weaken, thus driving an upwelling of warmer waters due to a deeper-than-normal main thermocline (Ji & Leetmaa, 1997). Biological responses to this phenomenon are exhibited by a wide variety of organisms. For example, primary production is severely reduced (Barber & Chavez, 1983) and large amounts of benthic macroalgae wash ashore during the strongest ENSO (i.e., 1982–1983). The latter affects the related benthic and grazing fauna (Tarazona et al., 1988; Arntz & Fahrbach, 1996; Fernandez et al., 1999). Furthermore, anchovy (*Engraulis ringens* Jenyns) concentrates in shallower refuge waters (Csirke, 1989; Muck et al., 1989a; Arntz & Fahrbach, 1996) where a large die off occurs due to a drastic habitat reduction (Bertrand et al., 2004). In addition, there is high mortality of top predators like seabirds (i.e., *Phalacrocorax bougainvilli* Lesson and *Sula variegate* Tschudi) and marine mammals (i.e., *Otaria byronia* Shaw) due to limited food availability (Arntz & Fahrbach, 1996; Jahncke et al., 2004). Such examples demonstrate how marine organisms off Peru and Chile respond to ENSO; however, there are few examples of how sea turtles respond.

The black turtle, *Chelonia mydas* (=*Chelonia agassizii* Bocourt), is distributed along the west coasts of North and South America. Main nesting grounds are at Michoacan (Mexico), the Galapagos Archipelago (Ecuador), and the Revillagigedos Islands (Mexico). Coastal primary foraging areas range from San Diego Bay (USA) to Mejillones (Chile) (Marquez, 1990). The feeding ecology of this species, which is widely accepted to be herbivorous, has been studied along most of its distribution. Macroalgae and seagrass were reported in the diet of turtles from Bahía de Los Angeles and Bahía Magdalena (Baja California, Mexico) (Seminoff et al., 2002). A more omnivorous diet, based mainly on algae but with an additional wide variety of animals, such as crustaceans, fish eggs, mollusks, and, to a lesser extent, jellyfish were recorded in turtles from Bahía de Sechura and San Andrés-Pisco (Paredes, 1969; Hays-Brown & Brown, 1982; de Paz et al., 2004; Kelez et al., 2004; Santillán Corrales, 2008). Because the effects of ENSO on marine organisms are seen at several levels of the food web, black turtle diet could change with respect to

non-ENSO years; however, the feeding ecology of this species has never been studied in relation to ENSO.

For several sea turtle species, oceanographic conditions at their foraging grounds prior to the nesting season determine their probability of nesting (Broderick et al., 2001; Wallace et al., 2006; Saba et al., 2007, 2008a, b). Within the large black turtle foraging area, it is reasonable to expect that events like ENSO could greatly affect their migration and foraging ecology; however, few reports are available that refer to ENSO-driven conditions on black turtle reproductive ecology (Hurtado, 1984; Zárate, 2003). Most recently, Seminoff et al. (2008) showed that black turtle migrations from the Galapagos to their foraging grounds are restricted by sea surface temperature (SST) $\leq$24–25°C; they suggested that periods of elevated SST (i.e., ENSO) could facilitate access of this species to its foraging habitats along the coast of South America. It is known that during ENSO, warmer waters (>22°C) reach the coast of South America (Wang, 1995), and in this scenario, sea turtle approach to the coast of Peru could be favored. This species might respond to environmental variability driven by ENSO, at least on its nesting grounds and possibly on its migration to foraging areas, but no conclusive evidence has been presented yet.

In Peru, sea turtles have been consumed by men since the pre-Hispanic era (Frazier & Bonavia, 2000). A traditional sea turtle fishery, with a well-developed trade along the southern coast (Hays-Brown & Brown, 1982), existed until 1995 when this fishery was banned (Morales & Vargas, 1996); however, some turtle carapaces are found sporadically on dump sites, suggesting that some captures still occur (Quiñones, pers. obs.). San Andrés was recognized as the main locality of this fishery (Fig. 1) (Aranda & Chandler, 1989; Vargas et al., 1994), while other Peruvian ports did not have fishermen specializing on turtle harvesting (Frazier, 1979). This fishery was artisanal, operating mostly during summer and early fall (Frazier, 1979; Hays-Brown & Brown, 1982). Shore-based boats of 4–8 m with engines of 25–40 HP were employed (Frazier, 1979; Pinedo, 1988). They used tangle-nets of different sizes and mesh, some of which were designed specifically to catch turtles (Frazier, 1979; Hays-Brown & Brown, 1982). In San Andrés port, sea turtle landings showed high inter-annual fluctuations, with some years having
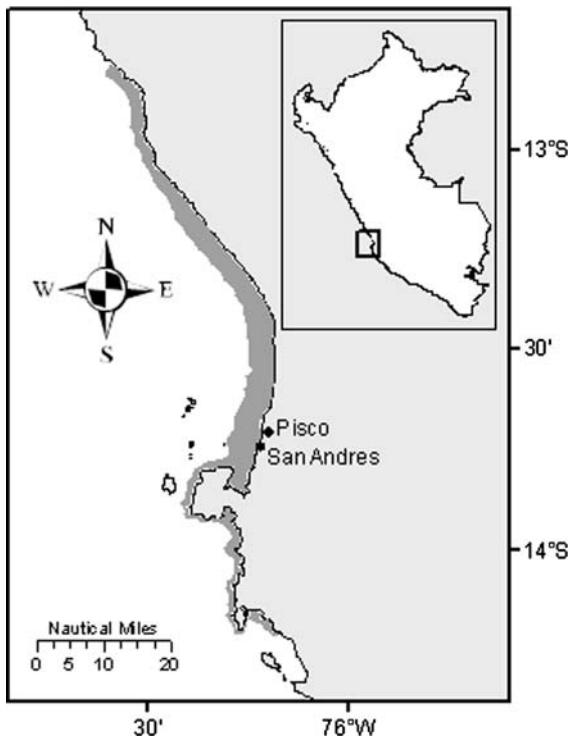
Fig. 1 Study area off the coast off Peru. Fishing grounds of the San Andrés turtle fishery during 1970–1988 are shown in *dark gray*

very large landings and other years having almost none. El Niño (EN), the warm phase of the ENSO, is believed to play an important role in this inter-annual fluctuation.

