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ORIGINAL ARTICLE

# Post-release survival of loggerhead sea turtles bycaught in demersal trawls in overwintering habitats of the Adriatic Sea

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**Abstract:** Fishery-related mortality is a major anthropogenic threat to marine megafauna, and gear-specific estimates are essential for effective conservation management of populations. We assessed cryptic post-release survival of loggerhead turtles (*Caretta caretta*) incidentally captured in a Croatian demersal-trawl fishery operating in overwintering habitats of the northern Adriatic Sea at depths of 45–84 m, with a mean tow duration of 390 ± 43 min. Ten individuals with a mean carapace length of 57.2 ± 9.4 cm were equipped with Argos-linked platform transmitter terminals with a pressure sensor and released after regaining activity following 15–90 min of on-board recovery. We inferred individual fate (dead/alive) from transmission continuity, movement trajectories, location-class composition and submergence records. Nine animals provided telemetry data and exhibited biologically plausible movements and repeated diving beyond the 15-day post-release threshold period, with total tracking durations of 94–512 days. Apparent survival was conservatively estimated at 90% (9/10; exact 95% confidence interval 55.5–99.7%), suggesting the conservation value of this on-board recovery procedure for the reduction of delayed mortality of sea turtles in demersal trawl fisheries.
***Keywords***: *Caretta caretta*; satellite telemetry; fishing mortality; incidental catch; on-board recovery; bycatch mitigation; Mediterranean Sea

**Sažetak:** PREŽIVLJAVANJE GLAVATIH ŽELVI SLUČAJNO ULOVLJENIH PRIDNENIM KOĆAMA U ZIMOVALIŠTIMA JADRANSKOG MORA. Ribolovna smrtnost predstavlja glavnu antropogenu prijetnju morskoj megafauni, a procjene smrtnosti koje su posljedica korištenja pojedinih ribolovnih alata nužne su za učinkovito upravljanje i zaštitu njihovih populacija. Ovim istraživanjem ocijenili smo kriptične stope preživljavanja glavate želve (*Caretta caretta*) nakon slučajnog ulova pridnenim koćama u zimovalištima hrvatskog akvatorija sjevernog Jadrana na dubinama od 45–84 m, sa srednjim trajanjem potega od 390 ± 43 min. Deset jedinki prosječne duljine oklopa 57,2 ± 9,4 cm opremljeno je satelitskim odašiljačima sa senzorom tlaka povezanim s Argos-satelitskim sustavom te pušteno u aktivnom stanju nakon 15–90 min oporavka na plovilu. Status preživljavanja svake jedinke (uginula/preživjela) nakon puštanja ocijenjen je na temelju kontinuiteta odašiljanja signala, putanje kretanja, sastava lokacijskih razreda i podataka o zaronima. Nakon prijelaznog perioda od 15 dana nakon puštanja, devet jedinki davalo je telemetrijske podatke koji su ukazivali na biološki vjerodostojna kretanja i opetovane zarone, uz ukupno vrijeme praćenja od 94 do 512 dana. Konzervativna procjena preživljavanja iznosila je 90 % (9/10; egzaktni 95 %-tni interval pouzdanosti: 55,5–99,7 %), što upućuje na konzervacijsku vrijednost primijenjenog postupka oporavka životinja na plovilu kao načina smanjenja naknadne smrtnosti morskih kornjača nakon slučajnog ulova u pridnene koće.
***Ključne riječi***: *Caretta caretta*; satelitska telemetrija; ribolovna smrtnost; prilov; oporavak na plovilu; smanjenje prilova; Sredozemno more

## INTRODUCTION

Fishery-related mortality is a major anthropogenic threat to marine megafauna and has contributed to population declines globally (Lewison *et al.,* 2004; Pacoureau *et al.,* 2021; VanCompernolle *et al*., 2026). Wide-ranging movements, extensive spatial overlap with fishing activity and repeated exposure to multiple gears increase the susceptibility of these taxa to both industrial and small-scale fisheries (Lewison *et al.,* 2004). Fisheries bycatch is consistently identified as one of the most widespread anthropogenic threats to sea turtles (Wallace *et al.,* 2011, 2013), and has been assessed as moderate to high globally and particularly high in the Mediterranean, substantially exceeding direct take, coastal development, pollution, and climate change (Wallace *et al.,* 2025). In the Mediterranean Sea alone, bottom-trawl, longline and set-net fisheries were estimated to capture more than 132,000 turtles and cause more than 44,000 incidental deaths annually (Casale, 2011). Life-history traits of sea turtles limit their capacity to compensate for additional fishery-related mortality, and population growth is espe-

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cially sensitive to the survival of large neritic juveniles and adults with high reproductive value (Heppell *et al.,* 2003; Wallace *et al.,* 2008). Fisheries that capture these stages may therefore exert demographic effects disproportionate to the number of animals removed from the population (Wallace *et al.,* 2008).

Demersal trawls are of particular concern because they operate in neritic feeding and overwintering habitats and capture large-sized turtles (Wallace *et al.,* 2008, 2013). A turtle entering a trawl remains forcibly submerged until it escapes or the net is retrieved, and mortality risk is influenced by animal condition and activity, tow duration, capture depth and the timing of entry into the net (Poiner and Harris, 1996; Sasso and Epperly, 2006; Fahlman *et al.,* 2017). Early assessments of seaturtle survival and mortality associated with demersal-trawl bycatch focused mainly on drowning during forced submergence and injuries sustained during capture and handling (Poiner and Harris, 1996; Casale *et al.*, 2004; Casale, 2011). However, more recent clinical studies have documented an unexpectedly high prevalence of intravascular gas embolism (GE) in several species of sea turtles, arising from gas-bubble formation within supersaturated blood and tissues after decompression, and have assessed the contribution of GE and decompression sickness to both direct and delayed mortality in animals incidentally captured in trawls and other demersal fishing gears (García-Párraga *et al.,* 2014; Fahlman *et al.,* 2017; Crespo-Picazo *et al.,* 2020; Parga *et al.,* 2020; Franchini *et al.*, 2021; García-Párraga *et al.,* 2023).

