

A first multi-sensor gear-based characterisation of the behaviour of target and bycatch species during pelagic longline capture

Antoine Landreau^{a,b,*}, Vincent Kerzérho^b, Olivier Derridj^a, Bertrand Wendling^c,
Nolwenn Cosnard^c, Amaury Boguais^b, Paul Leloup^b, Paulo Pimenta^b, Sylvain Bonhommeau^d,
Jéréemie Chanut^e, Anne-Elise Nieblas^e, Tristan Rouyer^a

^a MARBEC, Univ Montpellier, CNRS, IFREMER, IRD, Sète, France

^b LIRMM, Univ. Montpellier, CNRS, Montpellier, France

^c SATHOAN, 29, promenade J.B. Marty, Sète, 34200, France

^d UMR ENTROPIE, IFREMER DOI, Le Port, La Réunion, France

^e Company for Open Ocean Observations and Logging (COOOL), La Reunion, Saint Leu, France

ARTICLE INFO

Keywords:

Bycatch
Longline
Behaviour
Bio-logging
Bluefin tuna
Elasmobranchs

ABSTRACT

Little is known about the behaviour and stress responses of animals captured by longline gear from hooking until retrieval at the vessel, despite the importance of this process for bycatch mitigation and post-release survival. Most existing studies have relied on physiological sampling at haulback, which provides only a snapshot of stress at retrieval and requires invasive handling. This study used a custom multi-sensor data logger, the SMARTSNAP device, attached directly to the longline to continuously record the behaviour of individuals captured on commercial pelagic longlines in the Gulf of Lion and around Réunion Island between 2022 and 2023. A total of 40 individuals across 15 species, including target tuna species and elasmobranch bycatch, were recorded from hooking until retrieval. Within active capture phases, individual dive sequences were identified and characterised through metrics describing dive duration, depth, descent speed, and directional movement. Atlantic bluefin tuna showed a marked decline in fight intensity over successive dives, whereas blue shark and pelagic stingray displayed more stable patterns. Principal component analysis revealed that individuals which ultimately died following capture were characterised by elevated movement and depth metrics, while surviving individuals showed comparatively lower values. Similar mortality-associated behaviours were observed in other tuna species. These findings support the hypothesis that behavioural dynamics can serve as a proxy of capture-induced exhaustion, demonstrating the potential of gear-based instrumentation to directly assess animal condition during capture. Further work is needed to determine whether these observations can be translated into practical applications for bycatch mitigation, rapid release strategies, and the management of capture-related stress, with potential implications for animal welfare and flesh quality.

1. Introduction

Pelagic longline fisheries are characterised by prolonged hooking events during which captured animals undergo extended physical restraint, sustained energy expenditure, and acute stress responses, all of which can compromise animal welfare, post-release survival for animals returned to the water and affect the flesh quality and thus the price of landed individuals (Frick et al., 2010, Brooks et al., 2012, Addis et al., 2013). Yet the sequence of events unfolding between hooking and retrieval — how an animal fights, when it exhausts itself, and through

which mechanisms it ultimately survives or dies on the line — remains poorly described and understudied. The limited information available on behavioural responses during capture largely derives from recreational catch-and-release fisheries, where animals are individually targeted and retrieved rapidly, conditions that differ substantially from those experienced during commercial longline operations, where animals may remain on the line for several hours (Stokesbury et al., 2011, Lloret, Shulman, and Love, 2013, Gallagher et al., 2014). How stress and behavioural responses develop in hooked animals throughout the capture event therefore remains largely unknown in commercial longline

* Corresponding author at: MARBEC, Univ Montpellier, CNRS, IFREMER, IRD, Sète, France.

E-mail address: antoine.landreau@ifremer.fr (A. Landreau).

<https://doi.org/10.1016/j.fishres.2026.107892>

Received 25 June 2026; Received in revised form 15 September 2026; Accepted 6 October 2026

Available online 9 October 2026

0165-7836/© 2026 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

fisheries.

Existing approaches to characterise capture-induced stress have primarily relied on biological sampling conducted at haulback, when the animal is brought aboard (Mandelman and Skomal, 2009, Marshall et al., 2012). The behavioural responses of animals are tightly coupled to their physiological stress state and are specific to each species, with increasing fight intensity manifesting in measurable changes in movement patterns, activity levels and physiological perturbations (Lockridge, 1981, Beiting, 1990, Scott et al., 2023). In large pelagic species such as Atlantic bluefin tuna (ABFT) and sharks, swimming speed and tail beat frequency have been documented as indicators that vary in response to stress and physical exertion (Addis et al., 2013, Jerome et al., 2018, Wosnick et al., 2023). However, in commercial longline contexts, such behavioural data are difficult to obtain in situ, and stress assessment has therefore largely relied on physiological proxies. Stress hormones and markers of physical exhaustion such as blood lactate have been widely used to quantify the degree of stress and exhaustion experienced by individuals at the time of retrieval (Skomal, 2007, Jerome et al., 2018, Whitney et al., 2021). Nevertheless, these methods require direct handling of the animal, which is inherently invasive, time-consuming, even more stressful and operationally challenging in commercial fishing contexts, and they provide only a static snapshot of physiological condition at the point of retrieval, with no information on how stress and exhaustion developed throughout the capture event (Brooks et al., 2012, Whitney et al., 2021).

Understanding the individual's stress response during capture is nonetheless critical, particularly in the context of bycatch subsequently released, where the survival of incidentally captured animals upon release is highly variable and depends on the species, the time spent on the line, gear characteristics, and onboard handling practices (Davis, 2010, Poisson et al., 2019, Bowlby et al., 2021). These survival outcomes take on particular significance given the scale at which bycatch occurs in pelagic fisheries. Bycatch remains one of the most pressing challenges in the sustainable management of marine fisheries and the conservation of pelagic ecosystems (Botsford, Castilla, and Peterson, 1997, Lewison et al., 2004, Hazen et al., 2018). Global estimates suggest that bycatch accounts for more than 10% of total marine catches, of which longline fisheries alone contribute approximately 6% (Davies et al., 2009, Roda, M.A., 2019). Despite being considered relatively more selective than trawling or gillnetting, longlines still generate substantial bycatch of elasmobranchs, cetaceans, seabirds, and marine turtles, with a significant proportion of non-target animals arriving dead at the vessel (Carruthers, Schneider, and Neilson, 2009, Coelho et al., 2012, Roda, M. A., 2019). The large scale of some artisanal fleets, combined with limited observer or electronic monitoring coverage, further complicates the assessment of bycatch and its ecological impacts on affected species and ecosystems (Babcock and Pritchard, 2003, Read, Drinker, and Northridge, 2006). Better characterising the behavioural responses and stress experienced by hooked animals is therefore essential to improve post-release survival estimates and inform the development of more effective bycatch reduction strategies (Davis, 2002, Davies et al., 2009, Bellido et al., 2011).

Direct instrumentation of the fishing gear offers a promising avenue to characterise the behaviour of animals throughout the capture event. Advances in sensor miniaturisation have enabled the development of increasingly sophisticated bio-logging methods for monitoring individual animals in their natural environment (Block et al., 2011; Rouyer et al., 2023, Landreau et al., 2026). However, the direct application of bio-logging to animals captured on commercial longlines remains limited, as the probability that an electronically tagged individual is subsequently captured on a longline during the monitoring period is very low. Efforts to characterise animal behaviour on longlines have therefore relied on gear instrumentation, primarily through hook timers and time-depth recorders (TDRs) to identify capture events and describe gear dynamics (Campbell and Young, 2012, Peterson, Gartland, and Latour, 2017, Scott et al., 2022). TDR data have also been used to

characterise the behavioural responses of several shark species caught as bycatch on pelagic longlines, revealing species-specific patterns in post-capture behaviour, although the combined use of TDRs with accelerometer data was identified as necessary to more fully interpret these responses (Guida et al., 2017, Scott, Royer, and Hutchinson, 2023). Camera systems mounted directly on fishing lines have also been used to assess the species composition of catches, though scaling this approach to commercial longlines comprising hundreds or thousands of hooks presents considerable logistical and financial challenges (Ames, Leaman, and Ames, 2007). More broadly, existing gear instrumentation approaches remain limited in their capacity to provide continuous and multi-sensor records of individual animal behaviour throughout the capture event.

This study proposes a direct behavioural approach to characterise and quantify the response of large pelagic animals — including both target species and bycatch — captured on commercial pelagic longlines, using continuous multi-sensor data collected directly on the fishing gear from the moment of deployment until retrieval aboard the vessel, avoiding any manipulation of the animals. Individual behaviour at the end of the line is derived from sensor data, with sensor-derived metrics serving as proxies for capture-induced stress and fight intensity, allowing the progression of the capture event to be tracked continuously. This approach also enables behavioural differentiation between species, providing novel insights into the capture responses of large pelagic species under real commercial fishing conditions. The dataset generated constitutes, to our knowledge, one of the first continuous multi-sensor records of animal behaviour on pelagic longlines across multiple species and fishing areas. These data contribute to a deeper understanding of the stress experienced by hooked individuals, with direct implications for the estimation of post-release survival in discarded species and for the development of more effective bycatch reduction strategies. At the same time, characterising the behavioural dynamics of target species such as tuna opens new perspectives for assessing the effects of prolonged fighting on capture outcomes and potentially flesh quality, an aspect of growing commercial relevance.

2. Materials and methods

2.1. Behavioral electronic device

The SMARTSNAP is a self-contained underwater data logger designed to record the behaviour of animals captured on pelagic longlines (Nieblas et al., 2023, Landreau et al., 2024). Each unit consists of a waterproof housing enclosing a motherboard connected to a battery and a suite of sensors, including an accelerometer, magnetometer, gyroscope, and pressure and temperature sensors. Data retrieval and battery charging are performed via a USB connection.

The first prototype consisted of a fully waterproof, oil-filled enclosure with a silicone membrane allowing hydrostatic pressure transmission. Pressure-rating trials revealed sealing failures at the external USB interface, leading to seawater ingress and irreversible damage to the embedded circuitry. A second version was therefore developed from PVC pressure pipes rated to 15 bar (153 m depth), sealed with a dead-end cap and an O-ring inspection plug. Units were successfully deployed at sea at depths ranging from 90 to 300 m and further validated in the IFREMER hyperbaric chamber (Toulon), where the system withstood pressures of up to 37 bar (equivalent to 378 m depth) (Nieblas et al., 2023).

The system was built around a SMART ARM-based microcontroller (SAM D21 series, Atmel) interfaced with a pressure and temperature sensor (MS5837-30BA, TE Connectivity), operating across 0–30 bar and –20–85 °C with a depth resolution of 0.2 cm. An accelerometer/magnetometer module (FXOS8700CQ, NXP) and a 3-axis gyroscope (FXAS21002C, NXP) were mounted on the main motherboard, with sampling rates ranging from 1.5 to 400 Hz and 12.5–800 Hz respectively. All sensors were sampled at a fixed interval of 16 ms. Battery

autonomy exceeded 24 h, which was not a limiting factor as no deployment exceeded this duration and batteries were recharged between deployments (Pimenta et al., in prep).

Each device unit was equipped with a metal snap hook attached to the upper part of the housing, allowing the unit to be connected directly to the main longline. A fishing line loop was positioned underneath the housing, onto which the fisher attached the metal snap hook normally used to connect the leader line to the main longline (Fig. 1B). A 50 g weight was added to each unit and selected to achieve neutral buoyancy, thereby counteracting the positive buoyancy generated by the air contained within the housing. This was intended to minimise any alteration of the natural behaviour of the longline and to reproduce capture conditions as closely as possible to those encountered during regular fishing operations. The SMARTSNAP was thus positioned between the main line and the start of the leader leading to the hook (Nieblas et al., 2023, Landreau et al., 2024). A total of 180 units were manufactured and individually tested 24 h prior to each deployment.

2.2. Deployments

The SMARTSNAP devices were deployed on commercial pelagic longlines across two distinct fishing areas. Operations in the Gulf of Lion were conducted aboard French longline vessels targeting ABFT, with deployments carried out during autumn 2022 and spring 2023. In the waters surrounding Réunion Island, deployments were performed continuously throughout 2023 on vessels targeting predominantly albacore tuna (*Thunnus alalunga*), yellowfin tuna (*Thunnus albacares*), and swordfish (*Xiphias gladius*). A total of nine deployments were conducted in the Gulf of Lion, and six in the waters surrounding Réunion Island (Table 1).