In this study, we tested the hypothesis that environmental variability, driven by EN, may favor black turtle trophic migration to the San Andrés foraging ground. Because sea turtles are ectotherms, their distribution is restricted by sea temperature (Polovina et al., 2004; Wallace & Jones, 2008). Consequently, it is reasonable to expect that black turtle trophic migration to the San Andrés foraging ground is facilitated during warm events like EN and that their occurrence would increase. We used published data on the EN index and SST isotherms and constructed a sea turtle landing database for the local turtle fishery. Thus, historical records of sea turtle landings allowed us to study the response of this species to EN during a 19-year period. In addition, because black turtles migrate to Peruvian coastal waters to feed mostly on macroalgae (de Paz et al., 2004; de Paz & Alfaro Shigeto, 2008; Kelez

et al., 2004), and because the whole system of marine organisms (including macroalgae) responds to EN, we examined the stomach contents of black turtles landed in San Andres during one EN episode to determine if its diet was altered, potentially reflecting changes in food availability. Paradoxically, the information on sea turtle commercial landings served to improve our understanding of the effect of EN-driven environmental variability in the trophic migration of the endangered black turtles and also may provide the foundations for conservation of the species in the East Pacific Ocean.

Materials and methods

In this study, environmental variability driven by EN was represented by the Peruvian Oscillation Index (POI) and SST isotherm location along the Peruvian coast. To correlate these environmental indices with black turtle migration toward southern Peru, we used historical sea turtle fishery landings recorded in San Andrés from 1970 to 1988. Landings were used as a proxy of turtle occurrence and migration to this area. Then, to analyze if food availability also was altered by EN, diet analysis was performed on some of the turtles landed during EN 1987.

Environmental context

ENSO index

The official Oceanic Niño Index (ONI) is the SST of NIÑO 3.4 area (5–5°S, 170–140°W). This oceanic index does not necessarily reflect warming events restricted to the Peruvian coast, so the first principal component of SST of Peru, known as the POI, was considered to be more appropriate for this study. It was calculated from the means of monthly average SST during a 50-year time series (1950–1999) measured at five coastal stations along the Peruvian coast. Therefore, the POI best represents the coastal SST variation in Peru and is positively correlated with other indexes of EN and the Pacific Decadal Oscillation, thus reflecting conditions in the East Tropical Pacific region (Montecinos et al., 2003). In this study, monthly POI data were averaged by year and plotted with phases of EN episodes according to the ONI (onset = −1, peak = 0, and offset = +1)

and to warm events for the period 1970–1988. An EN episode is different from a warm event because an EN episode originates in the Central Pacific, while a warm event could originate in the East or West Pacific, and its effect is local.

SST isotherms

To illustrate the approach of warmer waters toward the San Andres foraging ground, the location of SST isotherms during EN episodes (1972, 1982–1983, and 1987) and a non-ENSO episode (1981) were plotted. We chose 1981 as a typical non-ENSO episode because the POI index was almost neutral throughout that year. SST isotherm maps were constructed based on previous works of Anónimo (1972), Zuta et al. (1984), Urquizo et al. (1987), Rivera (1988), and Muck et al. (1989b). For EN episodes of 1972, 1982–1983, and 1987, isotherms from March were represented. In 1981, only an average of the SST isotherms for January, February, and March was available.

Sea turtle landings

A sea turtle landing database for the San Andrés fishery was constructed using published data and interviews conducted for this study. Published data included monthly landings from 1970 to 1988 (Wosnitza-Mendo et al., 1988; Aranda & Chandler, 1989; Flores et al., 1994, 1998). Because landing reports for 1982–1983 were not reliable for the area, interviews with 32 San Andrés turtle fishermen, which represented 50% of all fishermen for 1982–1983, were conducted from April to July 2009. Data recorded during the interviews included the numbers of boats, days, trips, turtles landed, season, area fished, and turtle behavior. Sea turtle landings (L, in tons) for the years 1982–1983 were calculated as follows:

$$L = a * b * c * d/1000$$
$$a = x/z$$

where a is the mean effective fishing period calculated as the mean fishing period (x, in d) divided by mean trip duration (z, in d). Parameter b is the mean number of fishing boats, c is the mean number of turtles captured per boat, and d is the average turtle

weight (in kg) obtained from 1987 landings. To obtain an L value in tons, d was divided by 1000.

There were some limitations of this database. First, no species identification was available; however, it was known that 90% of the turtles landed corresponded to the black turtle (Aranda & Chandler, 1989) and was confirmed by our interviews. Second, monthly resolution could not be assessed in fishermen interviews, so L values plotted for 1982–1983 are not means. Finally, because of the artisanal nature of the San Andrés fishery, a reliable measure of fishing effort based on the number of fishing boats or fishing trips could not be established; therefore, we used the total landings in our analyses.

Sea turtle diet

Dead black turtles landed were recovered from San Andrés port from March to September 1987. Because diet varies throughout the sea turtle life history, curved carapace length (CCL), measured from the middle nucal scute to the posterior middle between supracaudal scutes, and weight were recorded. Adult and juvenile turtles were distinguished according to the minimum breeding size of CCL 60.7 cm for the Galapagos rookery (Zárate, 2003). Necropsies were performed on some of the turtles landed. Esophagus and stomachs were retrieved and immediately transported to the laboratory, where diet samples were analyzed. Prey items were identified to the lowest possible taxon. Plant matter, mollusks, fish, crustaceans, and jellyfish were identified according to Dawson et al. (1964), Alamo & Valdivieso (1987), Chirichigno (1974), Retamal (1981), Bowman & Gruner (1973), Brusca (1981), Stiasny (1937), and Mianzan & Cornelius (1999).