In demersal trawls, direct mortality at haulback represents only the immediately observable component of fishery-related mortality in sea turtles and may substantially underestimate total mortality because it excludes animals retrieved alive but comatose or physiologically compromised that may subsequently die on board or after release (Casale *et al.,* 2004; Parga *et al.,* 2020). The proportion of turtles classified as comatose at haulback in demersal trawls generally ranges from 21 to 34% (Poiner and Harris, 1996; Casale *et al.,* 2004, 2017), and these animals may contribute substantially to total mortality if released while unconscious and inactive (Sasso and Epperly, 2006; Franchini *et al*., 2021). Therefore, international guidance recommended keeping unresponsive turtles on board and applying a simple recovery protocol until regular breathing and spontaneous activity resume before release back into the sea (Gerosa and Aureggi, 2001; FAO, 2009). However, apparent recovery of activity on board does not necessarily indicate complete physiological recovery (Franchini *et al.,* 2021), making at-sea post-release fate an important but poorly quantified component of fishing mortality. Quantifying this cryptic post-release mortality is essential for understanding and managing fishery-related mortality, particularly in K-selected species. In sea turtles, most telemetry-based estimates of post-release mortality come from pelagic longline fisheries, whereas estimates for demersal trawls remain exceptionally scarce (Chaloupka *et al.,* 2022).

In the Mediterranean Sea, fishery bycatch has been recognized as a major anthropogenic threat to sea turtles (Casale *et al.,* 2018), with the resulting fisheries-induced mortality at unsustainable levels and slowing population recovery (Casale and Heppell, 2016; Omeyer *et al.*, 2021). The extensive continental shelf of the Adriatic Sea supports the largest neritic habitats for loggerhead turtles (*Caretta caretta*) in the region (Lazar *et al.,* 2011a; Casale *et al.,* 2018) and is used almost exclusively by individuals originating from Mediterranean nesting populations (Lazar *et al.,* 2004; Schofield *et al.,* 2010; Tolve *et al.,* 2018; Bertuccio *et al.,* 2019; Haywood *et al*., 2020). High turtle densities (Fortuna *et al.,* 2018; DiMatteo *et al*., 2022) and year-round residency (Jančič *et al.,* 2026) overlap spatially with intensive demersal fishing, especially on the shallow northern Adriatic shelf (Casale *et al.,* 2004; Lucchetti *et al.,* 2016; Jančič *et al*., 2025). The Adriatic is consequently recognized as a major Mediterranean bycatch hotspot, with an estimated 28,000 captures annually, including over 18,000 interactions with trawl fisheries (Carpentieri *et al.,* 2021; Carbonara *et al.,* 2025). Italian and Croatian demersal-trawl fisheries operating in the northern Adriatic mostly affect large-sized loggerhead turtles in overwintering habitats, resulting in direct mortality of 7.5–9.4%; however, when comatose cases are included, potential mortality may increase to 26.9–43.8% (Casale *et al.,* 2004; Lazar *et al.,* 2011b).

On-board recovery protocols have been promoted in the Mediterranean as a tool to reduce bycatch-related mortality (Gerosa and Aureggi, 2001) and implemented through several EU projects (e.g., the IPA Adriatic NETCET; LIFE15 NAT/HR/000997; LIFE12 NAT/IT/000937; LIFE18 NAT/IT/000103, and others). However, to the best of our knowledge, no study in the Mediterranean has evaluated the effectiveness of this conservation method by quantifying the at-sea survival of recovered trawl-caught turtles, particularly when animals were returned to a cold thermal environment. The present study therefore aimed to (i) estimate the apparent post-release survival of loggerhead turtles captured by demersal trawls under low-temperature conditions using satellite telemetry, thereby addressing a major knowledge gap in mortality rates of demersal-trawl fisheries, and (ii) assess the conservation value of on-board recovery for sea turtles incidentally captured by this fishing gear.

## MATERIAL AND METHODS

### Study animals, transmitters and data processing

We deployed Argos-linked platform transmitter terminals (PTTs) equipped with a pressure sensor (model TAM-4425-3, Telonics Inc., AZ, USA) on 10 loggerhead turtles with a curved carapace length (CCL) ranging from 47.0 to 74.0 cm (mean CCL: 57.2 ± 9.4 cm). All animals were incidentally captured during routine commercial bottom-trawl operations off Lošinj Island

in the north-eastern Adriatic Sea, Croatia, between 19 January and 1 March 2015, corresponding to the coldest period in the northern Adriatic (Jančič *et al.,* 2026). Trained on-board observers monitored fishing trips of collaborating vessels which operated at depths of 45–84 m, with a mean tow duration of 390 ± 43 min and a mean towing speed of 1.13 ± 0.05 m $s^{-1}$ (2.2 ± 0.1 knots), and targeted demersal fishes.