For each deployment, a single contiguous transect along the longline was instrumented, and its position — at the initial, central, or terminal segment of the gear — was determined by the fisher. Every hook within the selected transect was systematically equipped with an individual SMARTSNAP unit. Branchlines were made of monofilament and were 8 m long in the Gulf of Lion and 15 m long at Réunion Island. The diameter of the monofilament was not recorded. The length of the instrumented transect varied between deployments as it was directly determined by the fisher's gear configuration, including the spacing between successive hooklinks, which ranged from approximately 10 m

to over 50 m in the case of Réunion Island longlines, and the positioning of surface flotation elements. Installation was carried out in accordance with the operational settings defined by each fisher to minimise interference with standard fishing operations. However, this lack of uniformity in gear configurations may introduce sampling bias and was therefore considered when interpreting the results. Each unit was attached to the main line via a stainless-steel snap-link connector, and the corresponding hooklink was secured by the fisher to the dedicated attachment loop integrated into the device.

Each deployment campaign began with up to 180 operational units for the first deployment. The number of available devices decreased progressively across successive deployments within each campaign due to technical failures, including water ingress, logging system malfunctions, and battery failures, across all three deployment waves: Gulf of Lion 2022, Gulf of Lion 2023, and Réunion Island 2023.

Longline operations differed notably between the two study areas in terms of soak duration. In the Gulf of Lion, setting took approximately 3.5 h on average, followed by a soak period of 4–5 h, while hauling duration was variable and depended on the volume of catch present on the line (Landreau et al., 2026). In Réunion Island, setting duration was comparable to that observed in the Gulf of Lion, but soak times were substantially longer, averaging 12 h. Lines were typically set in the afternoon before sunset and hauled the following morning just before sunrise.

During hauling, all captures occurring on equipped hooks were systematically logged, and body length measurements were collected for a subset of individuals across all species (Table 1). However, some of the length measurements collected in the field were subsequently lost, resulting in heterogeneous data availability. Length data were available for 4 of 11 individuals in the Gulf of Lion and 14 of 29 individuals at Réunion Island. This limitation should be considered when interpreting results related to individual size.

2.3. Data recovery and analysis

After each field deployment, a data extraction and pre-processing phase was performed (Fig. 2). Each device was opened for physical inspection to verify integrity and reusability for subsequent deployments. Recorded datasets were retrieved via the onboard USB port, and the internal power source was recharged. System time synchronisation was

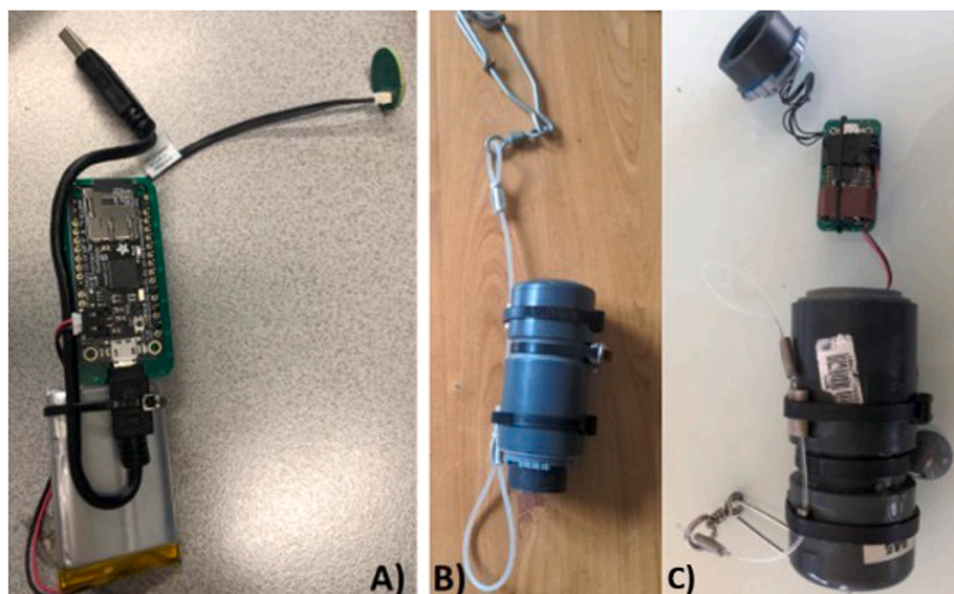
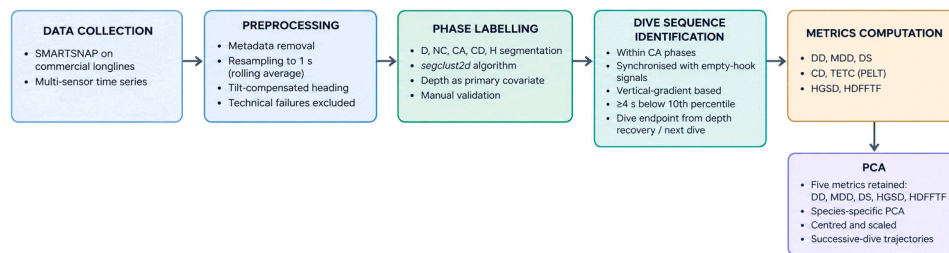


Fig. 1. Manufactured prototype of the SMARTSNAP device. Internal components with electronic system and battery (A), closed device with rigging system and snap ready to deploy (B) and opened device ready to connect (C). Adapted from (Landreau et al. 2024).

Table 1

Morphometric and deployment metadata for individuals caught by hooks equipped with devices.

DATE	AREA	#SNAP	SPECIES	LENGTH FL (cm)	STATUS AT HAULBACK	VESSELS	LABELLED
01/09/2022	Gulf of Lion	139	<i>Thunnus thynnus</i>	–	Alive	Trois Frères II	YES
02/09/2022	Gulf of Lion	58	<i>Thunnus thynnus</i>	–	Alive	Trois Frères II	YES
07/09/2022	Gulf of Lion	133	<i>Pteroplatytrygon violacea</i>	–	Alive	Trois Frères II	YES
07/09/2022	Gulf of Lion	181	<i>Thunnus thynnus</i>	–	Alive	Trois Frères II	YES
18/04/2023	Gulf of Lion	324	<i>Thunnus thynnus</i>	–	Dead	Trois Frères II	YES
19/04/2023	Gulf of Lion	264	<i>Mola mola</i>	–	Alive	Trois Frères II	YES
24/04/2023	Gulf of Lion	270	<i>Thunnus thynnus</i>	110	Alive	Trois Frères II	YES
24/04/2023	Gulf of Lion	276	<i>Thunnus thynnus</i>	116	Alive	Trois Frères II	YES
24/04/2023	Gulf of Lion	320	<i>Thunnus thynnus</i>	116	Alive	Trois Frères II	YES
24/04/2023	Gulf of Lion	400	<i>Prionace glauca</i>	120	Alive	Trois Frères II	YES
28/04/2023	Gulf of Lion	366	<i>Prionace glauca</i>	–	Alive	Trois Frères II	YES
24/02/2023	Reunion Island	250	<i>Prionace glauca</i>	213	Alive	Ichty	YES
24/02/2023	Reunion Island	258	<i>Xiphias gladius</i>	150	Dead	Ichty	YES
24/02/2023	Reunion Island	287	<i>Prionace glauca</i>	205	Alive	Ichty	NO (Missing data)
03/03/2023	Reunion Island	246	<i>Thyrstoides marleyi</i>	–	Alive	Ichty	NO (Insufficient activity)
03/03/2023	Reunion Island	284	<i>Coryphaena hippurus</i>	114	Alive	Ichty	YES
03/03/2023	Reunion Island	320	<i>Xiphias gladius</i>	120	Dead	Ichty	YES
03/03/2023	Reunion Island	337	<i>Sphyraena barracuda</i>	79	Alive	Ichty	YES
03/03/2023	Reunion Island	343	<i>Thyrstoides marleyi</i>	–	Alive	Ichty	YES
03/03/2023	Reunion Island	358	<i>Alepisaurus ferox</i>	–	Alive	Ichty	NO (Hardware failure)
14/06/2023	Reunion Island	225	<i>Thyrstoides marleyi</i>	180	Alive	Ichty	YES
14/06/2023	Reunion Island	246	<i>Pteroplatytrygon violacea</i>	35	Alive	Ichty	YES
14/06/2023	Reunion Island	372	<i>Tetraodontidae</i>	35	Alive	Ichty	NO (Insufficient activity)
14/06/2023	Reunion Island	384	<i>Thyrstoides marleyi</i>	–	Dead	Ichty	YES
28/06/2023	Reunion Island	319	<i>Thunnus albacares</i>	–	Dead	Ichty	YES
28/06/2023	Reunion Island	375	<i>Xiphias gladius</i>	135	Dead	Ichty	YES
17/11/2023	Reunion Island	237	<i>Coryphaena hippurus</i>	–	Alive	Petite crevette	NO (Insufficient activity)
17/11/2023	Reunion Island	339	<i>Prionace glauca</i>	–	Alive	Petite crevette	YES
17/11/2023	Reunion Island	346	<i>Xiphias gladius</i>	–	Alive	Petite crevette	YES
17/11/2023	Reunion Island	376	<i>Thunnus alalunga</i>	–	Alive	Petite crevette	YES
30/11/2023	Reunion Island	248	<i>Thunnus alalunga</i>	78	Dead	Petite crevette	YES
30/11/2023	Reunion Island	257	<i>Thyrstoides marleyi</i>	–	Alive	Petite crevette	YES
30/11/2023	Reunion Island	266	<i>Coryphaena hippurus</i>	–	Dead	Petite crevette	NO (Insufficient activity)
30/11/2023	Reunion Island	272	<i>Thyrstoides marleyi</i>	–	Alive	Petite crevette	NO (Insufficient activity)
30/11/2023	Reunion Island	277	<i>Coryphaena hippurus</i>	–	Dead	Petite crevette	YES
30/11/2023	Reunion Island	313	<i>Xiphias gladius</i>	200	Dead	Petite crevette	YES
30/11/2023	Reunion Island	332	<i>Thunnus alalunga</i>	74	Dead	Petite crevette	YES
30/11/2023	Reunion Island	352	<i>Thyrstoides marleyi</i>	–	Alive	Petite crevette	NO (Insufficient activity)
30/11/2023	Reunion Island	385	<i>Xiphias gladius</i>	110	Alive	Petite crevette	YES
30/11/2023	Reunion Island	391	<i>Pteroplatytrygon violacea</i>	–	Alive	Petite crevette	YES

Analytical workflow**Fig. 2.** Conceptual overview of the analytical workflow applied in this study.

repeated, and the data underwent cleaning procedures, including the identification of anomalous signals and diagnosis of defective mainboards or sensors. Following completion of these steps, curated data were archived in a relational database structured as an operational research repository. The stored data took the form of a multivariate time series combining all sensor outputs. All statistical analyses and data processing described in this study were performed using R version 2026.05.0–218.

2.3.1. Data pre-processing

A cleaning phase was first performed to remove metadata not relevant to this study and to produce a clean dataset consisting of the time series of each sensor (Fig. 2). Although raw data were recorded at a

sampling interval of 16 ms, all datasets were then resampled to a uniform frequency of 1 s prior to analysis using a rolling average. This downsampling was applied for two reasons: to reduce computational load during subsequent analyses, and because numerous electronic tagging studies have successfully characterised behavioural patterns in large pelagic species using sampling intervals equal to or greater than 1 s, making this frequency largely sufficient and the full 16 ms sampling rate unnecessary for the purposes of this study (Campana, Joyce, and Manning, 2009; Lotek, 2017; Arregui et al., 2018). Units that experienced technical malfunctions during deployment, as described in the previous section, yielded time series that were either too short for analysis or entirely unrecoverable and were excluded from further processing.

The magnetic heading, hereafter referred to as heading, was also computed from the raw magnetometer output to characterise the horizontal orientation of the device. As raw magnetometer measurements are reliable only when the sensor is perfectly horizontal, any tilt of the device causes the vertical component of the Earth's magnetic field to leak into the horizontal components, introducing systematic error in the heading estimate. The raw magnetometer measurements were therefore projected onto the horizontal plane using the pitch and roll angles derived from the accelerometer, following the tilt-compensated heading correction approach described in [Dominguez et al. \(2025\)](#). This correction yields a reliable heading regardless of the orientation of the sensor, which is particularly important given the continuous movement and changes in orientation experienced by the device on the line. Heading was expressed in degrees, ranging from 0° to 360°, and computed at each time step.

