Linking loggerhead locations: using multiple methods to determine the origin of sea turtles in feeding grounds

Alan F. Rees1,2 · Carlos Carreras2,3 · Annette C. Broderick2 · Dimitris Margaritoulis1 · Thomas B. Stringell2 · Brendan J. Godley2

Received: 26 July 2016 / Accepted: 5 December 2016 / Published online: 13 January 2017
© The Author(s) 2017. This article is published with open access at Springerlink.com

Abstract Many marine megavertebrate taxa, including sea turtles, disperse widely from their hatching or birth- ing locations but display natal homing as adults. We used flipper tagging, satellite tracking and genetics to identify the origin of loggerhead turtles living in Amvrakikos Gulf, Greece. This location has been identified as hosting regionally important numbers of large-juvenile to adult sized turtles that display long-term residency and/or association to the area, and also presents a male biased sex ratio for adults. A total of 20 individuals were linked to nesting areas in Greece through flipper tagging and satellite telemetry, with the majority (16) associated with Zakynthos Island. One additional female was tracked from Amvrakikos Gulf to Turkey where she likely nested. Mitochondrial DNA mixed stock analyses of turtles captured in Amvrakikos Gulf (n = 95) indicated 82% of individuals originated from Greek nesting stocks, mainly from Zakynthos Island (63%), with lesser contributions from central Turkey, Cyprus and Libya. These results suggest that the male-biased sex ratio found in Amvrakikos Gulf may be driven by the fact that males breed twice as frequently on Zakynthos, resulting in their using foraging grounds of greater proximity to the breeding site. Conservation measures in localised foraging habitats for the protection of marine vertebrates, such as sea turtles, may have positive impacts on several disparate breeding stocks and the use of multiple methods to determine source populations can indicate the relative effectiveness of these measures.

Introduction

Distribution and dispersal of many marine megavertebrate taxa involve large spatial scales (e.g. Pendoley et al. 2014 and additionally; tuna: Block et al. 2005; sharks: Domeier and Nasby-Lucas 2008; albatrosses: Weimerskirch et al. 2006; seals: Field et al. 2005; whales: Zerbini et al. 2006). Understanding and quantifying the intra-species connectivity between distant habitats is important for conservation and management (Webster et al. 2002; Gerber and Heppell 2004; Kennedy et al. 2014) and may necessitate international cooperation and collaboration for effective species protection (Jodice and Suryan 2010). Tagging and satellite tracking technologies have revealed a wealth of information on marine vertebrate life histories and migratory behaviour (Cooke 2008; Block et al. 2011) and genetic studies have revealed cryptic population structures (e.g. Blower et al. 2012) that are essential for the biological delineation of management units of endangered species (Moritz 1994).

Sea turtles may traverse oceans (Bowen et al. 1995; Hays et al. 2002) during their development and maturation that may take several decades (Heppell et al. 2003). Natal...
homming in these species contributes to genetic structuring of breeding populations so that adult turtles from different nesting areas can be identified genetically (Amorocho et al. 2012; Leroux et al. 2012). Furthermore, the pattern of adult dispersion from breeding areas has been shown to reflect the extent of passive dispersion that would be experienced by hatchlings; this, prevailing oceanography around nesting areas may be crucial to the selection of foraging sites used by adult sea turtles (Hays et al. 2010a). As for other taxa, tagging, tracking and genetic studies of sea turtles can reveal movements of individuals and stock composition in foraging grounds. For example, foraging assemblages have been shown to comprise of mixtures of turtle stocks, from often-distant rookeries (Lahanas et al. 1998; Luke et al. 2004; Bowen et al. 2007; Blumenthal et al. 2009; Nishizawa et al. 2014a).

Breeding populations and regional management units (RMUs) for loggerhead turtles have been defined using behavioural and genetic data respectively (Bowen et al. 2004; Wallace et al. 2010) and seasonal and ontogenetic movements have been identified at several locations (Limpus and Limpus 2001; Hawkes et al. 2007; McClellan and Read 2007; Casale et al. 2008; Mansfield et al. 2009; Hays et al. 2010a; Marcovaldi et al. 2010; Rees et al. 2010; Nishizawa et al. 2014b). The recent use of more variable genetic markers and extended coverage of nesting areas has increased the resolution of mitochondrial DNA (mtDNA) studies, aiding the identification of further sub-populations (Shamblin et al. 2014). This improved baseline can contribute to increased resolution in mixed stock analyses (MSAs) of foraging aggregations, which are used to highlight likely turtle origin and movements and possible conservation requirements (Roberts et al. 2005; Carreras et al. 2006; Reece et al. 2006; Monzón-Argüello et al. 2012; Garofalo and Rees 2011, Snape et al. 2016).

The Mediterranean Sea hosts an independent loggerhead turtle RMU but is also visited by individuals from two Atlantic RMUs (Wallace et al. 2010), with individuals from the Atlantic mainly occurring in the western Mediterranean basin (Clusa et al. 2014). Mediterranean loggerhead turtles are considered to form an isolated meta-population (Carreras et al. 2011; Clusa et al. 2013) with most nesting occurring in Greece, Turkey, Cyprus and Libya (Casale and Margaritoulis 2010). The life-history for this metapopulation has been presented in the literature; hatchlings enter oceanographic currents in which they disperse to varied locations away from the breeding area (Hays et al. 2010a; Casale and Mariani 2014). As the turtles increase in size they are capable of more directed movements and may undertake long migrations through oceanic and neritic waters (Bentivegna 2002; Casale et al. 2007; Hochscheid et al. 2010; Casale et al. 2012a) with a protracted switch from pelagic to benthic foraging (Laurent et al. 1998; Casale et al. 2008). In general, they complete maturation in locations closer to their natal origin than would be found by random dispersal (Laurent et al. 1998, Maffucci et al. 2006, Garofalo et al. 2013).

As adults, maternal philopatry to breeding areas has created several reproductive clades across the eastern Mediterranean as suggested through mtDNA analysis (Carreras et al. 2007; Garofalo et al. 2009; Yilmaz et al. 2011; Saied et al. 2012; Clusa et al. 2013), but some male mediated gene flow may reduce the overall depth of reproductive isolation (Carreras et al. 2007; Yilmaz et al. 2011). The neritic area off North Africa is an important foraging habitat away from the breeding areas, used by adult turtles from Greece (Margaritoulis et al. 2003; Zbinden et al. 2011; Schofield et al. 2013), Cyprus (Broderick et al. 2007; Snape et al. 2016) and Libya (Casale et al. 2013) with no published data for loggerhead turtles nesting in Turkey. The Adriatic Sea is also an important foraging/overwintering area for turtles that breed in Greece (Margaritoulis et al. 2003; Zbinden et al. 2011; Schofield et al. 2013; Giovannotti et al. 2010) with lower numbers recorded foraging elsewhere around the Mediterranean, including the Aegean Sea, the Levant coast and Cyprus (Margaritoulis et al. 2003; Margaritoulis and Rees 2011, Snape et al. 2016).

An important foraging aggregation of loggerhead turtles has been identified in Amvrakikos Gulf, western Greece, comprising numerous large-juvenile and adult individuals. Rees et al. (2013) revealed a male-biased sex ratio, which is at odds with established widespread female-biased hatching production (Witt et al. 2010a). To address the general lack of knowledge on the origins of loggerhead turtles in this important foraging area, we used a combination of flipper tagging, satellite tracking and genetic investigations to: (1) Identify direct linkages between the foraging area and breeding grounds. (2) Quantify composition of the foraging aggregation of loggerhead turtle breeding stocks. (3) Determine possible reasons for the previously highlighted male-biased sex ratio present in the Gulf.

Methods

Flipper tagging and sample collection

All turtles were obtained from an extensive (Ca. 16 km²) shallow region (<2 m deep) in the northeast part of Amvrakikos Gulf (39°1.3’ N, 21°3.6’ E; Fig. 1), except for 2013 when a number of turtles were captured in a similarly sized area further west (39°1.6’ N, 20°57.2’ E). Annual capture intensity varied over the period 2002–2015. In 2002 and 2003, turtles were encircled with a net to capture them. In subsequent years, captures were made using turtle rodeo technique (Ehrhart and Ogren 1999) from an inflatable
 dinghy. All captured turtles were hauled on-board the dinghy and flipper tagged. GPS location at the capture site, curved carapace length (CCL) measurements and skin samples, from one of the rear flippers, were also taken; samples were stored in 90% ethanol until analysis. See Rees et al. (2013) for further details on methods and location of captures.