At retrieval, four turtles were weakly responsive with slow flipper movements and occasional head lifting, whereas six showed no signs of activity and were provisionally classified as comatose. We precautionary applied an on-board recovery protocol adapted from Gerosa and Aureggi (2001) to all ten bycaught loggerhead turtles. Each turtle was kept sheltered on its plastron, with the posterior part of the body elevated so that the head was slightly lower, and was monitored until activity returned. No medication or other supportive treatment was administered. All turtles regained spontaneous activity (active movements of flippers and lifting of the head) within 15–90 min. After recovery, each animal was equipped with a PTT attached to the second vertebral carapace scute with a two-part epoxy resin (Power Fasteners) following a common cleaning protocol for hard-shell sea turtles (Witt *et al.,* 2010), and double-tagged with external tags attached to front or rear flippers. Seven turtles were released into the sea directly from fishing vessels in the area of capture, whereas three individuals, captured during the final haul before returning to the landing port, were released immediately upon arrival from a beach on the island of Lošinj (Fig. 1).

The PTTs were assigned one of the two duty cycles: 11 h on/37 h off or 11 h on/13 h off, with both schedules using a 45-s repetition interval and a daily limit of 300 messages to extend battery life. They were programmed to classify a continuous wet interval (submergence) from the saltwater switch longer than 5 seconds as a dive. During these dives, the PTT calculated the proportion of time spent at different depth layers during two 12-hour periods *per* day. The difference between the sum of these proportions and one represented the proportion of time spent at the surface (PTT wet for less than 5 seconds). Data were collected through the Argos satellite system and transferred automatically to the Satellite Tracking and Analysis Tool (STAT; Coyne and Godley, 2005). STAT also supplied sea-surface temperature (SST) associated with estimated locations from NOAA Geostationary Operational Environmental Satellites.

For each individual, we calculated tracking duration (number of days between release date and last uplink to Argos), and the number of locations based upon seven location classes (LCs) of accuracy level 3, 2, 1, A, B, 0, and Z, which is deemed an invalid location estimate (Witt *et al*., 2010). LC3–LC1 have nominal error estimates of decreasing precision (<250 m, 250–500 m and 500–1500 m, respectively), whereas LC0 denotes an error estimate >1500 m. LCA and LCB have no fixed nominal accuracy estimate (Hays *et al*., 2001; Royer




**Fig. 1**. Inactive, comatose loggerhead turtle following incidental capture in a bottom trawl in the northern Adriatic Sea **(A)**; release of turtles equipped with Argos-linked PTTs following application of the on-board recovery protocol from a beach on Lošinj Island **(B)** and at sea **(C)**. Authors of photographs: Bojan Lazar **(A, B)** and Tilen Genov **(C)**.

and Lutcavage, 2008), although empirical errors of 3.5 ± 9.2 km and 14.3 ± 135.6 km, respectively, have been reported for sea-turtle tracking data (Witt *et al.,* 2010). For subsequent analysis, we used the whole, unfiltered location dataset, while for track visualization purposes we removed locations on land and those with LCZ and filtered the remaining data to exclude locations requiring unrealistic speeds of movements (>8 km/h; Jančič *et al.,* 2026).

### Post-release fate and apparent survival

We used PTTs, rather than dedicated survivorship tags designed to detect mortality events. Hence, we inferred the fate of individual turtles (apparent survival or suspected mortality) indirectly, integrating multiple lines of evidence based on telemetry indicators: (i) continuity and temporal pattern of transmissions, (ii) movement trajectories, (iii) composition of Argos location classes, and (iv) dive records. The latter two indicators were split into the early post-release period (days 0–14) and a later period of tracking (day 15 to the end of transmission). We applied this 15-day cutoff as a conservative temporal threshold for estimating apparent post-release survival, as it exceeds the 6-day period within which, in previous studies, all observed post-release deaths occurred among satellite-tagged, trawl-caught turtles (Maxwell *et al.,* 2018; Parga *et al.,* 2020), and it encompasses the 2–13-day period over which radiographic gas emboli resolved in surviving loggerheads diagnosed with gas embolism (Franchini *et al.,* 2021). Every fate assignment required concordance among at least two types of telemetry indicators.

During normal diving, short and intermittent surfacing opportunities in sea turtles can limit the number and temporal spread of messages received during a satellite pass and thereby reduce the frequency of high-quality Argos positions (Hays *et al.,* 2001; Witt *et al.,* 2010). Hays *et al.* (2003) showed that inferred capture can produce the opposite signature: an abrupt increase in high-quality positions (LCs 3, 2 and 1) when a transmitter remains continuously exposed to air, particularly when the change is accompanied by cessation of submergence and movement towards or onto land. Accordingly, we evaluated temporal changes in the proportion of LCs and summarized the cumulative proportion of LC0, LCA, LCB and LCZ. The predominance of these low-quality LCs in the tracking data was an indication of apparent continued survival of the individual. In addition, a turtle was classified as an apparent survivor when the PTT continued to record biologically plausible movement and continuous submergence, indicating active dive patterns of free-ranging loggerheads (Hochscheid *et al*., 2005, 2007; Broderick *et al.,* 2007; Foley *et al.*, 2014). Conversely, suspected recapture or mortality was assigned when an abrupt and sustained rise in high-quality LCs coincided with cessation of diving and anomalous stationary, landward or inland movement, without the subsequent return to normal behaviour. Turtles for which telemetry indicators were conflicting or insufficient were classified as indeterminate.