2.3.2. Data labelling

The objective of the analysis was to characterise individual behaviour during the active phase of capture by identifying and describing dive sequences within this phase, allowing periods of active fighting to be distinguished from passive intervals. To this end, the time-series of devices associated with capture events were first labelled to identify deployment states prior to subsequent analysis ([Fig. 2](#)). Phases were defined according to their expected order of occurrence in the recorded signal. The Deploy (D) phase referred to the interval beginning when the device was submerged and oscillating and/or sinking, until the longline reached mechanical stabilisation. The No Catch (NC) phase corresponded to the pre-capture period, during which no organism was hooked. The Catch Alive (CA) phase started when the animal was hooked, corresponding to the onset of a disturbance in the otherwise stable sensor signals, which was detectable across the different sensors. This phase continued until the animal was either retrieved on board or its mortality was detected while it was still attached to the fishing line. The detection of mortality marked the beginning of the Catch Dead (CD) phase, corresponding to the period following the CA phase during which the animal was dead, inactive, and still attached to the hook. The Hauling (H) phase, when observable, corresponded to the mechanical winding action performed by the fisher during line retrieval, typically characterised by a sudden and continuous decrease in depth until the device exited the water. This segmentation procedure was conducted using the segmentation function implemented in the R package *seg-clust2d* ([Patin et al., 2020](#), [Patin et al., 2025](#)). Depth was selected as the primary segmentation covariate and applied systematically, as it exhibited the broadest range of variation and the lowest noise across phases, facilitating their visual identification. The model returned the segmented time series along with the identified segments and their corresponding start and end indices.

Segmentation outputs were systematically reviewed and validated against the expected phase structure, informed by biological and ecological knowledge of animal behaviour at the end of a longline. In some cases, labelling was not possible due to technical malfunctions during deployment or because the animal's activity at the end of the line prevented phase discrimination even with multiple covariates. These individuals were therefore excluded from subsequent behavioural analyses.

Within each Catch Alive (CA) phase, individual activity sequences, hereafter referred to as dives, were identified, as these periods represent the intervals during which the animal actively exerts effort against the line and during which behavioural analysis was conducted ([Fig. 2](#)). Prior to dive identification, the CA phase of each individual was extracted and synchronised with the median signal computed across all other devices deployed on the same longline. A two-sample *t*-test was performed to verify that the depth signal of the captured individual was significantly different ($p < 0.05$) from that of the remaining units, which recorded no capture events, thereby confirming that the signal reflected genuine animal activity rather than passive line movement.

Dive identification was based on the computation of vertical gradients, defined as the second-by-second change in depth (m/s), to represent vertical displacement throughout the CA phase. For each individual, the distribution of vertical gradients over the entire CA phase was computed, and the 10th and 90th percentiles were extracted as individual-specific thresholds. All candidate descent sequences were first identified across the CA phase as sequences of at least four consecutive vertical gradient values falling below the 10th percentile, indicating sustained downward movement. This threshold of four consecutive values was selected after testing alternative thresholds of 8, 10, and 15 values, all of which yielded consistent results; the more conservative threshold of four was retained to avoid missing brief but ecologically relevant descent sequences. Sensitivity analyses using multiple percentile thresholds (10th, 15th, and 20th; 80th, 85th, and 90th) yielded consistent results, indicating that the conclusions were not sensitive to the selected cutoff values. Therefore, the 10th and 90th percentiles were retained, as they provided the broadest characterization of extreme observations. For each identified candidate descent, the algorithm then searched for the corresponding dive endpoint. The end of a dive was defined as the point at which depth returned to within 0.1 m of the depth recorded at dive onset. In cases where this condition was not met — specifically when an individual performed stepwise descents without returning to the initial depth before initiating a subsequent dive — the dive was closed at the shallowest depth point recorded prior to the onset of the next candidate descent sequence. For the final dive of each CA phase, the end of the sequence was defined by the occurrence of at least four consecutive vertical gradient values exceeding the 90th percentile, indicating a sustained upward movement. Each identified dive was assigned a chronological index reflecting its order of occurrence within the CA phase time series. At least one dive was successfully identified within the CA phase of every individual retained for analysis ([Boniol et al., 2024](#)).

2.3.3. Statistical analyses

For each identified dive, a set of behavioural metrics was initially computed: dive duration (DD), maximum dive depth (MDD), descent speed (DS), changepoint depth (CD) and time elapsed to changepoint (TETC) derived from the first changepoint identified by the Pruned Exact Linear Time (PELT) algorithm, heading gradient standard deviation (HGSD), and heading dominant Fast Fourier Transform (FFT) frequency (HDFFTF) ([Fig. 2](#)). Maximum dive depth has been calculated as the relative depth in relation to the position of the housing during the NC (No Catch) phase.

The behavioural state of each captured individual was further characterised through changepoint analysis performed on the vertical gradient data of each dive using the PELT algorithm, implemented via the R package *changepoint* ([Killick and Eckley, 2014](#), [Killick et al., 2024](#)). In the present study, the changepoint represented a shift in the individual's depth-descent behaviour, marking the transition from active descent to a more stable period at depth. This algorithm is based on a change-point detection method that partitions a sequence into segments with distinct statistical properties while optimizing a penalized cost function. It was applied exclusively to the negative vertical gradient values of each dive sequence, corresponding to the descent phase, with the aim of identifying shifts in the descent dynamics of the individual. Specifically, the PELT model was used to detect changes in the mean of the negative gradient series using the Modified Bayesian Information Criterion (MBIC) penalty criterion, allowing localisation of the point at which the individual transitioned between distinct descent regimes. This first changepoint was interpreted as the moment at which the negative vertical gradients stabilised, indicating a transition from an initial phase of intense downward pulling against the line to a subsequent phase of reduced and more uniform descent effort. Although the algorithm was allowed to detect multiple changepoints, only the first was retained, as dives were generally short in duration and subsequent changepoints were rarely interpretable in a meaningful behavioural context. From this

changepoint, two additional metrics were derived: the depth of the changepoint, and the time elapsed between the onset of the dive and the changepoint. For dives in which no changepoint was detected by the algorithm, these two metrics were assigned a missing value and excluded from the corresponding analyses.

In addition to the metrics derived from the vertical gradients, two further metrics were computed from the heading signal on a dive-by-dive basis to characterise the rotational and lateral activity of each individual. The use of heading as a behavioural descriptor was supported by the observation that heading time series recorded by devices associated with capture events during active CA phases were significantly different from those recorded by empty hooks on the same deployment (t -test, $p < 0.05$), confirming that heading variations reflect genuine animal-induced movement rather than passive line dynamics. Heading gradients — defined as the second-by-second change in heading — were computed rather than the raw heading values, as these better capture the dynamics of directional change over time. The standard deviation of the heading gradient series (HGSD) was then computed for each dive as a measure of the overall variability of directional change, providing a robust indicator of lateral and rotational activity that is less sensitive to isolated extreme values than a simple range measure. The dominant frequency of directional oscillation (HDFFTF) was extracted for each dive using a Fast Fourier Transform (FFT) applied to the heading gradient series. The FFT was computed using R's native `fft()` function, decomposing the signal into its constituent frequency components. The power spectrum was obtained as the squared modulus of the FFT output, and only the non-redundant positive frequencies were retained, excluding the zero-frequency (DC) component. The dominant frequency was defined as the frequency corresponding to the maximum power in the spectrum and was expressed in Hz, given that the heading gradient series were sampled at 1 s intervals. The FFT was computed only for dives comprising at least four data points, a condition that was systematically met given that dive onset was defined by a minimum of four consecutive descent values. For dives where computation failed, the dominant frequency was assigned a missing value and excluded from the corresponding analyses.

To examine the temporal dynamics of behavioural metrics across successive dives and characterise inter-individual and inter-specific patterns, a Principal Component Analysis (PCA) was performed separately for each species using the `prcomp` function in R, with all variables centred and scaled prior to analysis (Fig. 2). Following examination of the distribution and variability of each metric across individuals and species, five metrics were retained for the PCA on the basis that they exhibited sufficient variance across individuals and species and provided non-redundant information on the behavioural state of the animal: dive duration (DD), maximum dive depth (MDD), descent speed (DS), heading gradient standard deviation (HGSD), and heading dominant FFT frequency (HDFFTF). Each observation corresponded to a single dive from a given individual, with the chronological position of each dive within the CA phase preserved. This approach allowed the trajectory of each individual to be tracked through the principal component space across successive dives, providing a means of visualising the progression of behavioural state over the course of the capture event. Although the deployment basin — Gulf of Lion or Réunion Island — was not included as an explanatory variable in the PCA, individuals from each basin were distinguished graphically in the ordination plots, allowing visual assessment of potential basin-level differences in behavioural patterns across species. To assess whether the patterns observed in the PCA reflected genuine behavioural dynamics rather than the disproportionate influence of individuals with more dives, a linear mixed-effects model was fitted using the `lme4` R package, with PC1 and PC2 scores as response variables, dive position as a fixed effect, and individual as a random effect (Bates et al., 2015).

3. Results

Between 2022 and 2023, a total of 15 deployments (monitored fishing sets) were conducted across the two study areas. During these deployments, the activity of 40 individuals captured on hooks equipped with SMARTSNAP devices was successfully recorded, including 11 individuals in the Gulf of Lion and 29 around Réunion Island (Table 1). In the Gulf of Lion, four species were represented in the catches. In the Gulf of Lion, four species were represented in the catches. Atlantic bluefin tuna (*Thunnus thynnus*, $n = 7$) is the target species of French longline fisheries in this area, while blue shark (*Prionace glauca*, $n = 2$), ocean sunfish (*Mola mola*, $n = 1$), and pelagic stingray (*Pteroplatytrygon violacea*, $n = 1$) were recorded as bycatch. Around Réunion Island, 11 species were identified across all deployments (Table 1). Target species included albacore tuna (*Thunnus alalunga*, $n = 3$), yellowfin tuna (*Thunnus albacares*, $n = 1$), and swordfish (*Xiphias gladius*, $n = 6$). Bycatch species comprised dolphinfish (*Coryphaena hippurus*, $n = 4$), snoek (*Alepisaurus ferox*, $n = 1$ and *Thyrstitoides marleyi*, $n = 7$), blue shark (*Prionace glauca*, $n = 3$), pelagic stingray (*Pteroplatytrygon violacea*, $n = 2$), great barracuda (*Sphyrna barracuda*, $n = 1$), and one unidentified species of Tetraodontidae ($n = 1$) (Table 1). Of the 40 captured individuals, 11 were hauled back dead.

Successful phase labelling was achieved for all 11 individuals captured in the Gulf of Lion. Around Réunion Island, labelling was completed for 19 of the 29 recorded captures (Table 1). In the remaining cases, labelling was not possible either due to data loss resulting from device malfunction, or because animal activity at the end of the line was too limited for the segmentation algorithm or manual inspection to reliably discriminate between phases.

The deployment phase was identifiable in most time series as a gradual increase in depth following submersion of the device (Fig. 3). In the Gulf of Lion, longlines stabilised at depths of between 5 and 20 m during the No Catch (NC) phase, while around Réunion Island, NC phase depths reached up to 150 m. During this phase, acceleration data exhibited low variability, fluctuating around a stable baseline value from submersion until the onset of a capture event. At the moment of hooking, a clear disturbance was visible in both depth and acceleration signals. During the CA phase, maximum depths reached 75 m in the Gulf of Lion, while around Réunion Island some individuals pulled the line to depths exceeding 150 m. Acceleration data during the CA phase oscillated between approximately -10 and 10 m/s², reflecting active struggling at the end of the line. The duration of CA phases ranged from 3 min to 19 h across all individuals. For individuals that arrived dead at the vessel, the Catch Dead (CD) phase was characterised by a stabilisation of depth over time following the large vertical excursions of the CA phase. In this phase, despite the animal's death, the acceleration shows a greater variation than in the NC phase, probably due to the combined effect of the waves and the current, coupled with the dead weight of the animal hanging at the end of the line (Fig. 3). In some cases, the Hauling (H) phase was also discernible in the time series as a continuous and rapid decrease in depth until the device exited the water.