Data analysis

To test for association between EN and sea turtle occurrence and migration toward San Andrés foraging ground, a Spearman correlation was carried out between sea turtle landings and the POI. A type I error (α) of 0.05 was considered significant.

Quantitative assessment of diet was based on the frequency of occurrence (FO) of each diet item and its relative wet weight (WW) in each sample was calculated as follows:

Fig. 2 Historical series of
sea turtle landings for the
San Andrés turtle fishery
during 1970–1988.
Correlation between the
POI anomalies and sea
turtle landings in tons was
statistically significant.
Warm events and EN
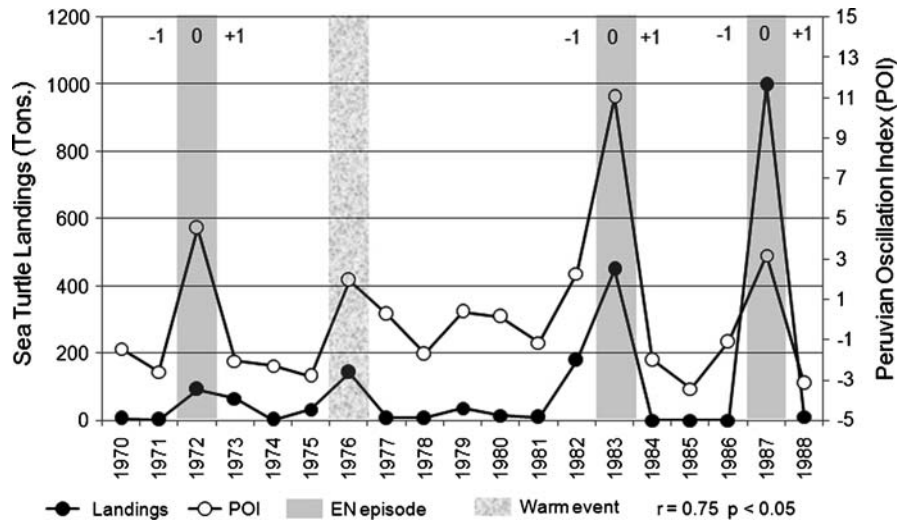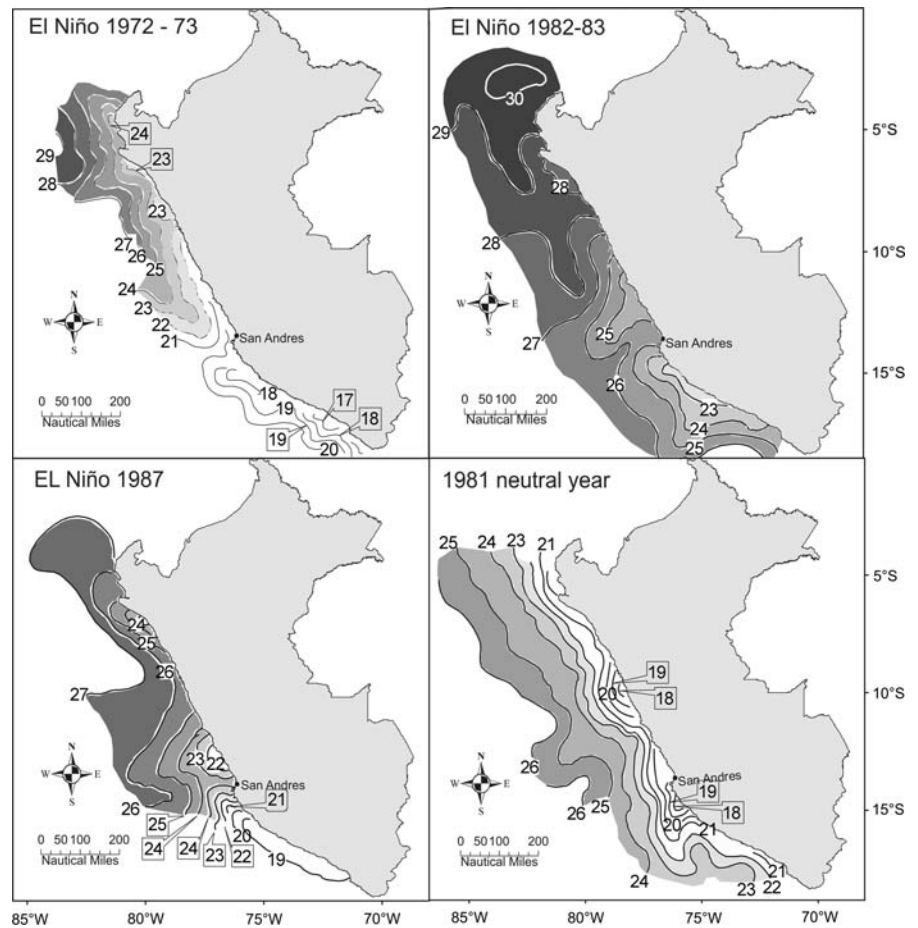phases (−1, 0, +1) are
indicated by *gray shading*

Fig. 3 SST isotherm
locations during EN
episodes **a** 1972–1973, **b**
1982–1983, **c** 1987, and
during a neutral year **d**
1981. Warmer waters can
be seen near the coast of
Peru during EN episodes

$$\%FO = (\text{number of samples in which diet item observed/total samples}) * 100$$

$$\%WW = (\text{wet weight of a diet item/total weight of all items}) * 100.$$

Results

POI, SST, and sea turtle landings

During a 19-year period, the POI varied inter-annually from a maximum of +9.54 to a minimum of −2.99. During this period, three EN episodes were observed; two strong EN occurred in 1972–1973 and 1982–1983 with POI anomalies of +4.43 and +9.36, respectively, and a moderate EN occurred in 1986–1987 with a maximum anomaly of +4.23. In addition, a warm event occurred during 1975–1976 with a maximum anomaly of +2.9 (Fig. 2).