For statistical comparisons between the early and later tracking periods, each turtle was treated as an independent sampling unit, to avoid pseudo-replication of dependent repeated measurements from the same individual (Hurlbert, 1984). We calculated the cumulative proportion of low-quality LC classes (A, B, 0 and Z) and the mean proportion of time assigned to dives longer than 5 s for each period separately. Differences between the two tracking periods were tested using a paired Wilcoxon signed-rank test, with p-values adjusted using the Holm procedure for multiple comparisons (Zar, 2010). This comparison was performed for submergence only, as the surface-associated time is the exact complement of time assigned to dives.

Apparent post-release survival was calculated as (i) the proportion of turtles classified as apparent survivors among all individuals with classifiable telemetry outcomes, comprising apparent survivors and suspected recaptures or mortalities, and (ii) a conservative apparent post-release survival estimate, calculated as a proportion of apparent survivors in the complete tagged sample, including also non-reporting or otherwise indeterminate individuals without classifying them as confirmed mortalities. We calculated confidence intervals (95% CI) of post-release survival according to the Clopper–Pearson exact method for a binomial distribution (Zar, 2010). Data processing, visualization and statistical analysis were performed in R statistical software (version 4.5.2; R Core Team, 2025), whilst sensor data were processed by the program TDC (Telonics Data Converter, Telonics Inc.). Maps were produced using QGIS (version 3.40; QGIS Development Team, 2026). Summary statistics are presented as mean ± standard deviation, unless otherwise specified.

## RESULTS

At the end of the 15–90 min on-board recovery period, all ten turtles exhibited spontaneous activity and were released with PTTs. Sea surface temperature at release ranged from 11.2 to 12.4 °C (12.0 ± 0.4 °C, n = 9). Nine transmitters returned usable telemetry data; PTT 140017 returned no Argos data, and the fate of this turtle was therefore classified as indeterminate. For the nine reporting PTTs, tracking duration ranged from 94 to 512 days (222.0 ± 155.6 days; median: 157 days), and 103–3,424 Argos locations were obtained per individual (1,054 ± 968; median: 714; Table 1). Turtles 140013 and 140012 were tracked for 475 and 512 days, respectively, whereas the remaining seven individuals were tracked for 94–161 days. All reporting turtles moved away from their release sites and generated non-stationary tracks in the northern and central Adriatic Sea (Fig. 2A). Several individuals crossed offshore parts of the basin, whereas others remained principally in the northern Adriatic.

**Table 1**. Summary of loggerhead turtles incidentally captured in a Croatian demersal-trawl fishery operating in overwintering habitats of the northern Adriatic Sea, transmitter deployments, release conditions, tracking performance and inferred post-release fate. CCL, curved carapace length; SST, sea-surface temperature; N/A, not available.

| Tag ID | CCL (cm) | Release date | SST (°C) | Last uplink | Tracking (days) | Locations (n) | Inferred fate |
|---|---|---|---|---|---|---|---|
| 140017 | 49.0 | 19 Jan 2015 | N/A | N/A | N/A | N/A | Indeterminate |
| 140011 | 47.0 | 21 Jan 2015 | 12.1 | 9 Jun 2015 | 139 | 617 | Apparent survivor |
| 140013 | 74.0 | 3 Feb 2015 | 11.9 | 23 May 2016 | 475 | 795 | Apparent survivor |
| 140010 | 50.5 | 13 Feb 2015 | 11.2 | 20 Jul 2015 | 157 | 1,469 | Apparent survivor |
| 140014 | 53.0 | 14 Feb 2015 | 12.4 | 25 Jul 2015 | 161 | 714 | Apparent survivor |
| 140016 | 50.0 | 19 Feb 2015 | 12.1 | 23 Jul 2015 | 154 | 683 | Apparent survivor |
| 140015 | 57.0 | 20 Feb 2015 | 12.4 | 15 Jul 2015 | 145 | 525 | Apparent survivor |
| 140018 | 70.0 | 21 Feb 2015 | 12.2 | 26 May 2015 | 94 | 103 | Apparent survivor |
| 140012 | 65.5 | 24 Feb 2015 | 11.8 | 20 Jul 2016 | 512 | 3,424 | Apparent survivor |
| 140009 | 56.0 | 1 Mar 2015 | 11.9 | 9 Aug 2015 | 161 | 1,160 | Apparent survivor |

Note: Means for SST, tracking duration and number of locations are based on the nine reporting PTTs; mean CCL is based on all ten turtles.

For all nine reporting loggerhead turtles, transmission continued beyond the 15-day post-release threshold for a minimum of 79 days (Fig. 2B) with LCs and dive records consistently obtained throughout both tracking periods (Tables 2 and 3). None of the individuals showed a sustained combination of stationary or landward movement, cessation of diving, or a predominant proportion of high-quality Argos positions in the later period. Hence, no telemetry indicator met criteria for suspected mortality or recapture. During the early period, individual PTTs yielded 12–100 locations, of which 22.2–72.7% were assigned to low-quality LCs (Table 2) while in the later period these LCs comprised 57.5–90.8% of locations. The proportion of low-quality LCs increased in seven turtles and decreased in two individuals (140011 and 140015; Table 2). The mean proportion of low-quality LCs significantly increased from 46.7 ± 16.9% in the early to 70.2 ± 10.7% in the late tracking period ($P = 0.020$; Holm-adjusted $P = 0.039$). During days 0–14, individual proportions of time assigned to dives longer than 5 s ranged from 53.1 to 94.6% (78.2 ± 17.9%), compared with 71.1–97.0% (85.7 ± 7.8%) from day 15 onwards. Dive-time proportions increased in five turtles and decreased in four, and the paired difference between periods was not statistically significant ($P = 0.426$; Holm-adjusted $P = 0.426$). The corresponding surface-associated proportions ranged from 5.4 to 46.9% during days 0–14 and from 3.0 to 28.9% during the later period.