For all labelled individuals, at least one dive sequence was successfully identified within the CA phase, with the total number of detected sequences per individual ranging from 1 to 72 (Fig. 4). Dive sequences are clearly distinguishable from the background depth signal, with each sequence delimited according to the identification criteria described previously. The number of identified sequences, their depth, and their distribution over time varied considerably between individuals. For instance, ABFT individuals tended to perform a small number of relatively long dive sequences, whereas elasmobranchs displayed a much larger number of short dive sequences. Depth amplitudes reached during dive sequences also differed between species. In the Gulf of Lion, ABFT reached amplitudes of up to 50 m, while pelagic stingray rarely exceeded 8 m (Fig. 4). Around Réunion Island, depth amplitudes spanned a comparable range across species, from approximately 10 m for some species to 30 m for dolphinfish and up to 70 m for yellowfin tuna, with

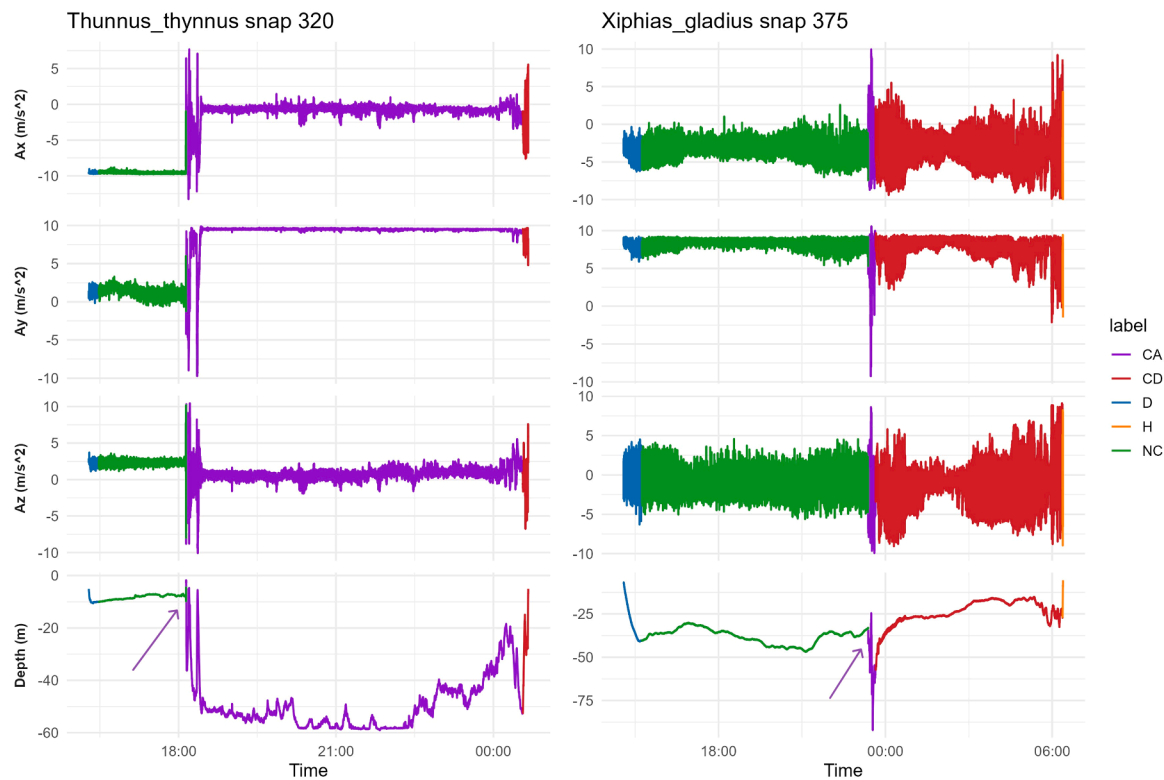


Fig. 3. Observed and labelled acceleration and depth sensor time series of *Thunnus thynnus* (device number 320) and *Xiphias gladius* (device number 375). The Deploy (D) phase corresponds to the period from device submersion until mechanical stabilisation of the longline; the No Catch (NC) phase corresponds to the period before an animal is hooked; the Catch Alive (CA) phase starts at hooking and continues while the animal is considered alive on the line; the Catch Dead (CD) phase corresponds to the period following mortality detection during which the animal remains dead and attached to the hook; and the Hauling (H) phase corresponds to line retrieval. Purple arrows indicate the hooking moment.

absolute depths reached being substantially greater than in the Gulf of Lion (Fig. 4). A progressive reduction in the depth of successive dive sequences was observable over the course of the CA phase in both individuals. Between identified sequences, depth data returned to a relatively stable baseline, corresponding to periods of reduced vertical activity at the end of the line.

These individual-level observations were further examined across all captured individuals of each species through the computation of dive-level metrics, allowing inter-individual and inter-specific patterns to be characterised across successive dive sequences. DD showed contrasting patterns between the two species, with high inter-individual variability and an overall increasing mean tendency in *Thunnus thynnus*, while values were generally lower and less variable in *Prionace glauca*, where the mean trend line remained relatively stable across successive dives. In *Thunnus thynnus*, dive durations did not exceed 2500 s during the first dives, whereas they reached up to 5000 s during the last dives. In contrast, dive durations in *Prionace glauca* remained below 2500 s throughout the successive dives (Fig. 5). In *Prionace glauca*, Gulf of Lion individuals showed a tendency towards increasing DD values across successive dives, whereas Réunion Island individuals exhibited more heterogeneous trajectories. MDD ranged approximately between 20 and 60 m in *Thunnus thynnus* and between 10 and 75 m in *Prionace glauca*, with the mean trend line showing an overall increasing tendency across successive dives in both species (Fig. 5). In *Prionace glauca*, however, one individual — notably the one exhibiting the highest number of dive sequences — showed a decreasing tendency in MDD, in contrast to the increasing trend observed in the remaining individuals. DS showed a decreasing trend across successive dive sequences in both species at the individual and mean levels, with values declining from approximately 1–3 m/s in early dives towards lower values in later sequences in *Thunnus thynnus*, and from approximately

1–2 m/s towards near-zero values in *Prionace glauca* (Fig. 5). Unlike DD and MDD, DS showed a consistent decreasing trend across successive dives in *Prionace glauca* regardless of the deployment basin.

The remaining dive metrics, namely CD, TECP, HGSD, and HDFSFTF, further highlighted the behavioural divergence between the two species (Fig. 6). CD showed contrasting patterns between the two species, with *Thunnus thynnus* exhibiting a tendency towards shallower changepoint depths across successive dives (approximately 20–55 m), while *Prionace glauca* displayed the opposite, with changepoint depths tending to increase over successive dives (approximately 20–80 m). TECP increased progressively across successive dives in both species, however the rate of increase differed notably. In *Thunnus thynnus*, values rose from near zero to approximately 200 s over only 9 dive sequences, while in *Prionace glauca*, values ranged from near zero to over 1000 s but across more than 60 dive sequences, suggesting a more rapid relative increase in *Thunnus thynnus* despite the lower absolute values reached (Fig. 6). HGSD displayed contrasting patterns between the two species. In *Thunnus thynnus*, values declined from approximately 20–70° in early dives to around 10–20° in later sequences. In *Prionace glauca*, values increased progressively from approximately 10–20° in early dives to around 40–60° in later sequences. HDFSFTF displayed contrasting patterns between the two species. In *Thunnus thynnus*, the majority of individuals exhibited a decreasing tendency in dominant frequency across successive dives, with values declining from around 0.25 Hz in early dives to below 0.15 Hz in later sequences for some individuals, with one individual departing from this general pattern (Fig. 6). In *Prionace glauca*, the opposite tendency was observed, with most individuals displaying increasing dominant frequencies across successive dive sequences, from approximately 0.2–0.3 Hz in early dives to values reaching 0.4–0.45 Hz towards the end of the CA phase, with the exception of one Gulf of Lion individual which did not follow this increasing pattern (Fig. 6).

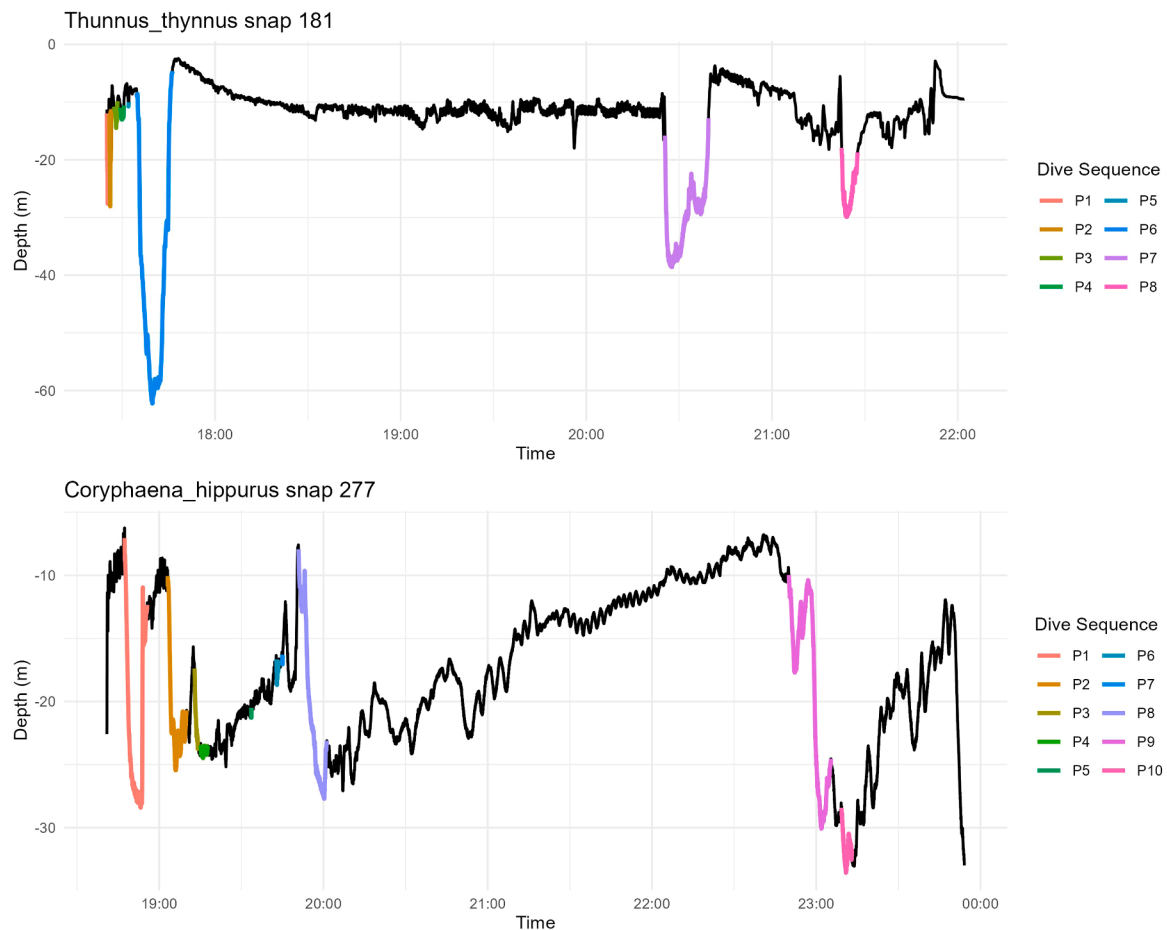


Fig. 4. Depth time series recorded during the Catch Alive (CA) phase for two representative individuals: Atlantic bluefin tuna (*Thunnus thynnus*, device 181, upper panel) and dolphinfish (*Coryphaena hippurus*, device 277, lower panel). The black line represents the raw depth signal throughout the CA phase. Identified dive sequences are highlighted in colour, each colour corresponding to a distinct dive sequence in chronological order (P1 to P8 for *T. thynnus*; P1 to P10 for *C. hippurus*).

These patterns were further examined across all remaining species recorded in this study, revealing additional inter-specific variation in dive-level metrics (Fig. 7). For DD, albacore tuna (*Thunnus alalunga*), yellowfin tuna (*Thunnus albacares*), ocean sunfish (*Mola mola*), and snoek (*Thyrsitoides marleyi*) exhibited a decreasing tendency across successive dives, while the remaining species showed relatively stable or increasing trends. For DS, albacore tuna and snoek displayed a clear increasing tendency across successive dive sequences, while the opposite pattern was observed for swordfish (*Xiphias gladius*) and pelagic stingray (*Pteroplatytrygon violacea*), and the remaining species showed relatively flat trends (Fig. 7). The absolute value of maximum dive depth (MDD) increased progressively across successive dives in the majority of species, with the exception of the two tuna species, ocean sunfish, and great barracuda (*Sphyraena barracuda*), which showed stable or decreasing tendencies. The absolute value of changepoint depth (CD) increased progressively across successive dives in the two tuna species and swordfish, while no clear pattern emerged for the remaining species (Fig. 7). TECP increased across successive dives in the majority of species, with yellowfin tuna and swordfish being the only exceptions. Regarding heading-based metrics, HGSD increased across successive dives in great barracuda and swordfish, while all other species displayed a decreasing tendency. HDEFTF showed a slight increasing tendency in great barracuda and albacore tuna, while all remaining species exhibited a decreasing trend across successive dive sequences (Fig. 7).