Sea turtle landings in San Andres also increased during EN episodes and the warm event (Fig. 2). Maximum catches were more than 90, 400, and 900 tons in EN 1972–1973, 1982–1983, and 1987, respectively, and 142 tons for the warm event of 1976. POI and sea turtle landings were significantly positively correlated ($r = 0.749$, $P = 0.0002$) during the 19-year period.

Warm-water intrusions (22–28°C) approached near the coast and reached San Andrés and other southern Peruvian areas in every EN during the 19-year period (Fig. 3a–c). In contrast, during the typical summer 1981, warm waters (22–26°C) remained approximately 100 nautical miles off the Peruvian coast (Fig. 3d).

Black turtle diet

From a total of 998 black turtles measured in San Andrés in 1987; 76% of the turtles were of adult size (Fig. 4). Food items in the stomach and esophagus of 192 of those turtles were analyzed: Jellyfish was the prey item most frequently consumed (70.8%), followed by mollusks (62.0%), crustaceans (47.4%), and macroalgae (37.5%). Anthropogenic debris, especially those made of plastic, also was consumed frequently (41.7%; Table 1).

In addition to being the most frequently consumed prey item, jellyfish represented the highest mean WW (49.5%), which was followed by mollusks (17.0%)
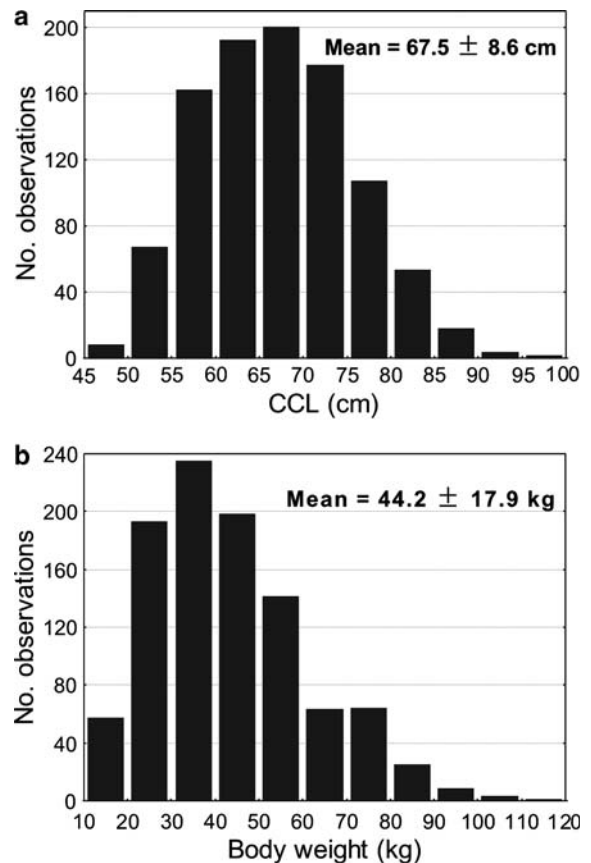

Fig. 4 **a** Curved carapace length and **b** body weight of black turtles, *C. mydas* (=*C. agassizii*), landed in San Andrés during EN 1987

and macroalgae (13.2%). Jellyfish represented ≥75% of gut content WW for more than 40% of the turtles analyzed (Table 1). The only jellyfish consumed was *Chrysaora plocamia* Péron & Lesueur (Scyphozoa). Jellyfish found in diet samples appeared as pieces and as partly digested liquefied jellyfish. Because of the coloration and consistency, this material could be identified as *C. plocamia*. "Other" items included all organic materials (i.e., pieces of wood, land plants, etc.) and stones that probably were consumed when the turtles ate other prey items. Among mollusks, *Donax marincovichi* Coan was consumed most frequently (67%). *Macrocystis pyrifera* Linnaeus was the most consumed macroalga (97%). Almost all crustaceans (99.9%) were amphipods, *Hyperia* sp. Latreille, which probably were living in, and were consumed with, the jellyfish. Finally, annelids, fishes, sponges, and echinoderms were considered to be

Table 1 Mean percent sample wet weight (%WW) and frequency of occurrence (%FO) of prey groups recovered in esophagus and stomach samples from black turtles *C. mydas* (=*C. agassizii* Bocourt) in San Andrés

Diet item	%W		%FO			
	Mean	SD	Present	≤5%WW	≥50%WW	≥75%WW
Jellyfish *Chrysaora plocamia*	49.5	41.2	70.8	32.3	53.1	41.7
Mollusks[a]	17.0	29.0	62.0	62.0	14.6	8.3
Crustaceans[b]	3.3	10.4	47.4	85.9	1.6	0.5
Anthropogenic debris	10.7	22.9	41.7	71.9	9.9	4.2
Macroalgae[c]	13.2	26.6	37.5	69.3	12.0	6.3
Others	2.9	10.3	36.9	88.5	1.6	1.0
Unknown	0.4	3.4	6.25	100	–	–
Annelids *Diopatra* sp. Audouin & Milne-Edwards	0.6	5.9	3.6	99.0	0.5	0.5
Fishes[d]	0.3	2.8	4.2	98.4	–	–
Sponges	T	–	1.0	100	–	–
Echinoderms *Ophiectis kröyeri* Lütken	T	–	0.5	100	–	–

T denotes presence in trace levels, *SD* standard deviation

[a] *Mulinia edulis* King & Broderip, *Donax marincovichi* Coan, *Nassarius gayi* Kiener, *Discinisca lamellosa* Broderip, *Semimytilus algosus* Gould, *Crepipatella dilatata* Lamarck, *Aulacomya ater* Molina, *Tegula atra* Lesson, *Polinices otis* Broderip & Sowerby, *Fisurella peruviana* Lamarck, *Sinum cymba* Menke