We detected no pattern among telemetry indicators meeting the criteria for suspected recapture or mortality in the nine reporting turtles during their tracking periods. All nine classifiable outcomes therefore met the criteria for apparent survival. Apparent post-release survival among turtles with classifiable telemetry outcomes was 100% (9/9; exact 95% CI: 66.4–100.0%). A conservative estimate, in which the indeterminate deployment was retained in the denominator and assigned no survival credit, yielded a minimum apparent survival of 90% (9/10; exact 95% CI: 55.5–99.7%).

## DISCUSSION

Although estimates of survival rates in sea turtles are increasingly available (Pfaller *et al.,* 2018), information on fishery-related mortality remains limited, particularly for cryptic post-release mortality (Chaloupka *et al.,* 2022). To the best of our knowledge, this study provides the first telemetry-based, at-sea assessment of post-release survival following incidental capture in a Mediterranean demersal-trawl fishery. No delayed mortality was previously detected among six trawl-caught turtles monitored for up to 66 h using ultrasonic transmitters and time–depth recorders in eastern Australia, although their diving behaviour had not returned to patterns considered normal by the end of monitoring (Robins and Mayer, 1998). Maxwell *et al.* (2018) confirmed 30-day survival of two of three comatose olive ridleys released after onboard recovery off Gabon; the third apparent mortality was consistent with possible predation, and the contribution of the preceding trawl interaction could not be resolved. In southern Brazil, Parga *et al.* (2020) reported 20% post-release mortality among 15 tagged turtles, with all deaths occurring within six days after release.

All nine loggerhead turtles with classifiable outcomes met the criteria for apparent survival beyond 15 days, yielding 100% apparent survival and a conservative minimum estimate of 90% for the complete tagged sample; both estimates had wide confidence intervals (95% CI: 66.4–100.0% and 55.5–99.7%, respectively). Continued movements of tracked animals and repeated

submergence for 94–512 days demonstrated their survival throughout tracking and recovery from capture. Although pop-up archival and survivorship tags have been commonly used in post-release studies (Swimmer *et al.,* 2006; Sasso and Epperly, 2007; Álvarez de Quevedo *et al.,* 2013; Swimmer *et al.,* 2014; James *et al.,* 2024), we used conventional Argos PTTs, which provided only movement and submergence data. Fate assessment therefore required concordance among at least two telemetry indicators. Hays *et al.* (2003), for example, inferred fisheries capture from PTTs only when improved Argos location quality coincided with cessation of submergence and movement towards or onto land. In our study, for all nine classifiable outcomes the predominance of low-quality LC positions after day 15 (Table 2) coincided with biologically plausible movement (Fig. 2) and continuous diving (Table 3). Turtle 140017 returned no telemetry data. However, cessation of PTT transmission does not necessarily indicate mortality and may result from tag loss, battery exhaustion, antenna damage or saltwater-switch malfunction (Hays *et al.,* 2007), so we conservatively classified this case as indeterminate fate.

Tracked turtles allocated 53.1–94.6% of recorded time to submergences longer than 5 s during days 0–14 and 71.1–97.0% thereafter (Table 3). The mean proportion increased from 78.2 to 85.7%, but the difference