To synthesise the temporal dynamics of behavioural metrics across successive dives and examine inter-individual and inter-specific patterns, a PCA was performed separately for *Thunnus thynnus* and *Prionace glauca* (Fig. 8). For some individuals, one or more metrics were

unavailable for certain dive sequences and were therefore excluded from the corresponding observations, resulting in the retention of five metrics for these analyses: DD, DS, MDD, HGSD, and HDEFTF. For *Thunnus thynnus*, the linear mixed-effects model fitted to test the effect of dive position on PC scores, with individual as a random effect, indicated a significant effect of position on PC2 ($t = -2.39$) but not on PC1 ($t = 0.25$), with intra-class correlation coefficients of 0.25 and 0.24 for PC1 and PC2 respectively, supporting the use of a single PCA at the species level. PC1 explained 38.2% of the total variance and was primarily associated with MDD, with higher values loading positively, and DS, with higher values loading negatively. DD contributed moderately to PC1 in the positive direction. PC2 explained 21.3% of the total variance and was primarily associated with HGSD and HDEFTF, both loading positively (Fig. 8a). Individual trajectories in the ordination space revealed two distinct behavioural patterns among *Thunnus thynnus* individuals. Individuals 320 and 324 initiated their first dive in the positive quadrant of the biplot. Individual 320 subsequently moved towards strongly positive values on PC2 before progressing towards positive PC1 values, with its final dive — followed by mortality — occurring at strongly positive PC1 values. Individual 324 moved closer to the origin during its second dive while remaining in the positive quadrant, before its final dive — also followed by mortality — returned to strongly positive PC2 values. In contrast, individuals 139, 181, 270, and 276 showed trajectories that progressively shifted towards negative PC2 values across successive dives, with their respective final dives — none of which were followed by mortality — all occurring at negative PC2 values. Within this group, individuals 181 and 270 initiated their first dive at values close to the PC2 origin, while individuals 139 and 276

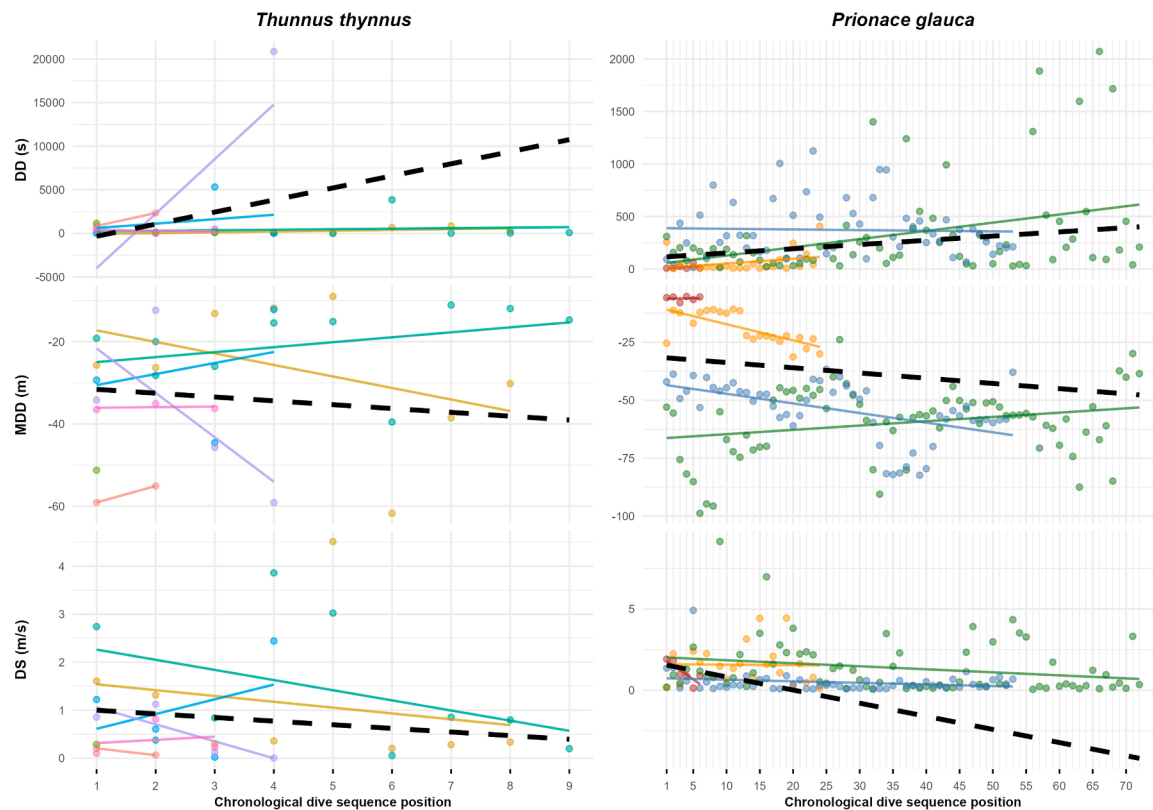


Fig. 5. Evolution of dive duration (DD), maximum dive depth (MDD), and descent speed (DS) across successive dive sequences for *Thunnus thynnus* (left, $n = 7$) and *Prionace glauca* (right, $n = 4$; Gulf of Lion individuals in red and orange, Réunion Island individuals in blue and green). Each individual is represented by a distinct colour. Each point corresponds to a dive for a given individual, solid lines show the linear trend for each individual, and the black dashed line represents the mean trend across all individuals.

started at negative PC2 values. Individual 58 performed only a single dive, positioned in the positive quadrant (Fig. 8a).

For *Prionace glauca*, the linear mixed-effects model fitted to test the effect of dive position on PC scores, with individual as a random effect, indicated significant effects of position on both PC1 ($t = 3.40$) and PC2 ($t = 2.06$), with intra-class correlation coefficients of 0.47 and 0.22 respectively. The high intra-class correlation on PC1, together with the unequal contribution of individuals to the principal components depending on their deployment basin, indicated that a single PCA at the species level would be biased by basin-level differences. Separate PCAs were therefore performed for individuals captured in the Gulf of Lion ($n = 2$) and around Réunion Island ($n = 2$). For Gulf of Lion individuals, PC1 explained 42.9% of the total variance and was primarily associated with DD and MDD, which loaded positively, while HGSD, HDFSFTF, and DS loaded negatively. PC2 explained 28.5% of the total variance and was primarily associated with DD, which loaded positively, while MDD and DS loaded negatively (Fig. 8b). The two recorded individuals showed contrasting trajectories. Individual 366 remained confined to the negative quadrant of PC1 throughout its CA phase, whereas individual 400 occupied a broader portion of the ordination space, with its earliest dives located in the negative region of PC1 before progressively shifting towards positive PC1 values across successive dives. The final dive of each individual was located at opposite ends of the PC1 axis and in the positive quadrant of PC2. Individual 366 ended its CA phase with a final dive characterised by elevated values of HGSD and HDFSFTF, and low values of DD and MDD, whereas individual 400 ended with the opposite pattern, with elevated DD and MDD and low values of HGSD and HDFSFTF. For Réunion Island individuals, PC1 explained 32.2% of the total variance and was primarily associated with DS, which loaded positively, while DD, MDD, and HDFSFTF loaded negatively. PC2 explained 20.7% of the total variance and was primarily associated with

HGSD, which loaded positively, with HDFSFTF contributing weakly in the positive direction (Fig. 8c). Both recorded individuals showed trajectories alternating between positive and negative values on PC1 across successive dives. Individual 250 tended to extend slightly further into the positive region of PC2 than individual 339. Both individuals ended their CA phase with a final dive located close to the origin of the ordination space. None of the four *Prionace glauca* individuals recorded in this study showed mortality following their final dive.

4. Discussion

Little is known about the behaviour of animals captured by longline gear and their progressive fight activity over time until retrieval at the vessel. This study analyses the evolution of behaviour from direct gear-based measurements throughout the capture event, rather than from observations made once the individual is brought aboard, based on the assumption that progressive changes in movement and fight intensity may reflect an underlying physiological decline. Understanding this process is essential not only to assess the level of stress experienced during capture, but also to inform the development of mitigation measures, particularly for species that are released alive and whose post-release survival is a critical conservation concern (Ellis, McCully Phillips, and Poisson, 2017, Cope et al., 2022). This study provides a first characterisation of the behaviour of several species captured on pelagic longlines in the Gulf of Lion and around Réunion Island through direct gear instrumentation. Given the small sample size for several species, results are interpreted with caution. Electronic tagging has been widely used to monitor large pelagic species, enabling the characterisation of individual behaviour, the tracking of movements, the understanding of phenology, and the estimation of post-release survival rates (Evans and Hammond, 2004, Rouyer et al., 2022, Landreau et al., 2026). In

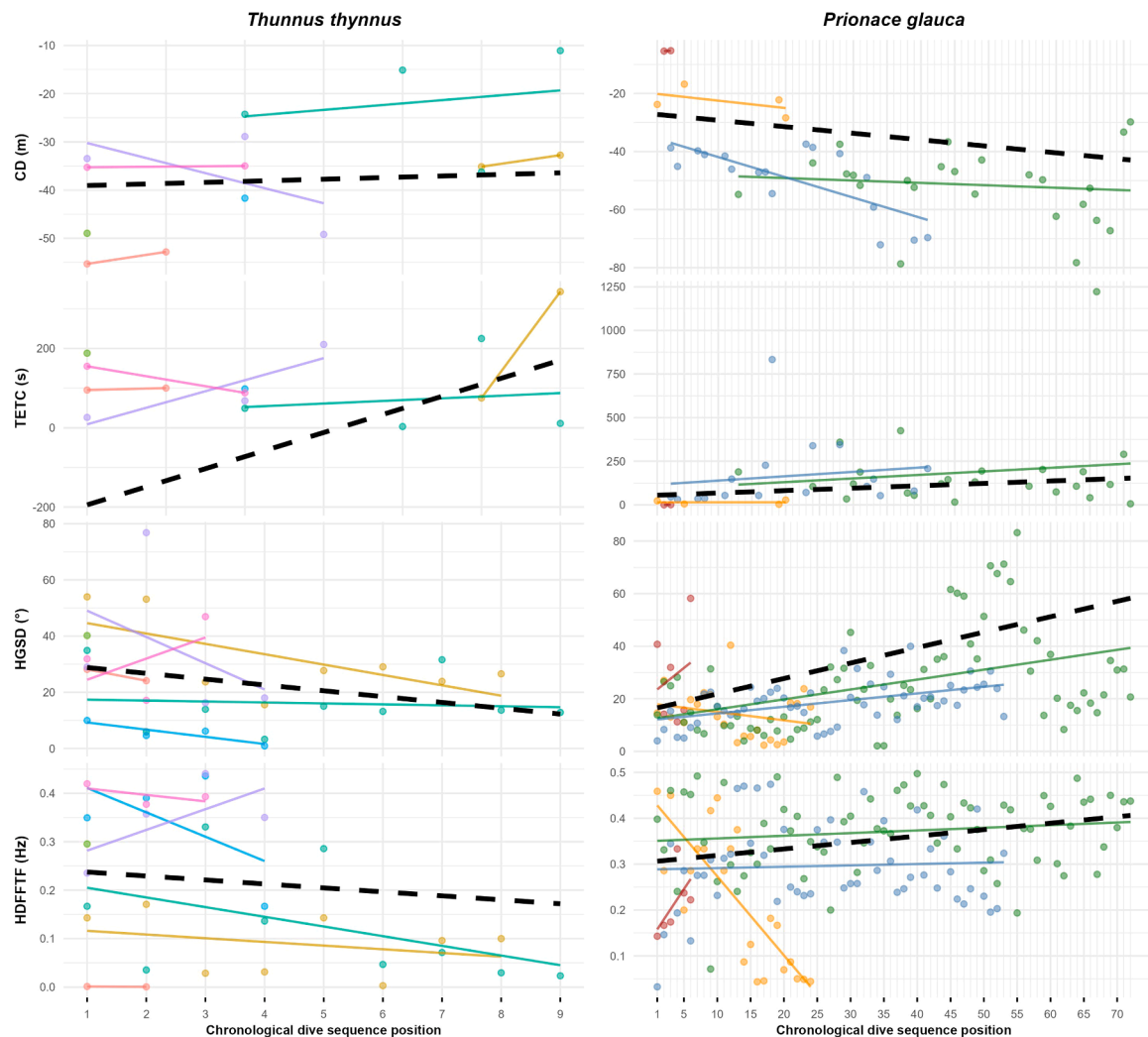


Fig. 6. Evolution of changepoint depth (CD), time elapsed to changepoint (TECP), heading gradient standard deviation (HGSD), and heading dominant FFT frequency (HDFFTF) across successive dive sequences for *Thunnus thynnus* (left, $n = 7$) and *Prionace glauca* (right, $n = 4$; Gulf of Lion individuals in red and orange, Réunion Island individuals in blue and green). Each individual is represented by a distinct colour. Each point corresponds to a dive for a given individual, solid lines show the linear trend for each individual, and the black dashed line represents the mean trend across all individuals.

contrast, methods for assessing exhaustion and stress following capture remain relatively limited. Several studies have used physiological methods with in situ sampling to estimate the stress level of the animal at the time of boarding (Skomal, 2007, Jerome et al., 2018, Whitney et al., 2021). Elevated blood lactate levels have been used as a proxy for the degree of stress and exhaustion experienced by animals during capture (Marshall et al., 2012). However, these methods have certain limitations. Results are not immediate, the procedure requires handling the animal, which may further increase its stress level, the biopsy and blood withdrawal can be invasive, and sampling conditions are sometimes too complex to ensure reliable and consistent results. Regarding longline instrumentation, a limited number of studies have reported results on gear behaviour and its position in the water column, but few findings exist on the actual behaviour of animals captured on the line (Campbell and Young, 2012, Peterson, Gartland, and Latour, 2017). The analysis of TDR depth data has nonetheless helped reveal behavioural differences between shark species incidentally captured on pelagic longlines (Guida et al., 2017).