**Satellite tracking**

We tracked 13 adult and juvenile turtles using Kiwisat Argos-linked satellite transmitters (Sirtrack Ltd., Havelock North, New Zealand). Three were deployed in June 2002, three in May 2003, six in June 2013 (three each from both the east and west capture locations) and one in August 2013 (from the eastern capture location). Captured turtles were taken ashore, close to the capture site, and retained in a shaded, wooden corral to affix the transmitters and were then released at the water’s edge. In 2002/2003, the fibreglass and polyester resin attachment method of Balazs et al. (1996) was employed and to extend battery life, transmitters were duty-cycled to be continuously on for the first 28 days, followed by 24 h on: 36 h off for the rest of the transmitter’s functional duration. In 2013, two-part epoxy was used to attach the transmitters to the turtles (Godley et al. 2002) and the transmitters were duty-cycled...
to be continuously on for their entire functional duration. Location data were calculated by the Argos system (http://www.argos-system.org/). Data from the 2002/2003 transmitters were manually retrieved through telnet on a daily basis. Compiled datasets were then uploaded into the Satellite Tracking and Analysis Tool (STAT; Coyne and Godley 2005) for processing and filtering. Data from the 2013 transmitters were automatically downloaded and processed in STAT. To determine turtle routes, raw Argos data were filtered in the following manner: Location Classes 3, 2, 1, A and B were used (Witt et al. 2010b) and locations requiring excessive speed (>5 km h<sup>-1</sup>) or unlikely turning angle (<25°) were omitted. Locations that passed filtering were averaged to produce a single daily location.

Additionally, to complement the results of our own investigation, we undertook a review of published literature on loggerhead turtle tracking in the Mediterranean to identify any turtles recorded as migrating into Amvrakikos Gulf.

**DNA extraction and sequencing**

Skin samples were processed from turtles captured in Amvrakikos Gulf between 2008 and 2011. DNA from 95 samples was extracted using the Phire® Animal Tissue Direct PCR Kit (Finnzymes) and ~800 bp fragment of the mtDNA D-loop control region was amplified by polymer chain reaction (PCR) using the primer pair LCM15382 (5’-GCTT AACCCTAAGCATTGG-3’) and H950 (5’-GTCTCGG ATTAGGGGT-TT-3’) (Abreu-Grobois et al. 2006). PCR protocol comprised an initial denaturation phase of 98 °C for 5 min followed by 40 cycles of 5 s at 98 °C, 5 s at 60.6 °C and 20 s at 72 °C, with a final 1 min at 72 °C before cooling to 4 °C to hold. The resulting PCR product was visualised in agarose gel before being purified by enzymatic reactions (Exo 1 and FastAP; Fermentas). Sequencing was undertaken on an Automatic Sequencer 3730XL, in both forward and reverse directions (Macrogen Europe, the Netherlands). These ~800 bp sequences were aligned in Geneious v5.5 (Drummond et al. 2011) or BioEdit v7.1.11 (Hall 1999) and compared to known loggerhead turtle haplotypes found in the database maintained by the Archie Carr Center for Sea Turtle Research (http://accstr.ufl.edu/).

**Mixed stock analysis**

A ‘one to many’ MSA using the genetic data was conducted to test the contribution of each nesting area to the foraging area of Amvrakikos using a Bayesian approach (Pella and Masuda 2001). Hierarchical Bayesian models also allow combination of genetic and ecological data, like rookery size, to avoid the over representation of extremely small populations typical of other Bayesian approaches (Okuyama and Bolker 2005). We used the programme Bayes and applied the BM2 model from previous studies, that used the rookery size as a weighting factor, as shown to be appropriate for sea turtle studies (Bass et al. 2004). As a baseline we used published haplotype frequencies of the Atlantic and Mediterranean nesting beaches (Shamblin et al. 2014). Mean annual nests per year were also obtained from the literature as an approximation of population size (López-Jurado et al. 2007; Casale and Margaritoulis 2010; Shamblin et al. 2012). The Gelman-Rubin shrink factor was used diagnostically to test for anomalous realizations of the Bayes predictive posterior distribution (Pella and Masuda 2001) 95% CI were obtained directly from the MCMC used diagnostically to test for anomalous realizations of the Bayes predictive posterior distribution. Values greater than 1.2 indicated a lack of convergence in the algorithm and the corresponding estimates were considered unreliable. A ‘many to many’ mixed stock analysis (Bolker et al. 2007) was not performed as it requires the inclusion of all available foraging areas, and so far only a few feeding grounds (Yilmaz et al. 2012, Garofalo et al. 2013) have been assessed using the ~800 bp fragment.

Additionally, we performed a similar MSA using the haplotype frequencies from loggerhead turtles captured at Drini Bay in Albania (Fig. 1; Yilmaz et al. 2012) in an MSA similar to that performed on the Amvrakikos haplotype frequency results in order to compare breeding stock contributions to foraging grounds separated by approximately 350 km.

**Results**

**Links from flipper tagging**

In over a decade of the capture-mark-recapture study in Amvrakikos Gulf, with records of almost 700 unique individuals, identified through tag recaptures (Rees et al. 2013 and unpubl data), linkage to several nesting areas in Greece has been confirmed through flipper tag observations at Greece’s main nesting areas, which are monitored by ARCHELON. A total of ten turtles tagged at Greek nesting beaches have so far been encountered in Amvrakikos Gulf. Four turtles originally tagged nesting on Zakynthos Island (180 km from Amvrakikos) and four from southern Kyparissia Bay (240 km from Amvrakikos) comprise the majority; the remainder were a single turtle that nested at Rethymno, Crete (600 km from Amvrakikos) and a turtle tagged nesting on Kefalonia Island (130 km from Amvrakikos) that was reported to the authors by local fishers. Additionally, four turtles tagged in the Gulf were subsequently observed nesting in southern Kyparissia (1), Zakynthos (2) and both southern Kyparissia and Zakynthos during a single breeding season (1). In total 50% (7 of 14)
of turtles linked to the Gulf from a nesting area were associated with Zakynthos. Details of these observations are provided in Table 1 and Fig. 1.

Links from satellite telemetry

The majority (11 of 13) satellite tracked turtles remained within the gulf and the behaviours of those from 2002/2003 (n = 6) are discussed in Rees et al. (2013). One turtle from June 2013 (probable adult, female, CCL = 75 cm) departed the gulf on 28th June and migrated into the Adriatic Sea where it resided until 18th May 2015, when its transmitter stopped functioning. Turtle nesting does not occur in that region; hence no nesting site linkage was determined. The remaining turtle (probable adult, female, CCL = 75 cm), tagged in May 2003, departed the Gulf and its movements are presented in Fig. 1. This turtle left the Gulf on 3rd July and made an oceanic migration, reaching Syria on 14th August, with a minimum possible distance travelled from origin of 1650 km. It then moved north and westwards following a more coastal route in Turkey. After undertaking a large oceanic loop, it returned to the Turkish coast and arrived at its overwintering spot near the Kale and Kumluca nesting areas on 23rd October, having travelled a total of 3425 km. It remained there through to May 2004 until it travelled westwards, with the last location received on 24th June (mid-nesting season in the Mediterranean), 15 km from Fethiye beach, a known loggerhead turtle nesting area in Turkey (Türkozan 2000). From the literature, we identified a total of six adult loggerhead turtles (three male and three female) that migrated into Amvrakikos Gulf; all from the Greek nesting area of Zakynthos (Zbinden et al. 2011; Schofield et al. 2013).