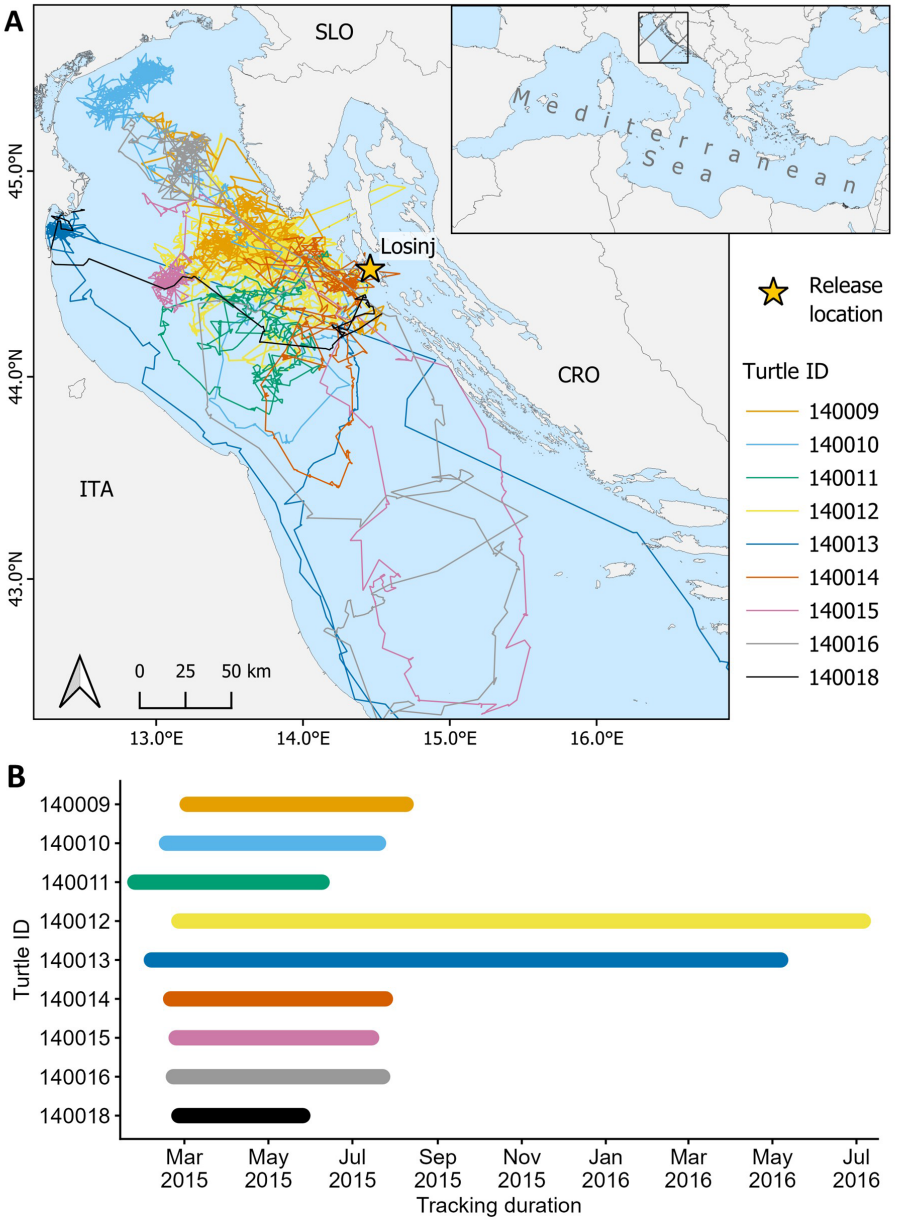



**Fig. 2**. Satellite tracks of nine loggerhead turtles in the Adriatic Sea **(A)** and their tracking durations **(B)**. Turtle identifiers correspond to PTT identifiers (tag ID) in Table 1. CRO - Croatia, ITA - Italy, SLO - Slovenia.

**Table 2.** Argos location-class summaries during the early post-release period (days 0–14) and from day 15 to the end of transmission for the nine loggerhead turtles incidentally captured in a Croatian demersal-trawl fishery operating in overwintering habitats of the northern Adriatic Sea that provided telemetry data. LC - location classes.

| Tag ID | Duty cycle | Days 0–14 | | Day 15–end | |
|---|---|---|---|---|---|
| | | Locations (n) | LC0/A/B (%) | Locations (n) | LC0/A/B (%) |
| 140009 | 11 h/13 h | 20 | 65.0 | 1,140 | 80.3 |
| 140010 | 11 h/13 h | 39 | 41.0 | 1,430 | 74.5 |
| 140011 | 11 h/13 h | 26 | 61.5 | 591 | 57.5 |
| 140012 | 11 h/13 h | 61 | 41.0 | 3,363 | 62.5 |
| 140013 | 11 h/13 h | 100 | 38.0 | 695 | 90.8 |
| 140014 | 11 h/37 h | 62 | 29.0 | 652 | 60.4 |
| 140015 | 11 h/37 h | 22 | 72.7 | 503 | 63.4 |
| 140016 | 11 h/37 h | 63 | 22.2 | 620 | 70.0 |
| 140018 | 11 h/37 h | 12 | 50.0 | 91 | 72.5 |

**Table 3.** Dive-behaviour summaries during the early post-release period (days 0–14) and from day 15 to the end of transmission for the nine loggerhead turtles incidentally captured in a Croatian demersal-trawl fishery operating in overwintering habitats of the northern Adriatic Sea that provided telemetry data.

| Tag ID | Days 0–14 | | | Day 15–end | | |
|---|---|---|---|---|---|---|
| | Records (n) | Surface-associated time (%) | Time in dives >5 s (%) | Records (n) | Surface-associated time (%) | Time in dives >5 s (%) |
| 140009 | 12 | 5.9 | 94.1 | 195 | 10.7 | 89.3 |
| 140010 | 13 | 11.4 | 88.6 | 207 | 12.0 | 88.0 |
| 140011 | 12 | 5.4 | 94.6 | 135 | 15.6 | 84.4 |
| 140012 | 13 | 21.2 | 78.8 | 557 | 18.5 | 81.5 |
| 140013 | 18 | 46.9 | 53.1 | 275 | 3.0 | 97.0 |
| 140014 | 19 | 45.7 | 54.3 | 104 | 28.9 | 71.1 |
| 140015 | 7 | 6.5 | 93.5 | 87 | 16.9 | 83.1 |
| 140016 | 10 | 41.8 | 58.2 | 95 | 18.1 | 81.9 |
| 140018 | 7 | 11.6 | 88.4 | 41 | 4.7 | 95.3 |

Note: Surface-associated time is the proportion not assigned by the PTT to dives longer than 5 s; it may include very brief wet intervals and should not be interpreted as exact time completely out of the water.

was not statistically significant, and individuals displayed heterogeneous diving patterns. Surface-associated time was especially variable early after release and may reflect differences in hypoxia, lactate burden and GE severity experienced by individual animals and, consequently, variable surfacing time required for physiological recovery. All turtles regained spontaneous activity within 15–90 min after being brought on board. However, restoration of ventilation and locomotor responsiveness does not necessarily imply complete metabolic recovery. Clearance of accumulated blood lactate may require approximately 20 h or longer and may be slower at low temperatures (Lutz and Dunbar-Cooper, 1987; Stabenau and Vietti, 2003). Moreover, up to two weeks were required for the disappearance of observable GE-related symptoms in trawl-caught loggerhead turtles (Franchini *et al.,* 2021), so variable surface-associated behaviour during days 0–14 is compatible with ongoing recovery. High submergence proportions are nevertheless consistent with the winter behaviour of Mediterranean loggerheads. In cold water, loggerheads may spend most of their time in resting dives lasting at least 3 h, with maximum dive durations of 270–480 min at temperatures as low as 11.8 °C, while continuing to

surface (Hochscheid *et al*., 2005, 2007). Release SST in our study (11.2–12.4 °C) overlapped this range. A recent tracking study has also demonstrated individual variation in seasonal space use and overwintering strategies of loggerhead turtles in the Adriatic (Jančič *et al*., 2026), so variability in dive patterns between animals and the absence of a uniform early-to-late shift in dive allocation is unsurprising. Nevertheless, all reporting turtles continued to alternate submergence and surfacing throughout tracking, consistent with voluntary diving in free-ranging loggerheads (Hochscheid *et al*., 2005, 2007; Broderick *et al.,* 2007; Foley *et al*., 2014).