[b] *Hyperia* sp. Latreille, *Ceratothoa gaudichaudii* Milne-Edwards, *Balanus* sp. Da Costa, *Hepatus chilensis* Edwards, *Lepas anatifera* Linnaeus, *Cancer porteri* Rathbun

[c] *Macrocystis pyrifera* Linnaeus, *Rhodymenia flabellifolia* Montagne, *Ulva costata* Howe, *Chondracanthus chamissoi* Kützing, *Gracilariopsis lemaneiformis* E. Y. Dawson, Acleto & Fold

[d] *Engraulis ringens* Jenyns, *Gaelichthys peruvianus* Lütken, *Schroederichthys chilensis* Guichenot

trace items because each group constituted <1%WW and ≤5%FO (Table 1).

Discussion

In this study, we present consistent evidence that warm episodes, including EN, favor black turtle trophic migration to southern Peruvian foraging grounds. High black turtle landings occurred during every EN and warm event observed from 1970 to 1988 (Fig. 2). Since turtles were the target species of this specialized fishery, an increase in sea turtle landings may reflect an increase in sea turtle occurrence during their migration to San Andrés. In fact, abundances of sea turtles changed from being considered a rare visitor most of the time to become common during EN episodes on Peruvian coasts (Arntz & Fahrbach, 1996). Landings alone, however, may not reflect sea turtle abundance because the fishing effort would vary.

The scarce literature on the San Andrés fishery revealed that since 1979, the turtle fleet contained 7–11 boats (see Frazier, 1979; Hays-Brown & Brown, 1982; Aranda & Chandler, 1989), indicating that the fishing effort was fairly consistent. Opportunistic fishermen might have fished during EN, probably because the other fishing resources declined. During EN 1987, up to 110 boats were recorded to land turtles in San Andrés (Zeballos, pers. obs.), encompassing the largest sea turtle harvest ever recorded in Peru (Aranda & Chandler, 1989). That year, however, about 14 boats (about the usual fleet size) captured up to 50% of the turtles during 50% of the total fishing trips reported, which suggests that even if the landings by the opportunistic boats are disregarded, very high sea turtle landings occurred during that EN episode (Zeballos, pers. obs.).

Among the various physical and biological factors that might be involved in the high black turtle occurrences in Peruvian coastal waters during EN

Table 2 Summary of diet studies on the black turtle along its distribution in the East Pacific

References	Location	N	Sampling year	Frequency of occurrence (%FO)		
				Algae	Jellyfish	Others
Seminoff et al. (2002)	Mexico, Baja California	108	1995–1999	Chlorophyta >24% Phaeophyta >19% Rhodophyta 100%	No	Overall animal matter was 38.5–42.8%
Amorocho & Reina (2007)	Colombia	84	2003–2004	18%	No	Tunicates 74% Mangrove 69% Crustaceans 63%
Paredes (1969)	Peru, San Andrés-Pisco	20	1969	100%	Unident. 60%	Mollusks 50% Fish eggs 60% Crustaceans 25%
Hays-Brown & Brown (1982)	Peru, San Andrés-Pisco	39	1979	51%	Unident. 31%	Mollusks 64% Polychaetes 49% Crustaceans 13%
Kelez et al. (2004)	Peru, San Andrés, and Chimbote	3	2000	100%	Unident. 33%	Mollusks 67%
de Paz et al. (2004)	Peru, San Andrés	13	1999–2000	43%	No	Mollusks 29%
Santillán Corrales (2008)	Peru, Bahía de Sechura	NR	2002–2004	>33%	Hydrom. 13%	Squid eggs 22%

NR not reported, N number of turtles analyzed, *unident.* unidentified, *hydrom.* hydromedusae

episodes, we focused on sea temperature. During average years, the west coast of South America is characterized by upwelling of cold subsurface waters (Brink et al., 1983), but during EN episodes, warmer waters propagate poleward along the entire coastlines of Peru and Chile (Hormazabal et al., 2001), as shown by SST fields with cold water extending 100 km offshore of the Peruvian coast in 1981, but warm waters >22°C reaching the San Andrés coast during EN 1982–1983 and 1987. Because the POI is calculated from SST data along the coast of Peru (i.e., Montecinos et al., 2003), it follows that temperature plays a key role determining sea turtle migration. Our results strongly support the idea that warm waters near the shore facilitate black turtle access to the San Andrés foraging grounds (Fig. 3).

Previous work on black turtle diet throughout its distribution showed that macroalgae were consumed most frequently, in combination with several invertebrate species, including jellyfish, to a lesser extent (Table 2). No previous study considered dietary preferences related to ENSO. During EN, primary productivity decreases triggering changes throughout the food web (Barber & Chavez, 1983; Muck et al., 1989a; Arntz & Fahrbach, 1996). Because benthic

macroalgae washes ashore during strong EN events (Arntz & Fahrbach, 1996), that food resource probably is limited during EN events, and thus, may affect the turtle's diet. During EN 1987 as reported here, 70.1% of black turtles fed on the large jellyfish *C. plocamia* and only 37.5% fed on macroalgae. Moreover, of the turtles feeding on *C. plocamia*, more than 40% had a stomach full (≥75%WW) of this species (Table 1). During La Niña episodes (i.e., 1999–2001 with negative POI values) and even during neutral or mild EN episodes (1979 and 2002–2003 with a maximum POI of +1.5), turtles probably have an omnivorous diet based mostly on macroalgae with some jellyfish consumed (see Fig. 2 and Table 2). Conversely, during moderate to strong EN episodes (1969, maximum POI of +3.2), jellyfish may predominate in the diet. To test this hypothesis, further research on black turtle diet during EN episodes is needed.