Behavioural differences between captured species appeared from the earliest stages of analysis. At the time-series labelling stage, certain datasets could not be labelled, mainly because some individuals showed too little activity at the end of the line. This was observed only in data collected around Réunion Island, and concerned individuals of snoek

(*Thyrstitoides marleyi*) and, for some individuals, dolphinfish (*Coryphaena hippurus*). These species likely have limited physical strength to pull against the line, and the relatively heavy and resistant gear deployed in this fishery may further limit the movements of individuals of these species, which are generally of modest body size (Coelho et al., 2014, Whitney et al., 2016). The duration of the Catch Alive (CA) phase varied greatly between individuals and species, largely depending on when the animal was hooked along the line, an aspect not directly analysed in the present study. Within these CA phases, however, the identification of dive sequences and the computation of several associated metrics revealed clearer behavioural differences between species, most notably between target and bycatch species such as ABFT and blue shark, although several species were represented by a single individual, calling for some caution in interpreting these patterns. Across both study areas combined, elasmobranchs (blue shark and pelagic stingray) tended to perform the highest number of dive sequences, each relatively short compared to other captured species. Conversely, ABFT performed fewer dive sequences, but of comparatively longer duration.

This behavioural divergence between the two species appears to be further supported by the analysis of dive-level metrics. Exhaustion-related behaviour at the end of a line is typically characterised by a progressive reduction in diving activity, with individuals increasingly remaining around the depth of the mainline as their ability to actively

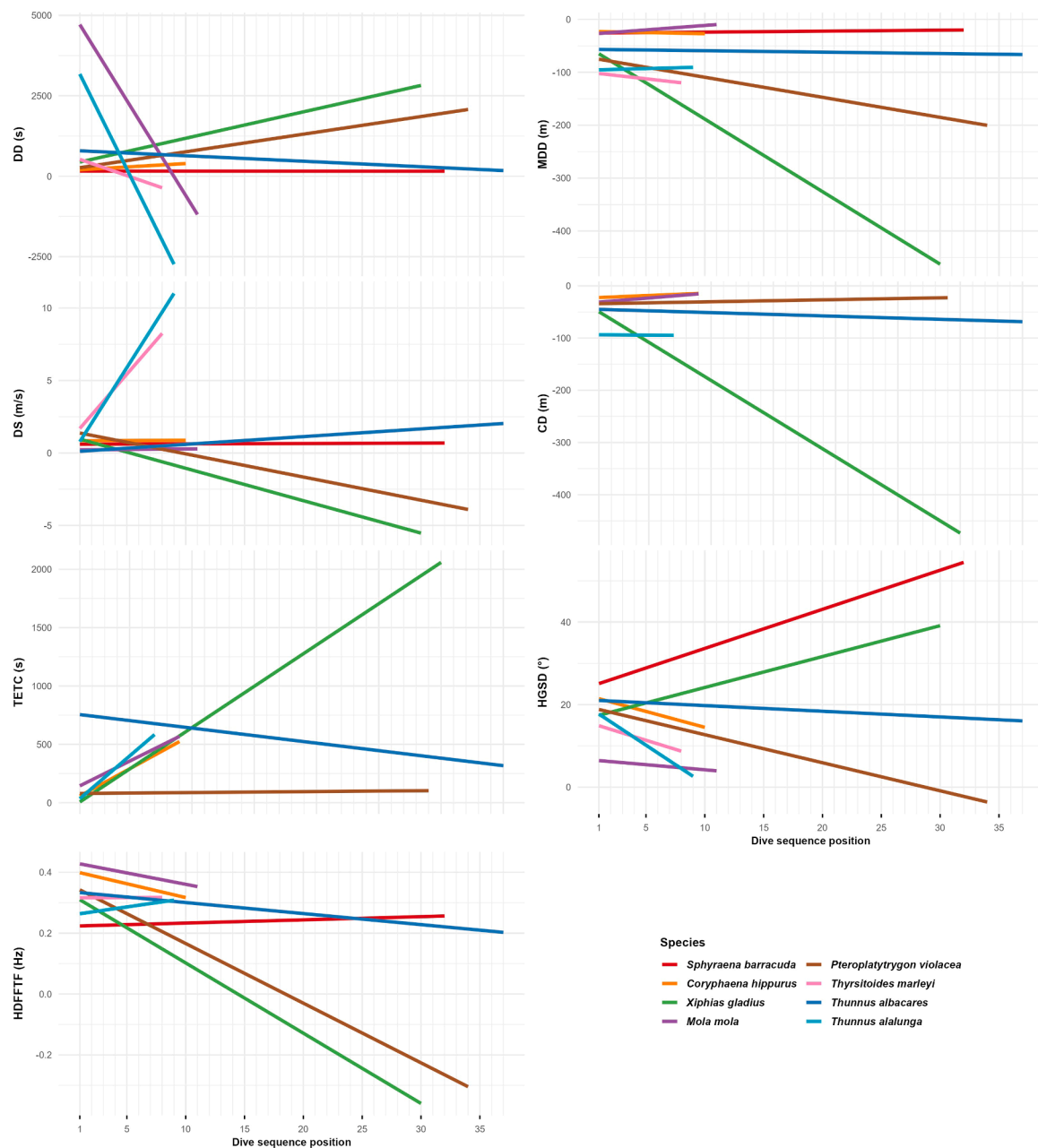


Fig. 7. Mean trend lines of all seven dive metrics — dive duration (DD), descent speed (DS), time elapsed to changepoint (TECP), heading dominant FFT frequency (HDFFTF), maximum dive depth (MDD), changepoint depth (CD), and heading gradient standard deviation (HGSD) — across successive dive sequences for all recorded species excluding *Thunnus thynnus* and *Prionace glauca*. Each line represents the mean trend for a single species.

move against the line decreases (Stokesbury et al., 2011, Mitchell et al., 2019). In ABFT, patterns of dive duration and maximum depth per sequence were highly variable between individuals (Fig. 5). A general decreasing trend in descent speed was nonetheless observed across successive dives. ABFT showed considerable fighting intensity during the first dive sequences, marked by sharp and short descents. These were followed by longer dives that were likely more costly in energy (Wood, 1991, Stokesbury et al., 2011). For blue sharks, two distinct patterns emerged. Individuals captured in the Gulf of Lion showed patterns of dive duration and maximum depth similar to those of ABFT. However, their descent speed stayed relatively constant over time, across a much higher number of dives than observed in ABFT. For individuals captured around Réunion Island, which were generally larger, behavioural trends were more variable between individuals (Table 1). Body size has previously been shown to affect capture-related behaviour in sharks

(Cortés, 2000, Raje, Thakurdas, and Sundaram, 2012). The difference between ABFT and blue shark was clearer for the CD, TECP, HGSD, and HDFFTF metrics (Fig. 6). The changepoint, marking the shift between the initial descent phase of a dive and the rest of the dive sequence, showed a progressive decline in the ability of ABFT to repeat intense pulling efforts against the line. Across successive dives, individuals not only reached a shallower changepoint but also took longer to reach it. This was not the case for blue sharks, which reached a progressively deeper changepoint, with a relatively stable time to reach it across dives. The two heading-based metrics, which reflect the intensity and rhythm of fighting movements, showed an opposite pattern in ABFT compared to blue sharks (Fig. 6). The amplitude and dominant frequency of movements declined over time in ABFT, potentially pointing to exhaustion-related behaviour. In fish, increased movement intensity is often seen as a proxy for stress during the early stages of capture, while a

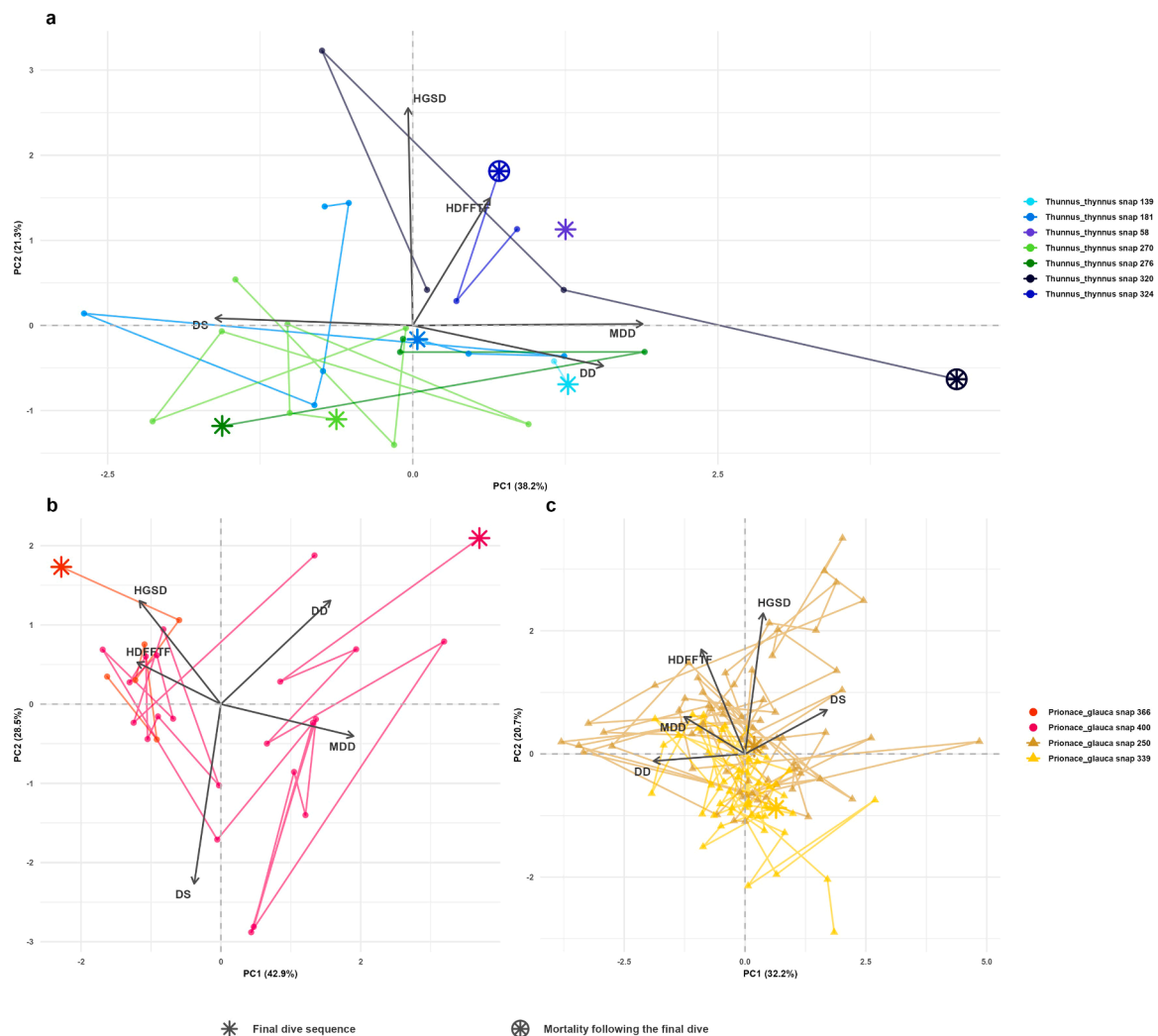


Fig. 8. PCA biplots of dive metrics across successive dive sequences for (a) *Thunnus thynnus* ($n = 7$), (b) *Prionace glauca* from the Gulf of Lion ($n = 2$; shown as circles in red and pink), and (c) *Prionace glauca* from Réunion Island ($n = 2$; shown as triangles in orange and yellow). Each point represents a single dive sequence, with trajectories connecting successive dives in chronological order for each individual. The final dive sequence of each individual is indicated by an asterisk (*), and individuals for which mortality was recorded following the final dive are identified by a circled asterisk (@).

later decline may reflect muscular fatigue and exhaustion (Kane et al., 2004, Davis, 2010). This pattern did not appear as a clear tendency in blue sharks, which may reflect greater physiological tolerance to sustained efforts. None of the elasmobranchs captured in this study arrived dead at the vessel, unlike ABFT. More broadly, blue sharks and stingrays incidentally captured on longlines are rarely retrieved dead (Campana, Joyce, and Manning, 2009, Carbonara et al., 2026, Landreau et al., 2026). Taken together, these results point to a broad contrast between ABFT, which appears to lose fighting intensity quickly, consistent with possible fast-onset exhaustion, and blue shark, which appears less affected by this process, probably exerting comparatively lower pulling forces against the line due to differences in physical capacity, but possibly showing greater endurance over the course of capture (French et al., 2015, Guida et al., 2017, Mitchell et al., 2019).