Links from genetics

A total of four haplotypes were recorded from Amvrakikos Gulf turtles (Table 2): the widespread haplotype CC-A2.1 (Genebank EU179445; Shamblin et al. 2012), the Crete haplotype CC-A2.8 (Genebank FM200217; Garofalo 2010), and the Greek haplotypes CC-A6.1 (Genbank JQ350705; Yilmaz et al. 2012; Clusa et al. 2013) and CC-A32.1 (Genebank JF837822; Clusa et al. 2013). A preliminary mixed stock analysis including all Atlantic and Mediterranean nesting areas showed that collectively the Atlantic nesting areas pooled was less than 1% of the Amvrakikos sea turtles (data not shown). A second analysis was performed excluding all these Atlantic nesting areas,

| Breeding | Sex | CCL (cm) | Origin | Re-observation | Source |
|----------|-----|----------|--------|----------------|--------|
| ZAK      | F   | 73.5     | AMV 2004 | ZAK 2011, AMV 2013 | Present study |
| ZAK      | F   | 73.5     | AMV 2005 | ZAK 2010, AMV 2010, 2011 | Present study |
| ZAK, KYP | F   | 73.5     | AMV 2007 | ZAK & KYP 2009 | Present study |
| KYP      | F   | 80.5     | AMV 2007 | KYP 2009, AMV 2012 | Present study |
| CRE      | F   | 78.5     | CRE     | AMV 2005 | Present study |
| KEF      | F   | –        | KEF     | AMV 2002 | Reported to ARCHELON |
| KYP      | F   | 81.0     | KYP     | AMV 2002 | Present study |
| KYP      | F   | 81.0     | KYP     | AMV 2013, 2014, 2015 | Present study |
| KYP      | F   | 85.0     | KYP     | AMV 2014 | Present study |
| ZAK      | F   | 77.0     | ZAK     | AMV 2005 | Present study |
| ZAK      | F   | 88.5     | ZAK     | AMV 2005, 2007, 2011, 2015 | Present study |
| KYP      | F   | 83.5     | KYP     | AMV 2005 | Present study |
| ZAK      | F   | 81.5     | ZAK     | AMV 2007 | Present study |
| ZAK      | F   | 88.0     | ZAK     | AMV 2008, 2010 | Present study |
| ZAK      | F   | 86.0     | ZAK 2007 | AMV 2007 | Zbinden et al. (2011)* |
| ZAK      | F   | 76.0     | ZAK 2007 | AMV 2007 | Zbinden et al. (2011)* |
| ZAK      | F   | 83.0     | ZAK 2009 | AMV 2009 | Schofield et al. (2013)* |
| ZAK      | M   | 90.0     | ZAK 2008 | AMV 2008, 2009 | Schofield et al. (2013)* |
| ZAK      | M   | 89.0     | ZAK 2009 | AMV 2009 | Schofield et al. (2013)* |
| ZAK      | M   | 88.0     | ZAK 2011 | AMV 2011 | Schofield et al. (2013)* |

See Fig. 1 for location of nesting areas

Breeding breeding area where turtles were observed, CCL curved carapace length, AMV Amvrakikos Gulf, KEF Mounda beach—Kefalonia, KYP southern Kyparissia Bay, ZAK Laganas Bay—Zakynthos, CRE Rethymno—Crete, Origin place first tagged including year of tagging for AMV tagged and ZAK satellite tracked turtles, Re-observation Location and year of subsequent observation(s)

Table 1 Links to nesting areas derived from flipper tag recaptures and satellite tracking(*)


| Haplotype | CC-A2.1 | CC-A2.8 | CC-A3.1 | CC-A3.2 | CC-A6.1 | CC-A10.4 | CC-A13.1 | CC-A20.1 | CC-A26.1 | CC-A29.1 | CC-A31.1 | CC-A32.1 | CC-A43.1 | CC-A50.1 | CC-A52.1 | CC-A53.1 | CC-A65.1 | CC-A68.1 | n | Ref. |
|-----------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|    |     |
| Amvrakikos Gulf, Greece—AMV | 88 1 | 4 | 2 | | | | | | | | | | | | | | | | | 95 | A |
| Drini Bay, ALBANIA—ITALY | 37 1 | 1 | 1 | | | | | | | | | | | | | | | | | 40 | G |
| Calabria—CAL | 22 | 14 | 2 | | | | | | | | | | | | | | | | | 38 | B |
| Misurata—LIBYA | 12 1 | 1 | | | | | | | | | | | | | | | | | | 14 | C |
| Sirte—SIR | 16 12 2 | | 4 | | | | | | | | | | | | | | | | | 1 | 35 | C |
| Zakynthos—GREECE | 16 | 2 | 1 | | | | | | | | | | | | | | | | | 19 | D |
| Kyparissia—KYP | 33 | 2 | 1 | | | | | | | | | | | | | | | | | 36 | E |
| Lakokos—LAK | 18 | 1 | | | | | | | | | | | | | | | | | | 19 | D |
| Crete—CYPRUS | 16 4 | | | | | | | | | | | | | | | | | | | 20 | D |
| CYP | 44 | | 1 | | | | | | | | | | | | | | | | | 45 | D |
| Dalyan—TURKEY | 25 | 15 | | | | | | | | | | | | | | | | | | 40 | F |
| Dalaman—DLM | 5 | 15 | | | | | | | | | | | | | | | | | | 20 | F |
| Western Turkey—WTU | 60 | 16 | | | | | | | | | | | | | | | | | | 76 | F |
| Mid—LEBANON | 46 | 1 | | | | | | | | | | | | | | | | | | 47 | F |
| Turkey—MTU | | | | | | | | | | | | | | | | | | | | | |
| Eastern Turkey—ETU | 60 | 8 1 | 1 1 1 | | | | | | | | | | | | | | | | | 72 | F |
| LEB | 17 | 2 | | | | | | | | | | | | | | | | | | 19 | D |
as previous studies suggested removing from the analysis those nesting areas whose contribution was biologically unrealistic and considering that no Atlantic exclusive haplotypes was found within our samples (Engstrom et al. 2002; Godley et al. 2010). This second mixed stock analysis showed that most of the Amvrakikos turtles (78%) originated from western Greece (Fig. 3; Supplemental Table S1), although notable contributions from Crete, Mid Turkey and Cyprus were also inferred (Figs. 2 and 3; Supplemental Table S1). Further analysis was undertaken for a fine scale assignation, considering western Greece nesting beaches (Zakynthos, southern Kyparissia and Lakanikos Bay) separately, justified by Zakynthos presents an exclusive haplotype. Zakynthos was the origin of most (63%) of western Greek turtles located in Amvrakikos, followed by southern Kyparissia (8%) and Lakanikos nesting areas (4%) (Fig. 3; Supplemental Table S1).

The turtles from Drini Bay, Albania (CCL Mean ± SD; 68.8 ± 10.3 cm, n = 40) were similar in size, and therefore life-stages, to those sampled from Amvrakikos (69.9 ± 8.3 cm, n = 94). MSAs using the Albanian haplotype frequencies presented by Yilmaz et al. (2012) indicated the majority (50%) of turtles present originated from western Greece, with larger contributions from the other same three other nesting units (Crete, Mid Turkey and Cyprus; Fig. 3) and if western Greece beaches were included separately in the MSA, Zakynthos was again shown to contribute the single largest proportion of turtles (22%), although far less dominant when compared to Amvrakikos (Fig. 3; Supplemental Table S1).

**Discussion**

Our results, from three differing research methods, indicate that turtles converge to use the same foraging areas from several breeding areas within 600 km distance. Thus further highlighting the utility of complementary studies in determining levels of reproductive and developmental isolation for widespread populations (Godley et al. 2003; Stewart et al. 2013).

**Links from flipper tagging and satellite telemetry**

Mark-recapture revealed links with proximate nesting areas in Greece, through cross-sighting of adult females tagged at a nesting beach and Amvrakikos Gulf. These breeding sites represent some of the largest populations in the Mediterranean (i.e. Laganas Bay, Zakynthos and southern Kyparissia Bay, the Peloponnese; Margaritoulis et al. 2003). The six turtles tracked from Zakynthos into Amvrakikos (Zbinden et al. 2011; Schofield et al. 2013) represent 9% of the total number of turtles tracked from that location over an
eight-year period. A single turtle tracked from Kefalonia (Hays et al. 1991) and another from Rethymno on Crete (Margaritoulis and Rees 2011) represent the only published tracks from other Greek nesting areas and consequently the biased effort precludes using satellite tracking data for direct comparison of the proportion of turtles from different breeding areas utilising Amvrakikos. Although no turtles tagged outside Greece have been recorded within Amvrakikos Gulf, tag recaptures from nesting females in Turkey (n = 1) and Cyprus (n = 1) have been recorded in the Adriatic Sea (Lazar et al. 2004), which necessitates passing the entrance to Amvrakikos Gulf.