For fate assessment of individual animals, we focused particularly on telemetry data obtained after the 15-day threshold, which was selected from the documented timing of delayed deaths in trawl-bycaught turtles. In satellite tracking studies, all confirmed post-release deaths occurred within six days (Maxwell *et al.,* 2018; Parga *et al.,* 2020), whilst Baldi *et al.* (2022) recorded 97.8% of deaths among turtles landed alive and transferred to a rescue center within one week. Severe untreated decompression sickness caused deterioration and death within 48–72 h (García-Párraga *et al.,* 2014), whereas Franchini *et al*. (2021) reported GE-associated deaths occurring within 6–8 h with disappearance of detectable intravascular gas over 2–13 days. These patterns place the 15-day boundary beyond the documented period of acute hypoxia-, drowning- and decompression-related mortality after trawl capture. Nevertheless, this threshold was treated as an operational endpoint for acute apparent survival, rather than a temporal point after which adverse effects are impossible. In longline fisheries, mortality associated with hooking injuries or retained gear has occurred much later, including events after approximately 79–177 days (Sasso and Epperly, 2007; James *et al*., 2024). Although the mechanisms of delayed mortality differ between longline and trawl capture, we accounted for the possibility of mortality after day 15 by evaluating telemetry indicators throughout the complete later tracking period.

Our results indicate high apparent survival of active turtles released after recovery; however, they are accompanied by a wide confidence interval, so they should be interpreted cautiously. Recent clinical studies provided significant insights in rates and physiological mechanisms of delayed mortality in sea turtles but are not directly comparable with at-sea survival. Franchini *et al.* (2021) reported 90% survival among 183 GE-affected loggerheads alive at admission and managed without supportive drug therapy, whereas 96% of 184 GE-positive trawl-caught turtles survived under clinical care and hyperbaric oxygen treatment (García-Párraga *et al.,* 2023). Most telemetry-based at-sea assessments of post-release mortality of sea turtles exist for pelagic longline fisheries. A meta-synthesis estimated pooled post-release mortality of 7.9% for shallow-hooked and 21.3% for deep-hooked loggerheads (Chaloupka *et al.,* 2022), while Álvarez de Quevedo *et al.* (2013) estimated 30.8–36.5% mortality over 90 days among loggerheads released with retained hooks and line in the Mediterranean. The two largest telemetry-based studies of trawl-bycaught loggerheads to date, Parga *et al.* (2020) and the present study, yielded conservative post-release mortality estimates of 20% and 10%, respectively, providing information on cryptic trawl-related mortality in loggerhead turtles that was missing in mortality assessments and is necessary for conservation planning (Pfaller *et al.,* 2018; Chaloupka *et al.,* 2022).

Six of ten turtles were unresponsive at haulback and required 15–90 min to regain spontaneous activity. Their condition indicates substantial physiological disturbance associated with forced apnoea, including hypoxia, metabolic acidosis, water aspiration and decompression-related injury (Lutz and Dunbar-Cooper, 1987; Stabenau *et al*., 1991; Parga *et al.,* 2020). In trawl-bycaught loggerheads, GE has been detected in 42.3–61.7% of cases and may occur in apparently active turtles or increase during the first hours after net retrieval (García-Párraga *et al.,* 2014; Parga *et al*., 2020; Franchini *et al.,* 2021; García-Párraga *et al.,* 2023). Its occurrence and severity are associated with tow duration, capture depth, ascent rate, turtle size or mass and temperature, although the relative importance of these variables differs among studies (Fahlman *et al.*, 2017; Franchini *et al.,* 2021; García-Párraga *et al.,* 2023). Long tow duration and forced submergence can cause marked metabolic acidosis (Stabenau *et al.,* 1991; Sasso and Epperly, 2006). The mean tow duration of 6.5 h in our study was at the upper end of prolonged dive durations recorded in loggerheads (Hochscheid *et al.,* 2005, 2007) and substantially exceeded those reported for Italian northern-Adriatic trawlers (111 ± 45 min; Casale *et al.,* 2004), the Gulf of Gabès (86.8 ± 11.4 min; Jribi *et al.,* 2007) and Mediterranean Egypt (3.1 h; Laurent *et al*., 1996). However, these comparisons concern nominal tow duration rather than actual forced-submergence time because the timing of entry into the trawl was unknown.