These contrasting patterns between ABFT and blue shark appeared to extend, to varying degrees, across the remaining species recorded in this study (Fig. 7). Tuna species captured around Réunion Island, namely yellowfin tuna (*Thunnus albacares*) and albacore tuna (*Thunnus alalunga*), showed patterns consistent with ABFT for the heading-based metrics (HGSD, HDFFTF) and for the changepoint-related metrics, except for TECP in yellowfin tuna. In contrast, the opposite pattern was observed for metrics describing dive characteristics themselves (DD, MDD, and DS), likely reflecting differences in gear configuration. Gear

characteristics specific to the Réunion Island fishery, such as float spacing, soak time, and branchline length, may explain these differences. Other biological factors that may influence diving behaviour could be taken into account, such as the thermal preferences of each species within the water column and the depth of the thermocline. Around Réunion Island, hooked individuals appear to have greater freedom of movement, but also access to deeper and cooler waters, where oxygen levels are likely higher, which may limit the energetic cost of capture (Wyrki, 1973, Rouyer et al., 2023). Nevertheless, these conditions did not prevent mortality in some tuna individuals, raising the question of the actual impact of capture on the physiological state of the animal. Tuna species have a higher basal metabolism than elasmobranchs and require continuous movement to maintain oxygen uptake. When restrained by a hooked line, this physiological constraint likely increases the energetic cost of restricted movement, leading to faster depletion of energy reserves and oxygen supply, and may explain why tuna species are more susceptible to capture-induced mortality despite having access to deeper, colder waters that are potentially richer in oxygen around Réunion Island. (Guppy, Hulbert, and Hochachka, 1979, Korsmeyer and Dewar, 2001). This may be taken into account in cases where individuals of target species (such as tuna) caught are below the minimum size limit and must be released.

The pelagic stingray individuals recorded in this study were

comparatively small-bodied, with seemingly limited strength to pull against the line. Despite this, they showed metric patterns broadly similar to blue shark across most dive sequences, suggesting that, like blue shark, they may not undergo the same rapid decline in fighting capacity observed in tuna species. Among the remaining bycatch species, swordfish stood out, showing trends closer to ABFT for most metrics except CD and HGSD. As with the tuna species discussed above, this may partly reflect gear characteristics specific to the Réunion Island fishery, which likely give captured individuals more freedom of movement. However, differences in environmental conditions and gear configurations between study areas make behavioural patterns difficult to compare directly, as these factors may strongly influence the observed responses. Incorporating environmental data, such as water column temperature, could help to better interpret these differences.

This contrast between a rapid decline in fight activity in tuna species and greater behavioural endurance in elasmobranchs, concerning, in this case, few blue sharks and pelagic stingrays, is further reinforced when considering the temporal continuity of behavioural states within each individual's CA phase, as revealed by the PCA trajectories (Fig. 8). The PCA trajectories provide further insight into this continuity across successive dives, suggesting that the behavioural state expressed during a given dive is closely linked to that of preceding dives. This continuity is particularly clear in ABFT, where the two individuals that ultimately died following their final dive (320 and 324) consistently occupied the positive quadrant of the ordination space throughout their CA phase, marked by elevated values of HGSD, HDTFF, MDD, and DD. In contrast, individuals that survived to retrieval showed dive sequences confined to the opposite region of the ordination space, with comparatively lower values across these same metrics. Notably, however, the final dive of each surviving individual was associated with reduced values along the heading-related axis (PC2), suggesting that some degree of exhaustion may nonetheless have been reached by the end of the CA phase, even without subsequent mortality. A similar pattern was observed in the two other tuna species (yellowfin and albacore tuna) recorded in this study, where individuals that ultimately died also showed dive trajectories moving towards the high-value quadrant of their respective ordination spaces, consistent with a progressive loss of fight capacity. Given that these tuna species are the main target catches in the Réunion Island fishery, this observation may have direct implications for the timing and consequences of capture-induced exhaustion in commercially important species, with potential consequences for flesh quality. As highlighted by Robb (2002), stressful conditions and high levels of activity before and during slaughter can negatively affect the subsequent quality of the flesh (Coelho et al., 2014; Kim and Na, 2022). For *Prionace glauca*, no mortality was recorded across the four individuals, regardless of the deployment basin. A common behavioural pattern emerged across these individuals, with dive sequences alternating between two contrasting states: deep and long dives associated with slow and low-amplitude rhythmic movements, and shorter and shallower dives marked by rapid descent speeds and high-amplitude rhythmic movements. Individual 366 from the Gulf of Lion stood out by displaying successive dive sequences characterised by sustained high-amplitude and high-frequency rhythmic movements. This individual was captured during the hauling of the gear, and the tension and vibrations transmitted along the line during this operation are known to elicit stress responses in sharks, which may explain this particular behavioural pattern (Skomal, Bernal, 2010; Carrier et al., 2022). A notable difference was observed in the position of the final dive of each individual within the ordination space, with Gulf of Lion individuals reaching extreme values of the biplot whereas Réunion Island individuals ended their CA phase close to the origin. This difference may partly reflect the larger body size and greater muscular capacity of Réunion Island individuals.

These mortality-linked behavioural trajectories in target tuna species illustrate the wider value of the approach developed in this study, which offers an unprecedented window into the behaviour of animals captured on pelagic longlines, raising the hypothesis of a link between behaviour

and the stress and exhaustion induced by fighting over the course of capture, across a range of target and bycatch species. Such information directly contributes to the overall characterisation of bycatch, which remains one of the most pressing challenges facing longline fisheries worldwide. More specifically, the results of this study contribute to characterising the behavioural and physiological responses of bycaught individuals during capture, an aspect that has received comparatively little attention to date. Beyond confirming that elasmobranchs (blue shark and pelagic stingray) and tuna (bluefin, yellowfin and albacore tuna) species differ markedly in how they respond behaviourally to capture, this approach is a first step to distinguish species based on their behaviour, as well as to assess their state of exhaustion and overall condition, without the need to wait for individuals to be hauled aboard. This has direct implications for the development of handling and mitigation measures, particularly for sensitive species, by avoiding the often invasive manipulations typically involved at release. This could have a crucial impact on the post-release survival of non-landed species, which depends on the time spent on the line and the level of stress accumulated. For longer-term development, equipping SMARTSNAP devices with a communication system linked to the vessel could provide fishers with new information on gear behaviour and catch volume in near real time. Coupled with a rapid release mechanism, this could also improve the survival of bycatch species through faster and less invasive release than if individuals had to wait to be brought aboard. Future deployments coupling this approach with physiological sampling, such as blood lactate measurements, could help confirm the hypothesised link between behaviour and exhaustion. At the same time, tracking the onset of exhaustion in target species such as tuna may help optimise the handling and release of undersized individuals, with benefits for survival and animal welfare, while also providing insights into potential consequences for flesh quality in retained fish, aspects of growing societal relevance. By linking behavioural data directly to the timing and intensity of exhaustion, this study therefore contributes both to bycatch conservation efforts and to the wider management of capture-related stress in commercial pelagic longline fisheries.

CRediT authorship contribution statement

Antoine Landreau: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation.

Funding

This work was supported by the SMARTSNAP project co-funded by European Fund for Maritime Affairs, Fisheries and Aquaculture (EMFAF) and France Filière Pêche (FFP).

SMARTSNAP2 project funded by European Fund for Maritime Affairs, Fisheries and Aquaculture (EMFAF).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgement

We thank the SATHOAN fishermen organization for their help and their constant support with field operations, as well as the crew of the longliner "Trois Frères II" (Renaud Frejafond) in the Gulf of Lion, whose skills and trust helped us to carry out this study in the best conditions. We also thank the Réunion Island fishermen, in particular the crews of the longliners "Ichtys" and "Petite Crevette", for their support during field operations. We are also grateful to the IFREMER and COOL teams for their assistance throughout the field operations.

Data availability

Data will be made available on request.