Fig. 2 Proportional contribution of Mediterranean nesting units to the foraging population in Amvrakikos Gulf using genetic markers. Circles Mediterranean nesting units that have been defined for mitochondrial haplotype frequencies in previous studies (Garofalo et al. 2009, Yilmaz et al. 2011, Clusa et al. 2013, Carreras et al. 2014) and considered for Mixed Stock Analysis of Amvrakikos (AMV) samples. Open circles indicate a nesting unit contribution of >2% to the Amvrakikos Gulf aggregation, with size denoting percentage contribution. Greece (ZAK Laganas Bay—Zakynthos Island, KYP southern Kyparissia Bay, LAK Lakonikos Bay, CRE Rethymno—Crete Island), Turkey (DLM Dalaman, DLY Dalyan, WTU western Turkey, MTU mid Turkey, ETU eastern Turkey), Cyprus (CYP), Lebanon (LEB), Israel (ISR), Libya (SIR Sirte, MIS Misurata), Tunisia (TUN Kuriat Islands), Italy (LAM Lampedusa Island, CAL Calabria).

Fig. 3 Mixed stock analysis (MSA) of loggerhead turtles from Amvrakikos Gulf foraging area, Greece (grey bars), and comparison with similar analysis on turtles from Drini Bay foraging area in Albania (white bars) (Yilmaz et al. 2012). a MSA using defined breeding units (see Fig. 2). b MSA with nesting areas in the western Greece unit (WGR) incorporated individually (ZAK, KYP, LAK) to identify likely source nesting beaches. See Fig. 2 for locations and abbreviations. Charts are truncated at the 2% contribution level; data for all areas are available in Supplemental Table S1. Error bars show 95% confidence interval range.
A modelling approach indicates hatchling turtles from Cyprus would disperse to the northern Ionian Sea region (Casale and Mariani 2014) and stable isotope analysis of breeding female loggerhead turtles from across the eastern Mediterranean indicates that a notable proportion from each location forages in the northern Ionian Sea or Adriatic Sea (Clusa et al. 2014). It is therefore intriguing that despite a long-term tracking programme on Cyprus (Snape et al. 2016), loggerhead turtles from there are yet to demonstrate northern Ionian/Adriatic directed migrations and the single flipper-tag recapture (Lazar et al. 2004) remains the only direct evidence of migration into the region.

**Life stage and sex bias**

All long-distance tag recaptures and satellite tracking results to date that relate to Amvrakikos Gulf have involved adult individuals and mainly females (13 females from 16 individuals), and yet the majority of the turtles found in Amvrakikos are juveniles, sub-adults and male (231 from 278 turtles; Rees et al. 2013). This bias in life stage representation may be due to different habitat preferences of males and females, as the study only takes place in a small part of the Gulf, but more likely relates to the opportunity for observation and tagging outside the foraging area. Nesting females are the most commonly encountered life stage and sex due to their predictable appearance on traditional nesting beaches and as such are the subject of the majority of flipper tagging and satellite tracking studies (reviewed in Godley et al. 2008; Jeffers and Godley 2016).

Tagging and tracking studies of male and juvenile loggerhead turtles in the eastern Mediterranean, have sourced animals from fisheries bycatch and/or rehabilitation facilities in three main locations, (1) the Adriatic Sea (White et al. 2011; Casale et al. 2012a), (2) southern Italian waters (Bentivegna 2002; Casale et al. 2007), and (3) waters of the African continental shelf off Tunisia and Libya (Hochscheid et al. 2010; Casale et al. 2012b, 2013), with some exceptions (Schofield et al. 2010; present study). There is a complete lack of published information from further east (Turkey, Cyprus, the Levant coast and Egypt). No individuals from the African continental shelf region have yet been recorded in the northern Ionian or Adriatic seas whereas there have been several recorded from the southern Italian waters. This is highly suggestive of geographical developmental segregation, with a large latitudinal component and the key driver stimulating any north–south movement in adulthood might be the need to undertake reproductive migrations (Margaritoulis et al. 2003; Broderick et al. 2007; Zbinden et al. 2011; Casale et al. 2013; Schofield et al. 2013).

**Links from genetics**

As with other sea turtle studies (Lahanas et al. 1998; Roberts et al. 2005; Reece et al. 2006; Prosdocimi et al. 2012), we have successfully used genetic markers to estimate breeding stock contributions to the Amvrakikos Gulf assemblage. Our results suggest the majority of the turtles in Amvrakikos are of Greek origin, supporting the assertion that loggerhead turtles locate their maturation and adult life stages closer to their nesting areas than would be expected from random settling after pelagic dispersal (Bowen et al. 2004; Reece et al. 2006; Casale et al. 2007; Pajuelo et al. 2012; Garofalo et al. 2013). Lack of fidelity to breeding areas witnessed in some individuals nesting in Greece (Margaritoulis 1998; present study) would support the western Greece grouping of breeding populations (Carreras et al. 2007; Clusa et al. 2013; Casale and Mariani 2014). However, when analysed in detail, the majority of turtles in Amvrakikos Gulf are indicated to originate from a single nesting area. Zakynthos is calculated to contribute 63% of the turtles characterised in genetic analysis, which is a similar level of contribution derived from flipper and satellite tracking studies incorporating only adults (see above).

Predominance of Greek and specifically Zakynthos contributions to foraging loggerhead turtles sampled in Drini Bay reinforce this assumption of proximal settlement to natal breeding area, with dispersal linked to original, passive movements in currents experienced by hatchlings (Hays et al. 2010a). Again these genetic data are further supported by two adult females tagged in Zakynthos being recaptured in Drini Bay (White et al. 2011) and no other tag recaptures linking the area to other nesting grounds.

Genetic analyses indicate Amvrakikos Gulf and Drini Bay are of international relevance, as turtles foraging in this region are the most productive (Cardona et al. 2014). Low contributions to both assemblages from Turkish and Cypriot nesting areas and tag returns from the Adriatic (Lazar et al. 2004) confirm that migrations to this region from these locations occur at low levels. However, mixed stock analysis using mtDNA relies on breeding isolation and characterisation of individual nesting areas. Despite the greater resolution the increased-length mtDNA sequences have provided over the previously used shorter sequences (Shamblin et al. 2012; Clusa et al. 2013), the Mediterranean loggerhead turtle populations remain linked through the common CCA2.1 haplotype that accounts for 80% or more of the samples in nine of the 15 nesting areas assessed (Table 2) and reaches over 95% in three (Lakonikos Bay in Greece, Cyprus & Mid Turkey). Additionally, not all haplotypes that have been described in the Mediterranean can be incorporated in MSA (as smaller datasets are dropped to avoid pseudoreplication, see Carreras et al. 2014) thus weakening their potential resolution.
No haplotypes apparently endemic to breeding areas outside Greece were obtained in our current analysis, thus when Greek endemic and common haplotypes are combined in a MSA with population size as a prior the results are likely to indicate contributions from larger non-Greek nesting areas. The Amvrakikos Gulf MSA results display wide confidence limits around average contribution levels reported here (Fig. 3; Supplemental Table S1); consequently, the smaller contributions of populations outside of Greece, namely Turkey, Cyprus and Libya, should be accepted with caution, until better supported by other lines of evidence (such as capture-mark-recapture investigations and satellite tracking).