In the Adriatic Sea, loggerhead turtles display a dichotomous pattern of seasonal habitat use, with most large-sized individuals (70.6%) overwintering close to their summer feeding habitats in the northern Adriatic (Jančič *et al*., 2026). Due to thermal constraints, overwintering habitats in the northern Adriatic are mostly situated in its eastern part (Casale *et al.,* 2004, 2007, 2012; Lazar, 2010). Overwintering of loggerheads elsewhere in the Mediterranean has been documented from shallow waters below 40 m (Hochscheid *et al.,* 2007; Broderick *et al.,* 2007; Rees *et al.*, 2026), whereas in the northern Adriatic it regularly occurs at 50–100 m (Jančič *et al.,* 2026). By overwintering at such depths, loggerheads in the Adriatic are more susceptible to GE risk through greater nitrogen uptake at elevated pressure. Clinical models suggested that an average trawl depth of 65 m corresponded to a 50% probability of GE-related mortality (Fahlman *et al.,* 2017), whereas larger loggerhead turtles captured in demersal trawls at a depth of

75 m had a >90% probability of GE and approximately 50% probability of developing a moderate-to-severe GE associated with high mortality if untreated (García-Párraga *et al.,* 2023). However, these modelled probabilities should not be applied as deterministic thresholds for development and effects of GE, because sea turtles are likely to have additional behavioural, anatomical and physiological mechanisms that limit nitrogen uptake, although these protective mechanisms may be disrupted by entrapment and struggling in trawl gear (Robinson *et al.,* 2021).

All our turtles were captured and released under low-temperature conditions, and overwintering of loggerheads in the Adriatic Sea was demonstrated to occur within a thermal range of 11–15 °C (Jančič *et al.,* 2026). Such low temperatures reduce metabolic rate and prolong voluntary dives but also increase the solubility of respiratory gases in body fluids (Hochscheid *et al*., 2004; García-Párraga *et al.,* 2014). This may increase dissolved nitrogen at depth, whereas warming after retrieval could favour supersaturation and bubble formation. Available data do not, however, show that cold conditions alone increase GE risk; Franchini *et al.* (2021) found a positive association between temperature and GE occurrence. Temperature effects are therefore opposing and difficult to infer, but prolonged benthic residence at low temperatures and seasonal overlap with demersal trawling increase capture probability (Hochscheid *et al.,* 2005, 2007; Domènech *et al.,* 2015).

Across demersal-trawl studies, approximately 19–34% of captured turtles were comatose or unresponsive at haulback (Poiner and Harris, 1996; Casale *et al.*, 2004; Lazar *et al.,* 2011b; Casale *et al.*, 2017). An inactive turtle unable to swim or lift its head is unlikely to surface if released immediately (Sasso and Epperly, 2006; Franchini *et al.,* 2021). Keeping comatose turtles sheltered on deck and allowing the lungs to drain until regular breathing and spontaneous activity resume has therefore been promoted as a simple procedure to reduce post-capture mortality (Gerosa and Aureggi, 2001; FAO, 2009). Apart from these recovery protocols, other methods and gear innovations have been introduced for the reduction of bycatch and bycatch-related mortality of sea turtles over the past decades. Besides reduction of fishing effort and spatio-temporal closures, turtle excluder devices (TEDs) have been successfully implemented in demersal-trawl fisheries, allowing turtles to escape from the gear (review by Lewison *et al.,* 2013). The success of TED implementation depends on fishery-specific design and correct installation, but also on fisher participation, enforcement, and financial support to fishermen, rather than on mandatory regulation alone (Eayrs, 2004; Lucchetti *et al.,* 2019; Jenkins, 2023; Baldi *et al*., 2025). In 2019, the purchase cost of a TED *per* net ranged from US$325 to 550 excluding installation, maintenance and potential catch loss costs (NOAA Fisheries, 2019). Experimental trials of Flexgrid TEDs in the Adriatic Sea suggested high efficiency in exclusion of turtles but have documented commercial catch losses of 16.6–19.7% and showed fisher reluctance to modify traditional gear (Lucchetti *et al.,* 2016, 2019; Baldi *et al.*, 2025). Because the fishery-wide effectiveness of TEDs depends not only on their technical performance but also on compliance and enforcement (Crowder *et al.,* 1994; Lewison *et al.,* 2003), lack of fisher acceptance coupled with limited enforcement capacity and the need for international coordination may impede efficient implementation in Adriatic demersal-trawl fisheries.

Long tow duration, capture depth and turtle size, coupled with prolonged submergence at low temperatures, make Adriatic loggerheads sensitive to seasonal demersal-trawl impacts, including delayed effects of GE. Although based on a limited sample, our findings showed high apparent survival among turtles that regained spontaneous activity following on-board recovery and therefore support the conservation value of this procedure (Maxwell *et al.,* 2018). The protocol requires no specialized equipment or gear modification and can be implemented through fisher education and training, making it a practical, low-cost measure when capture cannot be prevented. It is not, however, a treatment for severe decompression sickness; turtles that remain comatose or show persistent neurological abnormalities should be transferred to specialized veterinary care whenever feasible (García-Párraga *et al.,* 2014, 2023; Franchini *et al.,* 2021). Combining on-board recovery with measures that may reduce GE prevalence and related mortality, such as shorter tow duration and slower trawl retrieval, could further reduce mortality without gear modification. Such measures may be more readily adopted by fishers, and their uptake could be encouraged through eco-certification of products caught using sea turtle protection measures. However, larger multi-fishery studies combining dedicated survivorship tags, clinical screening and standardized operational covariates are needed before regional introduction of such integrated conservation measures.

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This study contributes to the PhD dissertation of MJ

as part of his doctoral studies at the Biotechnical Faculty, University of Ljubljana.

## AUTHOR CONTRIBUTIONS

B.L. formulated the ideas, and the authors jointly designed the methodology. B.L. led the fieldwork, conceptualized the paper, and drafted the manuscript. M.J. performed data processing and analysis and contributed to the preparation and editing of the manuscript.

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