Jellyfish are not trophic dead ends (Mianzan et al., 2001; Arai, 2005), as they are often mistakenly thought to be. Jellyfish have four to six times less gross energy than algae and seagrass (Doyle et al., 2007); however, some of the largest marine vertebrates like the leatherback sea turtle and the oceanic

sunfish, *Mola mola* Linnaeus, survive on diets mostly of jellyfishes (Arai, 2005; Houghton et al., 2006; Wallace et al., 2006). For those species, prey quantity probably prevails over quality, as for large terrestrial herbivores (Shrader et al., 2006; Doyle et al., 2007). Interestingly, initial analysis of concurrent jellyfish data suggests that their occurrences may be positively correlated with black turtle landings and EN episodes (Quiñones et al., in prep.). If jellyfishes are most abundant during EN episodes, sea turtles could exploit that resource opportunistically, as in EN 1987.

Most adult turtles foraging in coastal Peruvian waters come from their nesting beaches on the Galapagos Islands and, to a lesser extent, on the mainland of Ecuador (Green, 1984; Aranda & Chandler, 1989). Because both nesting and sea turtle fishing seasons occur from summer to early fall in these latitudes (Aranda & Chandler, 1989), adult turtles feeding in Peru probably do not reproduce that same year in the Galapagos Islands. In fact, during EN 1982–1983 and the warm event of 1975–1976, fewer turtles nested in the Galapagos than in non-EN years (Zárate, 2003). Although nesting records are not complete for the period 1970–1988, the numbers of turtles nesting in the Galapagos (apparently driven by EN) were opposite to the numbers landed in the San Andrés foraging ground. Furthermore, during EN 1987, and possibly during every EN between 1970 and 1988, adult-sized black turtles were captured in southern Peru to the detriment of Galapagos nesting population. Additional research is needed to understand how physical and biological factors governed by ENSO drive the ecology of endangered species like black turtles. The effects of environmental factors need to be considered in combination with the effects of anthropogenic factors, such bycatch or direct capture mortality, on sea turtle population dynamics.

References

Alamo, V. & V. Valdivieso, 1987. Lista sistemática de moluscos marinos del Perú. Boletín Instituto del Mar del Perú & Deutsche Gesellschaft füf Technische Zusammenarbeit, Volumen Extraordinario, Callao, Perú: 1–205.

Amorocho, D. F. & R. D. Reina, 2007. Feeding ecology of the East Pacific green sea turtle *Chelonia mydas agassizii* at Gorgona National Park, Colombia. Endangered Species Research 3: 43–51.

Anónimo, 1972. Cartas promedio de temperatura superficial del mar en Marzo, Abril, Mayo y Junio de 1972, Vol. 109. Serie de informes especiales del Instituto del Mar del Perú, Callao: 1–15.

Arai, M. N., 2005. Predation on pelagic coelenterates: a review. Hydrobiologia 451: 523–536.

Aranda, C. & M. Chandler, 1989. Las tortugas marinas del Perú y su situación actual. Boletín de Lima 62: 77–86.

Arntz, W. E. & E. Fahrbach, 1996. El Niño experimento climático de la naturaleza, causas físicas y efectos biológicos. Fondo de Cultura Económica, México: 1–311.

Ayón, P., S. Purca & R. Guevara-Carrasco, 2004. Zooplankton volume trends off Peru between 1964 and 2001. ICES Journal of Marine Science 61: 478–484.

Barber, R. T. & F. P. Chavez, 1983. Biological consequences of El Niño. Science 222: 1203–1210.

Bertrand, A., M. Segura, M. Gutierrez & L. Vásquez, 2004. From small-scale habitat loopholes to decadal cycles: a habitat-based hypothesis explaining fluctuation in pelagic fish populations off Peru. Fish and Fisheries 5: 296–316.

Bowman, T. E. & H. E. Gruner, 1973. The families and genera of *Hyperiidea* (Crustacea: Amphipoda). Smithsonian Contributions to Zoology 146: 1–64.

Brink, K. H., D. Halpern, A. Huyer & R. L. Smith, 1983. The physical environment of the Peruvian upwelling system. Progress in Oceanography 12: 185–305.

Broderick, A. C., B. J. Godley & G. C. Hays, 2001. Trophic status drives interannual variability in nesting numbers of marine turtles. Proceedings of the Royal Society 268: 1478–1481.

Brusca, R. C., 1981. A monograph on the isopoda Cymothoidae (Crustacea) of the eastern Pacific. Zoological Journal of the Linnean Society 73: 117–199.

Chavez, F. P., P. G. Strutton, G. E. Friederich, R. A. Feely, G. C. Feldman, D. G. Foley & M. G. McPhaden, 1999. Biological and chemical response of the equatorial Pacific Ocean to the 1997–1998 El Niño. Science 286: 2126–2131.

Chavez, F. P., A. Bertrand, R. Guevara-Carrasco, P. Soler & J. Csirke, 2008. The northern Humboldt current system: brief history, present status and a view towards the future. Progress in Oceanography 79: 95–105.

Chirichigno, N., 1974. Clave para identificar los peces marinos del Perú, Vol. 44. Informe Instituto del Mar del Perú, Callao: 1–388.

Csirke, J., 1989. Changes in the catchability coefficient in the Peruvian anchoveta (*Engraulis ringens*) fishery. In Pauly, D., P. Muck, J. Mendo & I. Tsukayama (eds), The Peruvian Upwelling Ecosystem: Dynamics and Interactions, Vol. 18. ICLARM Studies and Reviews, Manila: 207–219.

Dawson, E. Y., C. Acleto & N. Foldvik, 1964. The seaweeds of Perú. Nova Hedwigia 13: 1–111.

de Paz, N., J. C. Reyes & M. Echegaray, 2004. Capture and trade of marine turtles at San Andres, Southern Peru. In Coyne, M. S. & R. D. Clark (eds), Proceedings of the Twenty-First Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS–SEFSC-528: 52–54.

de Paz, N. & J. Alfaro Shigeto, 2008. Foraging grounds for sea turtles in inshore Peruvian waters. In Kalb, H., A. Rhode, K. Gayheart & K. Shanker (eds), Proceedings of the Twenty-Fifth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-582: 1–118.