Furthermore, mtDNA only assesses matrilineal reproductive isolation. Some levels of male mediated gene flow, demonstrated by lower differentiation in nuclear DNA compared to mtDNA have been recorded in the Mediterranean (Schröth et al. 1996; Carreras et al. 2007; Yilmaz et al. 2012). Nuclear DNA revealed that Crete and Cyprus nesting areas play pivotal roles in homogenising Mediterranean stocks (Carreras et al. 2007). However, these islands might not be exclusive locations for potential genetic mixing. Loggerhead turtle mating has been reported in Amvrakikos Gulf (Teneketzis et al. 2003) and hence the potential for individuals that hatched on beaches separated by thousands of kilometres to interbreed in distant foraging areas. This genetic mixing may increase the genetic variability of loggerhead turtle nesting aggregations, making the smaller aggregations more robust against inbreeding depression (Bell et al. 2009). However, natal philopatry in females means that recovery in nesting levels for compromised or near extirpated populations requires recruitment of individuals with ancestral origins at the affected sites (Carreras et al. 2007; Watanabe et al. 2011). It is therefore important to protect established nesting areas as well as foraging hot-spots to properly conserve the extant genetic diversity within the meta-population. Conservation measures adopted within Amvrakikos Gulf, which hosts year-round, regionally important numbers of loggerhead turtles (Rees et al. 2013) will help preserve both the larger breeding populations of Greece, including that of Zakynthos and the distant, more depleted nesting areas in Turkey, Cyprus and Libya.

Theory to explain male-biased sex ratio
An unexplained, high proportion of male turtles has been reported in Amvrakikos Gulf, with male-biased sex ratios in the largest size classes (Rees et al. 2013). This is contrary to the female-biased sex ratios produced at most Mediterranean nesting areas (Witt et al. 2010a with additional data in Uçar et al. 2012). This male bias is likely a consequence of several factors.

Approximately 60% of turtles in Amvrakikos Gulf originate from the large breeding aggregation at the relatively nearby Zakynthos. The sex ratio of hatchlings from that Island is vary variable, with a long-term average of around 50% male hatchling production (Compare Zbinden et al. 2007 with Katselidis et al. 2012). Additionally, fieldwork in the Gulf has been carried during the Mediterranean turtle nesting season, hence a cohort of adult females would be absent from the Gulf to breed, but the males would have already departed from the nesting areas to return to foraging areas such as Amvrakikos Gulf (Hays et al. 2010b). Furthermore, there is growing evidence that adult male turtles remain closer to the nesting areas than female conspecifics. This has been shown in loggerhead turtles (Arendt et al. 2012; Schofield et al. 2013) and hawksbill turtles Eretmochelys imbricata (Van Dam et al. 2008) and may facilitate more frequent remigration in males (Wright et al. 2012; Hays et al. 2014).

Conclusions
Through the integration of flipper tagging, satellite tracking and genetic markers we have garnered a number of insights, both fundamental and applied. We advance understanding of factors affecting natal homing and location-specific variation in sex ratios in foraging grounds (see Pilcher et al. 2015). Congruence in data obtained from low- and high-tech methodologies validate genetic designations of statistical ambiguity, generating defensible results that may serve as a template for other foraging ground studies. To take this work further for the site in question would involve aerial surveying to better understand heterogeneity of habitat use (e.g. Seminoff et al. 2014) that can be followed up by focussed in-water work.

It is likely that advances in genetic marker resolution, in tandem with increased sample sizes and sampling from some of more sparsely nested areas, would reveal further structuring within foraging turtle aggregations. This could lead to more assured individual-level assignments regarding natal origins, in contrast to the few individuals that may currently be assigned through low-frequency endemic haplotypes. Additional methods of characterising individuals to a geographical area, such as use of biochemical markers like stable isotopes (Zbinden et al. 2011; Ceriani et al. 2012; Shimada et al. 2014), even in the absence of external markers, could enhance our understanding of a specific foraging area’s region-wide links to nesting sites through complementary sampling of individuals observed nesting.

Finally, data sharing through publication and collaboration produces enhanced datasets that can be subjected to more rigorous analysis from which more robust inferences drawn. These stepwise contributions of complementary
insights into the life-histories of sea turtles may directly impact conservation measures, as management plans are revised in line with the latest ecological findings (Fujioji and Halpin 2014).

Acknowledgements The Authors would like to thank ETANAM for assistance during the 2002/2003 telemetry fieldwork. BJG and ACB are funded by NERC and the Darwin Initiative. CC is supported by the Beatriu de Pinós programme of the Departament d’Universitats, Recerca i Societat de la Informació de la Generalitat de Catalunya. AFR would like to thank Sonja Baker, Christopher Dean, Kimon Fassiniou, Andrew Haigh, Ben Hawksbee, Andreas Koutsodendrihs, Jason Margaritoulis, Robert Newman, Thomas Riggall, Giannis Rou-sopoulos, Paul Tsaros and others for field assistance. Local support for field teams has been provided by the Kopraina Centre for Environmental Education. ARCHELON’s activities in the Gulf are supported by the Management Agency of the Amvrakikos Wetlands National Park and the local Coast Guard stations at Menidi and Preveza. Thanks also to the many hundreds of ARCHELON volunteers have worked at the different nesting areas around Greece.

Funding Fieldwork in 2002/2003 was part-funded by EU LIFE project LIFE99NAT/006475. The British Chelonia Group provided a grant to support surveys in 2012. The 2013 fieldwork and tracking took place in the context of the project ‘PRO ACT NATURA 2000/Protection Actions for Cross-Border and Joint Management of Marine Sites of Community Interest (NATURA 2000)’ (Subsidy code 11.32.01 of the European Territorial Cooperation Programme Greece–Italy 2007–2013).

Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval The research was carried out with permission from the Ministries of Agriculture and Environment (Greece) and all applicable international, and/or institutional guidelines for the care and use of animals were followed.

Open Access This article is distributed under the terms of the Creative Commons Attribution 4.0 International License (http://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made.

References

Abreu-Grobois F, Horrocks J, Formia A, Leroux R, Velez-Zuazo X, Dutton P, Soares L, Meylan P, Browne D (2006) New mtDNA D-loop primers which work for a variety of marine turtle species may increase the resolution capacity of mixed stock analysis. In: Frick M, Panagopoulou A, Rees AF, Williams K (eds) Book of abstracts. 26th Annual symposium on sea turtle biology and conservation. International Sea Turtle Society, Athens, Greece

Amorosco DF, Abreu-Grobois FA, Dutton PH, Reina RD (2012) Multiple distant origins for green sea turtles aggregating off Gorgona Island in the Colombian Eastern Pacific. PLoS One 7(2):e31486

Arendt MD, Segars AL, Byrd JJ, Boynton J, Schwenter JA, Whitaker JD, Parker L (2012) Migration, distribution, and diving behavior of adult male loggerhead sea turtles (Caretta caretta) following dispersal from a major breeding aggregation in the Western North Atlantic. Mar Biol 159:113–125

Balazs G, Miya RK, Beaver SC (1996) Procedures to attach a satellite transmitter to the carapace of an adult green turtle, Chelonia mydas. In: Keinath JA, Bernard DE, Musick JA, Bell BA (eds) Proceedings of the 15th annual symposium on sea turtle biology and conservation. NOAA technical memorandum NMFS-SEFSC-387, pp. 21–26

Bass AL, Epperly SP, Braun-McNeill J (2004) Multi-year analysis of stock composition of a loggerhead turtle (Caretta caretta) foraging habitat using maximum likelihood and Bayesian methods. Conserv Genet 5:783–796

Bell CD, Blumenthal JM, Broderick AC, Godley BJ (2009) Investigating potential for depensation in marine turtles: How low can you go? Conserv Biol 24:226–235

Bentivegna F (2002) Intra-Mediterranean migrations of loggerhead sea turtles (Caretta caretta) monitored by satellite telemetry. Mar Biol 141:795–800

Block B, Teo SLH, Walli A, Boustany A, Stokesbury MJW, Farwell CJ, Weng KC, Dewar H, Williams TD (2005) Electronic tagging and population structure of Atlantic bluefin tuna. Nature 434:1121–1127

Block BA, Jonsen ID, Jorgensen SJ, Winship AJ, Shaffer SA, Bograd SJ, Hazen EL., Foley DG, Breed GA, Harrison AL, Ganong JE, Swwiheitenbank A, Castleton M, Dewar H, Mate BR, Shillinger GL, Schafer KM, Benson SR, Weise MJ, Henry RW, Costa DP (2011) Tracking apex marine predator movements in a dynamic ocean. Nature 475:86–90

Blower DC, Pandolfo JM, Bruce BD, Gomez-Cabrera Mdc, Oven-den JR (2012) Population genetics of Australian white sharks reveals fine-scale spatial structure, transoceanic dispersal events and low effective population sizes. Mar Ecol Prog Ser 455:229–244

Blumenthal JM, Abreu-Grobois FA, Austin TJ, Broderick AC, Bruford MW, Coyne MS, Ebanks-Petrie G, Formia A, Meylan PA, Meylan AB, Godley BJ (2009) Turtle groups or turtle soup: dispersal patterns of hawksbill turtles in the Caribbean. Mol Ecol 18:4841–4853. doi:10.1111/j.1365-294X.2009.04403.x

Bolker BM, Okuyama T, Bjorndal KA, Bolten AB (2007) Incorporating multiple mixed-stocks in mixed stock analysis: ‘many-to-many’ analyses. Mol Ecol 16:685–695

Bowen BW, Abreu-Grobois FA, Balazs GH, Kamezaki N, Limpus CJ, Ferl RJ (1995) Trans-Pacific migrations of the loggerhead turtle (Caretta caretta) demonstrated with mitochondrial DNA markers. Proc Natl Acad Sci USA 92:3731–3734

Bowen BW, Bass AL, Chow S-M, Bostrom M, Bjornal KA, Bolten AB, Okuyama T, Bolker BM, Epperly S, Lascasella E, Shaver D, Dodd M, Hopkins-Murphy SR, Musick JA, Swingle M, Rankin-Barnarsky K, Teas W, Witzell WN, Dutton PH (2004) Natal homing in juvenile loggerhead turtles (Caretta caretta). Mol Ecol 13:3797–3808

Bowen BW, Grant WS, Hillis-Starr Z et al (2007) Mixed-stock analysis reveals the migrations of juvenile hawksbill turtles (Eretmochelys imbricata) in the Caribbean Sea. Mol Ecol 16:49–60

Broderick AC, Coyne MS, Fuller WJ, Glen F, Godley BJ (2007) Fidelity and over-wintering of sea turtles. Proc R Soc B 274:1533–1538

Cardona L, Clusa M, Eder E, Demetropoulos A, Margaritoulis D, Rees AF, Hamza AA, Khalil M, Levy Y, Türkozan O et al (2014) Distribution patterns and foraging ground productivity determine clutch size in Mediterranean loggerhead turtles. Mar Ecol Prog Ser 497:229–241
Carreras C, Pont S, Maffucci F, Pascual M, Barcelo A, Bentivegna F, Cardona L, Alegre F, SanFelix M, Fernandez G, Aguilar A (2006) Genetic structuring of immature loggerhead sea turtles (Caretta caretta) in the Mediterranean Sea reflects water circulation patterns. Mar Biol 149:1269–1279

Carreras C, Pascual M, Cardona L, Aguilar A, Margaritoulis D, Rees A, Türkozan O, Levy Y, Gaith S, Aureggi M, Khalil M (2007) The genetic structure of the loggerhead sea turtle (Caretta caretta) in the Mediterranean as revealed by nuclear and mitochondrial DNA and its conservation implications. Conserv Genet 8:761–775

Carreras C, Pascual M, Cardona L, Marco A, Bellido JJ, Castillo JJ, Tomas J, Raga JA, Sanfelix M, Fernandez G, Aguilar A (2011) Living together but remaining apart: Atlantic and Mediterranean loggerhead sea turtles (Caretta caretta) in shared feeding grounds. J Hered 102:666–677

Carreras C, Rees AF, Broderick AC, Godley BJ, Margaritoulis D (2014) Mitochondrial DNA markers of loggerhead marine turtles (Caretta caretta) nesting at Kyparissia Bay, Greece, confirm the western Greece unit and regional structuring. Sci Mar 78(1):115–124

Casale P, Mariani P (2014) The first ‘lost year’ of Mediterranean sea turtles. J Exp Mar Biol Ecol 160:703–718

Casale P, Abbate G, Freggi D, Conte N, Olivero M, Argano R (2008) A model of connectivity of juvenile loggerhead turtles (Caretta caretta) tracked using satellite telemetry and stable isotopes. PLoS One 7(9):e45335. doi:10.1371/journal.pone.0045335

Clusa M, Carreras C, Pascual M, Demetropolis A, Margaritoulis D, Rees AF, Hamza AA, Khalil M, Aureggi M, Levy Y, Türkozan O, Marco A, Aguilar A, Cardona L (2013) Mitochondrial DNA reveals Pleistocene colonisation of the Mediterranean by loggerhead turtles (Caretta caretta). J Exp Mar Biol Ecol 439:15–24

Cunja C, Carreras C, Pascual M, Gaughan SJ, Piovano S, Giai-coma C, Fernandez G, Levy Y, Thomas J, Rara JA, Maffucci F, Hochscheid Aguilar A, Cardona L (2014) Fine-scale distribution of juvenile Atlantic and Mediterranean loggerhead turtles (Caretta caretta) in the Mediterranean Sea. Mar Biol 161:509–519

Cooke SJ (2008) Biotelemetry and biologging in endangered species research and animal conservation: relevance to regional, national, and IUCN Red List threat assessments. Endang Spec Res 4:165–185

Coyne MS, Godley BJ (2005) Satellite tracking and analysis tool (STAT): an integrated system for archiving, analyzing and mapping animal tracking data. Mar Ecol Prog Ser 271:7–17

Domeier ML, Nasby-Lucas N (2008) Migration patterns of white sharks Carcharodon carcharias tagged at Guadalupe Island, Mexico, and identification of an eastern Pacific shared offshore foraging area. Mar Ecol Prog Ser 370:221–237

Drummond AD, Ashton B, Buxton S, Cheung M, Cooper A, Heled J, Kearse M, Moir R, Stones-Havas S, Sturrock S, Thirier T, Wilson A (2011) Geneious v5.5. http://www.geneious.com

Ehrhart LM, Ogren LH (1999) Studies in foraging habitats: capturing and handling turtles. In: Eckert KL, Bjorndal KA, Abreu-Grobois FA, Donnelly M (eds) Research and management techniques for the conservation of sea turtles. IUCN/SSC Mar Turtle Spec Group Publ No. 4, pp 61–64

Engstrom TN, Meylan PA, Meylan AB (2002) Origin of juvenile loggerhead turtles (Caretta caretta) in a tropical developmental habitat in Caribbean Panama. Anim Conserv 5:125–133

Field IC, Bradshaw CIA, Burton HR, Sumner MD, Hindell MA (2005) Resource partitioning through oceanic segregation of foraging juvenile southern elephant seals (Mirounga leonina). Oecologia 142:127–135

Fujiko e, Halpin PN (2014) Spatio-temporal assessments of biodiversity in the high seas. Endang Species Res 24:181–190. doi:10.3354/esr00591

Garofalo L (2010) The Genetics of the loggerhead turtle (Caretta caretta) in Italy: from scientific data to public knowledge—PhD dissertation. Università Tor Vergata, Roma

Garofalo L, Mingozi T, Mico A, Novello A (2009) Loggerhead turtle (Caretta caretta) matrilines in the Mediterranean: further evidence of genetic diversity and connectivity. Mar Biol 156:2085–2095

Garofalo L, Mastrogiacomo A, Casale P, Carlini R, Eleni C, Freggi D, Gelli D, Knittweis L, Mifsud C, Mingozi T, Novarini N, Scaravelli D, Scillitani G, Oliverio M, Novello A (2013) Genetic characterization of central Mediterranean stocks of the loggerhead turtle (Caretta caretta) using mitochondrial and nuclear markers, and conservation implications. Aquat Conserv 23:868–884. doi:10.1002/aqc.2338

Gerber LR, Heppell SS (2004) The use of demographic sensitivity analysis in marine species conservation planning. Biol Conserv 120:121–128