Doyle, T. K., J. D. R. Houghton, R. McDevitt, J. Davenport & G. C. Hays, 2007. The energy density of jellyfish: estimates from bomb-calorimetry and proximate-composition. Journal of Experimental Marine Biology and Ecology 343: 239–252.

Fernandez, E. C., C. Cordova & J. Tarazona, 1999. Condiciones del bosque submareal de Lessonia trabeculata en la Isla Independencia durante el evento El Niño 1997–1998. In Tarazona, J. & E. Castillo (eds), El Niño 1997–98 y su impacto sobre los ecosistemas marino y terrestres. Revista Peruana de Biología, Volumen Extraordinario, Lima: 47–59.

Fiedler, P. C., V. Philbrick & F. P. Chavez, 1991. Oceanic upwelling and productivity in the eastern tropical Pacific. Limnology and Oceanography 36: 1834–1850.

Flores, M., S. Vera, R. Marcelo & E. Chirinos, 1994. Estadísticas de los desembarques de la pesquería marina Peruana 1983–1992, Vol. 105. Informe Instituto del Mar del Perú, Callao: 1–202.

Flores, M., S. Vera, R. Marcelo & E. Chirinos, 1998. Estadísticas de los desembarques de la pesquería marina Peruana 1970–1982, Vol 134. Informe del Instituto del Mar del Perú, Callao: 1–256.

Frazier, J., 1979. Marine Turtles in Peru and the East Pacific. Office of Zoological Research, National Zoological Park, Smithsonian Institution (unpublished manuscript).

Frazier, J. & D. Bonavia, 2000. Prehispanic marine turtles in Peru: where were they? In Abreu-Grobois, F. A., R. Briseño-Dueñas, R. Marquez & L. Sarti (eds), Proceedings of the Eighteenth International Sea Turtle Symposium. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SEFSC-436: 243–245.

Green, D., 1984. Long distance movements of Galapagos green turtles. Journal of Herpetology 18: 121–130.

Hays-Brown, C. & W. M. Brown, 1982. Status of sea turtles in the southeastern Pacific: emphasis on Peru. In Bjorndal, K. (ed.), Biology and Conservation of Sea Turtles. Smithsonian Institution Press, Washington, DC: 235–240.

Hormazabal, S., G. Shaffer, J. Letelier & O. Ulloa, 2001. Local and remote forcing of sea surface temperature in the coastal upwelling system off Chile. Journal of Geophysical Research 106: 16657–16672.

Houghton, J. D. R., T. K. Doyle, M. W. Wilson, J. Davenport & G. C. Hays, 2006. Jellyfish aggregation and leatherback turtle foraging patterns in a temperate coastal environment. Ecology 87: 1072–1967.

Hurtado, M., 1984. Registros de anidación de la tortuga negra, Chelonia mydas, en las Islas Galápagos, Vol. 6. Boletín Científico y Técnico, Instituto Nacional de Pesca, Guayaquil: 77–104.

Jahncke, J., D. Checkley & G. L. Hunt Jr., 2004. Trends in carbon flux to seabirds in the Peruvian upwelling. Fisheries Oceanography 13: 208–223.

Ji, M. & A. Leetmaa, 1997. Impact of data assimilation on ocean initialization and El Niño prediction. Monthly Weather Review 125: 742–753.

Kelez, S. A., C. Manrique, X. Velez-Suazo & M. Williams, 2004. Green turtle (Chelonia mydas agassizii) diet differences in two Peruvian coastal localities. In Coyne, M. S. & R. D. Clark (comps), Proceedings of the Twenty-First Annual Symposium in Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-528: 305–307.

Marquez, R., 1990. Sea turtles of the world. FAO Species Catalogue 125: 1–81.

Mianzan, H. W. & P. F. S. Cornelius, 1999. Cubomedusae and Scyphomedusae. In Boltovskoy, D. (ed.), South Atlantic Zooplankton. Backhuys Publishers, Leiden: 513–559.

Mianzan, H. W., M. Pájaro, G. Alvarez Colombo & A. Madirolas, 2001. Feeding on survival-food: gelatinous plankton as a source of food for anchovies. Hydrobiologia 451: 45–53.

Montecinos, A., S. Purca & O. Pizarro, 2003. Interannual to interdecadal sea surface temperature variability along the western coast of South America. Geophysical Research Letters 30: 1570.

Morales, V. R. & P. Vargas, 1996. Legislation protecting marine turtles in Peru. Marine Turtle Newsletter 75: 22–23.

Muck, P., A. Z. De Moreno & C. Aranda, 1989a. The seasonal dynamics of sea surface temperature and its impact on anchoveta distribution off Peru. In Pauly, D., P. Muck, J. Mendo & I. Tsukayama (eds), The Peruvian Upwelling Ecosystem: Dynamics and Interactions, Vol. 18. ICLARM Studies and Reviews, Manila: 33–44.

Muck, P., I. Tsukayama & E. Ferrandis, 1989b. Temperaturas superficiales del mar a lo largo de la costa Peruana para el período 1950–1988, Vol. 95. Informe Instituto del Mar del Perú, Callao: 1–29.

Paredes, R., 1969. Introducción al estudio biológico de Chelonia mydas agassizii en el perfil Pisco. Thesis. Universidad Nacional Federico Villareal, Lima: 1–83.

Pennington, J. T., K. L. Mahoney, V. S. Kuwahara, D. D. Kolber, R. Calienes & F. P. Chavez, 2006. Primary production in the eastern tropical Pacific: a review. Progress in Oceanography 69: 285–317.

Pinedo, M., 1988. La pesqueria artesanal en la caleta de San Andrés - Pisco. In Wosnitza-Mendo, C., M. Espino & M. Veliz (eds), La pesquería artesanal en el Perú durante junio 1986 a junio 1988, Vol 93. Informe Instituto del Mar del Perú, Callao: 127–130.

Polovina, J. J., G. H. Balazs, E. A. Howell, D. M. Parker, M. P. Seki & P. H. Dutton, 2004. Forage and migration habitat of loggerhead (Caretta caretta) and olive ridley (Lepidochelys olivacea) sea turtles in the central North Pacific Ocean. Fisheries Oceanography 13: 36–51.

Retamal, M. A., 1981. Catalogo ilustrado de los crustáceos decápodos de Chile, Vol. 44. Universidad de Concepción, Gayana: 1–110.

Rivera, T., 1988. Temperaturas del mar frente al Perú durante Enero – Marzo de 1987. In Salzwedel, H. & A. Landa (eds), Recursos y Dinámica del Ecosistema de Afloramiento Peruano. Boletín del Instituto del Mar del Perú, Volumen Extraordinario: 11–15.

Saba, V. S., P. Santidrian-Tomillo, R. D. Reina, J. R. Spotila, J. A. Musik, D. A. Evans & F. V. Paladino, 2007. The effect of the El Niño southern oscillation on the reproductive frequency of eastern Pacific leatherback turtles. Journal of Applied Ecology 44: 395–404.

Saba, V. S., G. L. Shillinger, A. M. Swithenbank, B. A. Block, J. R. Spotila, J. A. Musik & F. V. Paladino, 2008a. An oceanographic context for the foraging ecology of eastern Pacific leatherback turtles: consequences of ENSO. Deep-Sea Research I 55: 646–660.

Saba, V. S., J. R. Spotila, F. P. Chavez & J. A. Musick, 2008b. Bottom-up and climatic forcing on the worldwide population of leatherback turtles. Ecology 89: 1414–1427.

Santillán Corrales, L. A., 2008. Composición del contenido estomacal de Chelonia mydas en Bahía de Sechura. In Kelez, S., F. Van Oordt, N. de Paz & K. Forsberg (eds), Libro de Resúmenes II Simposio de tortugas marinas en el Pacífico Sur Oriental, Lima: 16.

Seminoff, J. A., A. Resendiz & W. J. Nichols, 2002. Home range of green turtles Chelonia mydas at a coastal foraging area in the Gulf of California, Mexico. Marine Ecology Progress Series 242: 253–265.

Seminoff, J. A., P. Zárate, M. Coyne, D. G. Foley, D. Parker, B. N. Lyon & P. H. Dutton, 2008. Post-nesting migrations of Galápagos green turtles Chelonia mydas in relation to oceanographic conditions: integrating satellite telemetry with remotely sensed ocean data. Endangered Species Research 3: 1–16.

Shrader, A. M., N. Owen-Smith & J. O. Ogutu, 2006. How a megagrazer copes with the dry season: food and nutrient intake rates by white rhinoceros in the wild. Functional Ecology 20: 376–384.

Stiasny, G., 1937. Scyphomedusae. John Murray Expedition 1933–1934, Scientific Reports 4: 203–242.

Tarazona, J., C. Paredes, L. Romero & S. Guzmán, 1988. La recolonización de las comunidades de mitílidos en la costa central del Perú después de El Niño 1982–1983. In Salzwedel, H. & A. Landa (eds), Recursos y dinámica del ecosistema de afloramiento Peruano. Boletín Instituto del Mar del Perú. Volumen Extraordinario, Callao: 115–120.

Tourre, Y. M., C. Cibot, L. Terray, W. B. White & B. Dewitte, 2005. Quasi-decadal and inter-decadal climate fluctuations in the Pacific Ocean from a CGCM. Geophysical Research Letters 32: 1–4.

Urquizo, W., C. Wosnitza-Mendo, E. Valdivia & C. Moreno, 1987. Catálogo de datos oceanográficos (T, S y O_2) por estaciones del año en diferentes profundidades frente a la costa Peruana, período 1970–1985. Boletín Instituto del Mar de Perú, Volumen Extraordinario, Callao: 1–445.

Vargas, P., P. Tello & C. Aranda, 1994. Sea turtle conservation in Peru: the present situation and a strategy for immediate action. In Bjorndal, K. A., A. B. Bolten, D. A. Johnston & P. J. Eliazar (eds), Proceedings of the Fourteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-351: 159–161.

Wallace, B. P. & T. T. Jones, 2008. What makes marine turtles go: a review of metabolic rates and their consequences. Journal of Experimental Marine Biology and Ecology 356: 8–24.

Wallace, B. P., S. S. Kilham, F. V. Paladino & J. R. Spotila, 2006. Energy budget calculations indicate resource limitation in eastern Pacific leatherback turtles. Marine Ecology Progress Series 318: 263–270.

Wang, B., 1995. Transition from a cold to a warm state of the El Niño-Southern Oscillation cycle. Meteorology and Atmosphere Physics 56: 17–32.

Wosnitza-Mendo, C., M. Espino & M. Veliz, 1988. La pesquería artesanal en el Perú durante Junio 1986 a Junio 1988, Vol 93. Informe Instituto del Mar del Perú, Callao: 127–130.

Wyrtki, K., 1975. El Niño the dynamic response to the equatorial Pacific Ocean to Atmospheric Forcing. Journal of Physical Oceanography 5: 572–584.

Zárate, P., 2003. First results of the East Pacific green turtle, Chelonia mydas, nesting population assessment in the Galápagos Islands. In Seminoff, J. A. (ed.), Proceedings of the Twenty-Second Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-503: 80–81.

Zuta, S., M. Farfán & O. Morón, 1984. Características principales del mar frente a Perú durante la evolución del evento El Niño 1982–83, Vol. 15. Revista de la Comisión Permanente del Pacífico Sur, Quito: 141–178.