Giovannetti M, Franzellitti S, Cerioni PN, Fabbri E, Guccione S, Val-lini C, Tinti F, Caputo V (2010) Genetic characterization of log-gerhead turtle (Caretta caretta) individuals stranded and caught by bycatch from the North-Central Adriatic Sea. Amphibia-Reptilia 31:127–133

Godley BJ, Richardson S, Broderick AC, Coyne MS, Glen F, Hays GC (2002) Long-term satellite telemetry of the movements and habitat utilisation by green turtles in the Mediterranean. Ecogra phy 25:352–362

Godley BJ, Lima EHS, Åkesson S, Broderick AC, Glen F, Godfrey MH, Luschi P, Hays GC (2003) Movement patterns of green turtles in Brazilian coastal waters described by satellite tracking and flipper tagging. Mar Ecol Prog Ser 253:279–288

Godley BJ, Blumenthal JM, Broderick AC, Coyne MS, Godfrey MH, Hawkes LA, Witt MJ (2008) Satellite tracking of sea turtles: Where have we been and where do we go next? Endang Species Res 4:3–22

Godley BJ, Barbosa C, Bruford M, Broderick AC, Catry P, Coyne MS, Formia A, Hays GC, Witt MJ (2010) Unravelling migratory connectivity in marine turtles using multiple methods. J Appl Ecol 47:769–778. doi:10.1111/j.1365-2664.2010.01817.x

Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symp Ser 41:95–98
Hawkes LA, Broderick AC, Coyne MS, Godfrey MH, Godley BJ (2007) Only some like it hot—quantifying the environmental niche of the loggerhead sea turtle. Diversity Distrib 13:447–457

Hays GC, Hayes JP, Priede IG, French J (1991) Satellite tracking of a loggerhead turtle (Caretta caretta) in the Mediterranean. J Mar Biol Ass UK 71:743–746

Hays GC, Broderick AC, Lovell P, Martin C, McConnell BJ, Richardson S (2002) Biphonal long-distance migration in green turtles. Anim Behav 64:895–898

Hays GC, Rosso S, Katselidis KA, Mariani P, Schofield G (2010a) Ontogenetic development of migration: lagrangian drift trajectories suggest a new paradigm for sea turtles. J R Soc Interface 7:1319–1327

Hays GC, Rosso S, Katselidis KA, Mariani P, Schofield G, Gravenor MB (2010b) Breeding periodicity for male sea turtles, operational sex ratios, and implications in the face of climate change. Conserv Biol 24:1636–1643

Hays GC, Mazaris AD, Schofield G (2014) Different male vs female breeding periodicity helps mitigate offspring sex ratio skews in sea turtles. Front Mar Sci 1:43. doi:10.3389/fmars.2014.00043

Heppell SS, Snover ML, Crowder LB (2003) Sea turtle population ecology. In: Lutz PL, Musick JA, Wyneken J (eds) The biology of sea turtles, vol II, CRC Press, Boca Raton, pp 275–306

Hochscheid S, Bertivegna F, Hamza A, Hays GC (2010) When suffered do not dive: multiple significance of extended surface times in marine turtles. J Exp Biol 213:1328–1337

Jeffers VF, Godley BJ (2016) Satellite tracking in sea turtles: How do we find our way to the conservation dividends? Biol Conserv 199:172–184. doi:10.1016/j.biocon.2016.04.032

Jodice PGR, Suryan RM (2010) The translational nature of seabird ecology. In: Trombulak SC, Baldwin RF (eds) Landscape-scale conservation planning. Springer, Dordrecht, pp 139–165

Kennedy AS, Zerbini AN, Rone BK, Clapham PJ (2014) Individual variation in movements of satellite tracked humpback whales Megaptera novaeangliae in the eastern Aleutian Islands and Bering Sea. Endang Species Res 23:187–195. doi:10.3354/ers00570

LaCasella EL, Epperly SP, Jensen MP, Stokes L, Dutton PH (2013) Genetic stock composition of loggerhead turtles Caretta caretta bycaught in the pelagic waters of the North Atlantic. Endang Species Res 22:73–84. doi:10.3354/ers00535

Lahanas PN, Bjornadal KA, Bolten AB, Encalada SE, Miyamoto MM, Valverde RA, Bowen BW (1998) Genetic composition of a green turtle (Chelonia mydas) feeding ground population: evidence for multiple origins. Mar Biol 130:345–352

Laurent L, Casale P, Bradai MN, Godley BJ, Gerosa G, Broderick AC, Schrot W, Schierwater B, Levy AM, Freggi D, Abd El-Mawla EM, Hadoud DA, Gomati HE, Domingo M, Hadjichristophorou M, Kornaraki L, Demirayak F, Gautier C (1998) Molecular resolution of marine turtle stock composition in fishery bycatch: a case study in the Mediterranean. Mol Ecol 7:1529–1542

Lazar B, Margaritoulis M, Tvrkovic N (2004) Tag recoveries of loggerhead sea turtle Caretta caretta in the eastern Adriatic Sea: implications for conservation. J Mar Biol Ass UK 84:475–480

Leroux RA, Dutton PH, Abreu-Grobois FA, Lagueux CJ, Campbell CL, Delcroix E, Chevalier J, Horrocks JA, Hillis-Starr Z, Tréong S, Harrison E, Stapleton S (2012) Re-examination of population structure and phylogeography of hawksbill turtles in the wider Caribbean using longer mtDNA sequences. J Hered 103(6):806–820

Limpus CJ, Limpus DJ (2001) The loggerhead turtle, Caretta caretta, in Queensland: breeding Migrations and fidelity to a warm temperate feeding area. Chelon Conserv Biol 4:142–153

López-Jurado LF, Sanz P, Abella E (2007) Loggerhead nesting on Boa Vista, República de Cabo Verde. The State of the World’s Sea Turtles, Report

Luke K, Horrocks JA, LeRoux RA, Dutton PH (2004) Origins of green turtle (Chelonia mydas) feeding aggregations around Barbados, West Indies. Mar Biol 144:799–805

Maffucci F, Kooistra WHCF, Bentivegna F (2006) Natal origin of loggerhead turtles, Caretta caretta, in the neritic habitat off the Italian coasts, Central Mediterranean. Biol Conserv 127:183–189

Mansfield K, Saba VS, Keinath JA, Musick JA (2009) Satellite tracking reveals a dichotomy in migration strategies among juvenile loggerhead turtles in the Northwestern Atlantic. Mar Biol 156:2555–2570

Marcovaldi MA, Lopez GG, Soares LS, Lima EHS, Thomé JCA, Almeida AP (2010) Satellite-tracking of female loggerhead turtles highlights fidelity behavior in northeastern Brazil. Endang Species Res 12:263–272

Margaritoulis D (1998) Interchange of nesting loggerheads among Greek beaches. In: Epperly S P, Braun J (eds) Proceedings of the 17th annual sea turtle symposium, NOAA Tech Memo. NMFS-SEFSC-415: 225-227

Margaritoulis D, Rees AF (2011) Loggerhead turtles nesting at Rethymno, Greece, prefer the Aegean Sea as their main foraging area. Mar Turtle Newslett 131:12–14

Margaritoulis D, Argano R, Baran I, Bentivegna F et al (2003) Loggerhead turtles in the Mediterranean Sea: present knowledge and conservation perspectives. In: Bolten AB, Witherington BE (eds) Loggerhead sea turtles. Smithsonian Books, Washington, pp 175–198

McClellan CM, Read AJ (2007) Complexity and variation in loggerhead sea turtle life history. Biol Lett 3:592–594

Monzón-Argüello C, Dell’Amico F, Morinière P, Marco A, López-Jurado LF, Bolten GC, Scott R, Marsh R, Lee PLM (2012) Lost at sea: genetic, oceanographic and meteorological evidence for storm-forced dispersal. J R Soc Interface 9:1725–1732

Moritz C (1994) Applications of mitochondrial DNA analysis in conservation: a critical review. Mol Ecol 3:401–411

Nishizawa H, Narazaki T, Fukuoka T, Sato K, Hamabata T, Kinoshita M, Arai N (2014a) Juvenile green turtles on the northern edge of their range: mtDNA evidence of long-distance westward dispersals in the northern Pacific Ocean. Endang Species Res 24:171–179. doi:10.3354/ers00592

Nishizawa H, Narazaki T, Fukuoka T, Sato K, Hamabata T, Kinoshita M, Arai N (2014b) Genetic composition of loggerhead turtle feeding aggregations: migration patterns in the North Pacific. Endang Species Res 24:85–93. doi:10.3354/ers00588

Okuyama T, Bolker BM (2005) Combining genetic and ecological data to estimate sea turtle origins. Ecol Appl 15:315–325

Pajuelo M, Bjornadal KA, Reich KJ, Vander Zanden HB, Hawkes LA, Bolten AB (2012) Assignment of nesting loggerhead turtles to their foraging areas in the Northwest Atlantic using stable isotopes. Ecosphere 3:89. doi:10.1890/ES12-00220.1

Pella J, Masuda M (2001) Bayesian methods for analysis of stock mixtures from genetic characters. Fish Bull 99:151–167

Pendoley KL, Schofield G, Whittock PA, Ierodiaconou D, Hays GC (2014) Protected species use of a coastal marine turtle migratory corridor connecting Australian MPAs. Mar Biol 161:1455–1466

Pilcher NJ, Al-Masmali I, Williams J, Gasang R, Chikhi A (2015) Population structure of marine turtles in coastal waters of Qatar. Endang Species Res 28:163–174. doi:10.3354/esr00688

Prosdocimi L, Garman VG, Albareda DA, Remis MJ (2012) Genetic composition of green turtle feeding grounds in coastal waters of Argentina based on mitochondrial DNA. J Exp Mar Biol Ecol 412:37–45

Reece JS, Ehnhart LM, Parkinson CL (2006) Mixed stock analysis of juvenile loggerheads (Caretta caretta) in Indian River Lagoon, Florida: implications for conservation planning. Conserv Genet 7:345–352
Shamblin BM, Bolten AB, Bjorndal KA, Dutton PH, Nielsen JT, Rees AF, Margaritoulis D, Newman R, Riggall TE, Tsaros P, Zbinden JA, Godley BJ (2013) Ecology of loggerhead marine turtles Caretta caretta in a neritic foraging habitat: movements, sex ratios and growth rates. Mar Biol 160:519–529

Roberts MA, Anderson CJ, Stender B et al (2005) Estimated contribution of Atlantic coastal loggerhead turtle nesting populations to offshore feeding aggregations. Conserv Genet 6:133–139

Saied A, Maffucci F, Hochscheid S, Dryag S, Swayeb B, Borra M, Ouerghi A, Procaccini Bentivegna F (2012) Loggerhead turtles nesting in Libya: an important management unit for the Mediterranean stock. Mar Ecol Prog Ser 450:207–218

Schofield G, Hobson VJ, Fossette S, Lilley MKS, Katselidis KA, Hays GC (2010) Fidelity to foraging sites, consistency of migration routes and habitat utilization of home range by sea turtles. Divers Distrib 16:840–853

Schofield G, Dimadi A, Fossette S, Katselidis KA, Koutsoubas D, Lilley MKS, Luckman A, Pantis JD, Karagouni AD, Hays GC (2013) Satellite tracking large numbers of individuals to infer population level dispersal and core areas for the protection of an endangered species. Divers Distrib 19:834–844. doi:10.1111/dad.12077

Schroth W, Streit B, Schierwater B (1996) Evolutionary handicap for turtles. Nature 384:521–522

Seminoff JA, Eguchi T, Carretta J, Allen CD, Prosperi D, Rangel R, Gilpatrick JW Jr, Forney K, Peckham SH (2014) Loggerhead sea turtle abundance at a foraging hotspot in the eastern Pacific Ocean: implications for at-sea conservation. Endang Species Res 24:207–220. doi:10.3354/esr00601

Shamblin BM, Bolten AB, Bjordal KA, Dutton PH, Nielsen JT, Abreu-Grobois FA, Reich KJ, Witherington BE, Bagley DA, Den JA, Godley BJ (2013) Reproductive ecology of the loggerhead turtle, Caretta caretta, on Fethiye and Kizilot beaches, Turkey. Chelon Conserv Biol 3:686–692

Uçar A, Kaska Y, Ergene S, Aymak C, Kaçar Y, Kaska A, Ili P (2012) Sex ratio estimation of the most eastern main loggerhead sea turtles nesting site: Anamur Beach, Mersin, Turkey. Isr J Ecol Evol 58:87–100

Van Dam RP, Diez CE, Balazs GH, Colon Colon LA, McMillan WO, Schroeder B (2008) Sex-specific migration patterns of hawksbill turtles breeding at Mona Island, Puerto Rico. Endang Spec Res 4:85–94

Wallace BP, DiMatteo AD, Hurley BJ, Finkbeiner EM, Bolten AB et al (2010) Regional management units for marine turtles: a novel framework for prioritizing conservation and research across multiple scales. PLoS One 5:e15465. doi:10.1371/journal.pone.0015465

Watanabe KK, Hatase H, Kinoshita M, Oikawa B, Tando N, Kamegake K, Nato K, Matsuzawa Y, Goto K, Nakashima Y, Takeshi H, Aoyama J, Tsukamoto K (2011) Population structure of the loggerhead turtle Caretta caretta, a large marine carnivore that exhibits alternative foraging behaviors. Mar Ecol Prog Ser 424:273–283

Webster MS, Peter P, Haig SM, Bensch S, Holmes RT (2002) Links between worlds: unraveling migratory connectivity. Trends Ecol Evol 17:64–68

Weimerskirch H, Åkesson S, Pinaud D (2006) Postnatal dispersal of wandering albatrosses Diomedea exulans: implications for the conservation of the species. J Avian Biol 37:23–28

White M, Haxhiu H, Kararaj E, Mitro M, Petri L, Saçdanakë E, Trehznjëvna B, Boura L, Grimanis K, Robinson P, Venizelos L (2011) Monitoring and conservation of important sea turtle feeding grounds in the Patok Area of Albania 2008–2010. Final Project Report (Unpublished), pp 68

Witt MJ, Hawkes LA, Godfrey MH, Godley BJ, Broderick AC (2010a) Predicting the impacts of climate change on a globally distributed species: the case of the loggerhead turtle. J Exp Biol 213:901–911

Witt MJ, Åkesson S, Broderick AC, Coyne MS, Ellick J, Formia A, Hays GC, Luschi P, Stroud S, Godley BJ (2010b) Assessing accuracy and utility of satellite-tracking data using Argos-linked Fastloc-GPS. Anim Behav 80:571–581

Wright LL, Stokes KL, Fuller WJ, Godley BJ, McGowan A, Snape R et al (2012) Turtle mating patterns buffer against disruptive effects of climate change. Proc R Soc B 279:2122–2127. doi:10.1098/rspb.2011.2285

Yilmaz C, Türköz O, Bardacki F (2011) Genetic structure of loggerhead turtle (Caretta caretta) populations in Turkey. Biochem Systemat Ecol 39:266–276

Yilmaz C, Türköz O, Bardacki F, White M, Kararaj E (2012) Loggerhead turtles (Caretta caretta) foraging at Drini Bay in Northeastern Albania: Genetic characterisation reveals new haplotypes. Acta Herpetol 7:155–162

Zbinden JA, Davy C, Margaritoulis D, Arlettaz R (2007) Large spatial variation and female bias in the estimated sex ratio of loggerhead sea turtle hatchlings of a Mediterranean rookery. Endang Spec Res 3:305–312

Zbinden JA, Bearthop S, Bradshaw P, Gill B, Margaritoulis D, Newton J, Godley BJ (2011) Migratory dichotomy and associated phenotypic variation in marine turtles revealed by satellite tracking and stable isotope analysis. Mar Ecol Prog Ser 421:291–302

Zerbini AN, Andriolo A, Heide-Jorgensen MP, Pizzorno JL et al (2006) Satellite-monitored movements of humpback whales Megaptera novaeangliae in the Southwest Atlantic Ocean. Mar Ecol Prog Ser 313:295–304