References

- Addis, P., Corrias, S., Garau, C., et al., 2013. Physiologic responses to stress and changes in atlantic bluefin tuna (*T. thynnus*) meat color during trap fisheries capture and processing in sardinia (W. Mediterranean). *J. Aquat. Food Prod. Technol.* 22 (3), 298–309. <https://doi.org/10.1080/10498850.2011.647596>.
- Ames, R.T., Leaman, B.M., Ames, K.L., 2007. Evaluation of Video Technology for Monitoring of Multispecies Longline Catches. *North. Am. J. Fish. Manag.* 27 (3), 955–964. <https://doi.org/10.1577/M06-029.1>.
- Arregui, I., Galuardi, B., Goñi, N., et al., 2018. Movements and geographic distribution of juvenile bluefin tuna in the Northeast Atlantic, described through internal and satellite archival tags. *ICES J. Mar. Sci.* 75 (5), 1560–1572. <https://doi.org/10.1093/icesjms/fsy056>.
- Babcock, E.A., Pikitch, E.K., 2003. How Much Observer Coverage Is Enough to Adequately Estimate Bycatch. https://www.pew.org/-/media/legacy/uploadedfiles/wwwpewtrustsorg/reports/protecting_ocean_life/oceanabycatch110403pdf.pdf.
- Bates, D., Mächler, M., Bolker, B., et al., 2015. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Beitinger, T.L., 1990. Behavioral Reactions for the Assessment of Stress in Fishes. *J. Gt. Lakes Res. Fish. Community Health: Monitoring and Assessment in Large Lakes*, 1990; 16(4):495–528. [https://doi.org/10.1016/S0380-1330\(90\)71443-8](https://doi.org/10.1016/S0380-1330(90)71443-8).
- Bellido, J.M., Santos, M.B., Pennino, M.G., et al., 2011. Fishery discards and bycatch: solutions for an ecosystem approach to fisheries management? *Hydrobiologia* 670 (1), 317–333. <https://doi.org/10.1007/s10750-011-0721-5>.
- Block, B.A., Jonsen, I.D., Jorgensen, S.J., et al., 2011. Tracking apex marine predator movements in a dynamic ocean. *art. 7354 Nature* 475 (7354). <https://doi.org/10.1038/nature10082>.
- Boniol P., Liu Q., Huang M. et al. Dive into Time-Series Anomaly Detection: A Decade Review, arXiv:2412.20512. Preprint, arXiv, 29 Dec. 2024. <https://doi.org/10.48550/arXiv.2412.20512>.
- Botsford, L.W., Castilla, J.C., Peterson, C.H., 1997. The Management of Fisheries and Marine Ecosystems. *Science* 277 (5325), 509–515. <https://doi.org/10.1126/science.277.5325.509>.
- Bowlby, H.D., Benoît, H.P., Joyce, W., et al., 2021. Beyond Post-release Mortality: Inferences on Recovery Periods and Natural Mortality From Electronic Tagging Data for Discarded Lamnid Sharks. *Front. Mar. Sci.* 8. <https://www.frontiersin.org/articles/10.3389/fmars.2021.619190>, 5 Feb. 2024, date last accessed.
- Brooks, E.J., Mandelman, J.W., Sloman, K.A., et al., 2012. The physiological response of the Caribbean reef shark (*Carcharhinus perezi*) to longline capture. *Comp. Biochem. Physiol. A Mol. Integr. Physiol. Sel. Pap. A Symp. Physiol. Stress. Response Elasmobranch Fishes* 162 (2), 94–100. <https://doi.org/10.1016/j.cbpa.2011.04.012>.
- Campana, S.E., Joyce, W., Manning, M.J., 2009. Bycatch and discard mortality in commercially caught blue sharks *Prionace glauca* assessed using archival satellite pop-up tags. *Mar. Ecol. Prog. Ser.* 387, 241–253. <https://doi.org/10.3354/meps08109>.
- Campbell, R.A., Young, J.W., 2012. Monitoring the behaviour of longline gears and the depth and time of fish capture in the Australian Eastern Tuna and Billfish Fishery. *Fish. Res.* 119–120, 48–65. <https://doi.org/10.1016/j.fishres.2011.12.006>.
- Carbonara, P., Bellodi, A., Prato, G., et al., 2026. Resilience in the line: insights on post-release survival from long-term monitoring and satellite tagging of blue sharks (*Prionace glauca*) in the Southern Adriatic Sea. *Biol. Conserv.* 321, 111939. <https://doi.org/10.1016/j.biocon.2026.111939>.
- Carrier, J.C., Simpfendorfer, C.A., Heithaus, M.R., et al., 2022. *Biology of Sharks and Their Relatives*. n.p. CRC Press.
- Carruthers, E.H., Schneider, D.C., Neilson, J.D., 2009. Estimating the odds of survival and identifying mitigation opportunities for common bycatch in pelagic longline fisheries. *Biol. Conserv.* 142 (11), 2620–2630. <https://doi.org/10.1016/j.biocon.2009.06.010>.
- Coelho, Rui, Santos, Miguel N, Amorim, Sérgio, 2012. Effects of Hook and Bait on Targeted and Bycatch Fishes in an Equatorial Atlantic Pelagic Longline Fishery. *Bulletin of Marine Science* 88 (3), 449–467. <https://doi.org/10.5343/bms.2011.1064>. <http://openurl.ingenta.com/content/xref?genre=article&issn=0007-4977&volume=88&issue=3&page=449>.
- Coelho R., Nikolic N., Evano H. et al. Reunion island pelagic longline fishery characterization and standardization of albacore catch rates, paper delivered at IOTC. 1 Jul. 2014. <https://archimer.ifremer.fr/doc/00208/31926/> (22 Jun. 2026, date last accessed).
- Cope, H.R., McArthur, C., Dickman, C.R., et al., 2022. A systematic review of factors affecting wildlife survival during rehabilitation and release. *PLOS ONE* 17 (3), e0265514. <https://doi.org/10.1371/journal.pone.0265514>.
- Cortés, E., 2000. Life History Patterns and Correlations in Sharks. *Rev. Fish. Sci.* 8 (4), 299–344. <https://doi.org/10.1080/10480340308951115>.
- Davies, R.W.D., Cripps, S.J., Nickson, A., et al., 2009. Defining and estimating global marine fisheries bycatch. *Mar. Policy* 33 (4), 661–672. <https://doi.org/10.1016/j.marpol.2009.01.003>.
- Davis, M.W., 2002. Key principles for understanding fish bycatch discard mortality. *Can. J. Fish. Aquat. Sci.* 59 (11), 1834–1843. <https://doi.org/10.1139/f02-139>.
- Davis, M.W., 2010. Fish stress and mortality can be predicted using reflex impairment. *Fish Fish* 11 (1), 1–11. <https://doi.org/10.1111/j.1467-2979.2009.00331.x>.
- Dominguez, S.C., Pao, J., Paradela, I., et al., 2025. Autonomous Drone-Ground Robot Alignment Through Ground Robot Visual Servo Control With Drone Detection and Tilt Correction. *IEEE Robot. Autom. Lett.* 10 (7), 6648–6655. <https://doi.org/10.1109/LRA.2025.3569125>.
- Ellis, J.R., McCully Phillips, S.R., Poisson, F., 2017. A review of capture and post-release mortality of elasmobranchs. *J. Fish. Biol.* 90 (3), 653–722. <https://doi.org/10.1111/jfb.13197>.
- Evans, P.G.H., Hammond, P.S., 2004. Monitoring cetaceans in European waters. *Mammal. Rev.* 34 (1–2), 131–156. <https://doi.org/10.1046/j.0305-1838.2003.00027.x>.
- French, R.P., Lyle, J., Tracey, S., et al., 2015. High survivorship after catch-and-release fishing suggests physiological resilience in the endothermic shortfin mako shark (*Isurus paucus*). *Conserv. Physiol.* 3 (1), cov044. <https://doi.org/10.1093/conphys/cov044>.
- Frick, L.H., Reina, R.D., Walker, T.I., 2010. Stress related physiological changes and post-release survival of Port Jackson sharks (*Heterodontus portusjacksoni*) and gummy sharks (*Mustelus antarcticus*) following gill-net and longline capture in captivity. *J. Exp. Mar. Biol. Ecol.* 385 (1), 29–37. <https://doi.org/10.1016/j.jembe.2010.01.013>.
- Gallagher, A.J., Orbesen, E.S., Hammerschlag, N., et al., 2014. Vulnerability of oceanic sharks as pelagic longline bycatch. *Glob. Ecol. Conserv.* 1, 50–59. <https://doi.org/10.1016/j.gecco.2014.06.003>.
- Guida, L., Dapp, D.R., Huveneers, C.P.M., et al., 2017. Evaluating time-depth recorders as a tool to measure the behaviour of sharks captured on longlines. *J. Exp. Mar. Biol. Ecol.* 497, 120–126. <https://doi.org/10.1016/j.jembe.2017.09.011>.
- Guppy, M., Hulbert, W.C., Hochachka, P.W., 1979. Metabolic Sources of Heat and Power in Tuna Muscles: II. Enzyme and Metabolite Profiles. *J. Exp. Biol.* 82 (1), 303–320. <https://doi.org/10.1242/jeb.82.1.303>.
- Hazen, E.L., Scales, K.L., Maxwell, S.M., et al., 2018. A dynamic ocean management tool to reduce bycatch and support sustainable fisheries. *Sci. Adv.* 4 (5), eaar3001. <https://doi.org/10.1126/sciadv.aar3001>.
- Jerome, J.M., Gallagher, A.J., Cooke, S.J., et al., 2018. Integrating reflexes with physiological measures to evaluate coastal shark stress response to capture. *ICES J. Mar. Sci.* 75 (2), 796–804. <https://doi.org/10.1093/icesjms/fsx191>.
- Kane, A.S., Salerno, J.D., Gipson, G.T., et al., 2004. A video-based movement analysis system to quantify behavioral stress responses of fish. *Water Res.* 38 (18), 3993–4001. <https://doi.org/10.1016/j.watres.2004.06.028>.
- Killick, R., Haynes, K., Hullait, H., 2024. Changepoint: Methods for Changepoint Detection, version 2.3. 4 Nov. 2024. <https://cran.r-project.org/web/packages/changepoint/index.html> (8 Jun. 2026, date last accessed).
- Killick, R., Eckley, I.A., 2014. changepoint: An R Package for Changepoint Analysis. *J. Stat. Softw.* 58, 1–19. <https://doi.org/10.18637/jss.v058.i03>.
- Kim, J., Na, H., 2022. Interannual Variability of Yellowfin Tuna (*Thunnus albacares*) and Bigeye Tuna (*Thunnus obesus*) Catches in the Southwestern Tropical Indian Ocean and Its Relationship to Climate Variability. *Front. Mar. Sci.* 9. <https://doi.org/10.3389/fmars.2022.857405>.
- Korsmeyer, K.E., Dewar, H., 2001. Tuna metabolism and energetics. In: *Tuna: Physiology, Ecology, and Evolution*, Fish Physiology, 19. n.p.: Academic Press, pp. 35–78. [https://doi.org/10.1016/S1546-5098\(01\)19003-5](https://doi.org/10.1016/S1546-5098(01)19003-5).
- Landreau, A., Kerzéro, V., Derridj, O., et al., 2026. Post-Release Survival of the Pelagic Stingray (*Pteroplatytrygon violacea*, Bonaparte, 1832) in French Longline Fisheries in the Northwestern Mediterranean Sea. *Fish. Manag. Ecol.* n/a (n/a). <https://doi.org/10.1111/fme.70053>.
- Landreau, A., Nieblas, A.E., Bonhommeau, S., et al., 2024. Ongoing Proj. Under Mitigate Bycatch Longline Bluefin Tuna Fish. *Fr. Mediterr.* https://www.iccat.int/Document/s/CVSP/CV081_2024/n_4/CV08104048.pdf.
- Lewis, R.L., Crowder, L.B., Read, A.J., et al., 2004. Understanding impacts of fisheries bycatch on marine megafauna. *Trends Ecol. Evol.* 19 (11), 598–604. <https://doi.org/10.1016/j.tree.2004.09.004>.
- Lloret, J., Shulman, G., Love, R.M., 2013. *Condition and Health Indicators of Exploited Marine Fishes*. n.p.: John Wiley & Sons.
- Lockridge, K.A., 1981. *Fish Stress and Health in Aquaculture*. n.p.: Cambridge University Press.
- Lotek. LAT2000 Series – Light Geolocation | LotekLotek. Lotek | 26 Oct. 2017. <https://www.lotek.com/products/lat2000-series/> (24 Jun. 2026, date last accessed).
- Mandelman, J.W., Skomal, G.B., 2009. Differential sensitivity to capture stress assessed by blood acid–base status in five carcharhinid sharks. *J. Comp. Physiol. B* 179 (3), 267–277. <https://doi.org/10.1007/s00360-008-0306-4>.
- Marshall, H., Field, L., Afadara, A., et al., 2012. Hematological indicators of stress in longline-captured sharks. *Comp. Biochem. Physiol. A Mol. Integr. Physiol. Sel. Pap. A Symp. Physiol. Stress. Response Elasmobranch Fishes* 162 (2), 121–129. <https://doi.org/10.1016/j.cbpa.2012.02.008>.
- Mitchell, J.D., McLean, D.L., Collin, S.P., et al., 2019. Shark depredation and behavioural interactions with fishing gear in a recreational fishery in Western Australia. *Mar. Ecol. Prog. Ser.* 616, 107–122. <https://doi.org/10.3354/meps12954>.
- Nieblas, A.E., Rouyer, T., Bonhommeau, S., et al., 2023. SMARTSNAP: A new device to aid in the reduction of bycatch mortality in longline fisheries | Bycatch Management Information System (BMIS). <https://otcorgmeetings19th-Work.-Part.-Ecosyst.-Bycatch-Meet.-Wpbe19>. <https://www.bmis-bycatch.org/references/rgf2ljlj>, 4 Apr. 2024, date last accessed.
- Patin, Rémi, Etienne, M.P., Lebarbier, E., et al., 2020. Identifying stationary phases in multivariate time series for highlighting behavioural modes and home range settlements. *J. Anim. Ecol.* 89 (1), 44–56. <https://doi.org/10.1111/1365-2656.13105>.
- Patin, Rémi, Etienne, M.P., Lebarbier, E., et al., 2025. segclust2d Bivariate Segm. /Clust. Methods Tools 0.3.3. <https://doi.org/10.32614/CRAN.package.segclust2d>.

- Peterson, C.D., Gartland, J., Latour, R.J., 2017. Novel use of hook timers to quantify changing catchability over soak time in longline surveys. *Fish. Res.* 194, 99–111. <https://doi.org/10.1016/j.fishres.2017.05.010>.
- Poisson, F., Sidonie, C., Caroline, C., et al., 2019. The effect of hook type and trailing gear on hook shedding and fate of pelagic stingray (*Pteroplatytrygon violacea*): New insights to develop effective mitigation approaches. *Mar. Policy* 107, 103594. <https://doi.org/10.1016/j.marpol.2019.103594>.
- Raje, S.G., Thakurdas, Sundaram, S., 2012. Relationship between body size and certain breeding behavior in selected species of Elasmobranchs off Mumbai. *J. Mar. Biol. Assoc. India* 54 (2), 85–89.
- Read, A.J., Drinker, P., Northridge, S., 2006. Bycatch of Marine Mammals in U.S. and Global Fisheries. *Conserv. Biol.* 20 (1), 163–169. <https://doi.org/10.1111/j.1523-1739.2006.00338.x>.
- Robb, D., 2002. The Killing of Quality: The Impact of Slaughter Procedures on Fish Flesh. In: Alasalvar, C., Taylor, T. (Eds.), *Seafoods — Quality, Technology and Nutraceutical Applications*. Springer, Berlin, Heidelberg, pp. 7–16. https://doi.org/10.1007/978-3-662-09836-3_2.
- Roda P., M.A. (ed.), Gilman et al. *A Third Assessment of Global Marine Fisheries Discards*. n. p.: FAO, 2019. <https://openknowledge.fao.org/handle/20.500.14283/ca2905en> (30 Jan. 2025, date last accessed).
- Rouyer, T., Bonhommeau, S., Bernard, S., et al., 2023. A novel protocol for rapid deployment of heart rate data storage tags in Atlantic bluefin tuna reveals cardiac responses to temperature and feeding. *J. Fish. Biol.* n/a (n/a). <https://doi.org/10.1111/jfb.15507>.
- Rouyer, Tristan, Bernard, S., Kerzerho, V., et al., 2022. Electronic tagging of Bluefin Tunas from the Maltese spawning ground suggests size-dependent migration dynamics, 30 Apr Environ. Biol. Fishes Publ. Online. <https://doi.org/10.1007/s10641-022-01262-4>.
- Scott, M., Cardona, E., Scidmore-Rossing, K., et al., 2022. What's the catch? Examining optimal longline fishing gear configurations to minimize negative impacts on non-target species. *Mar. Policy* 143, 105186. <https://doi.org/10.1016/j.marpol.2022.105186>.
- Scott, M., Royer, M., Hutchinson, M., 2023. Time of death: behavioral responses of an oceanic whitetip shark, *Carcharhinus longimanus*, to capture by a longline fishing vessel. *Anim. Biotelemetry* 11 (1), 34. <https://doi.org/10.1186/s40317-023-00346-x>.
- Skomal, G., Bernal, D., 2010. *Physiological Responses to Stress in Sharks. Sharks and Their Relatives II*. n.p.: CRC Press.
- Skomal, G.B., 2007. Evaluating the physiological and physical consequences of capture on post-release survivorship in large pelagic fishes. *Fish. Manag. Ecol.* 14 (2), 81–89. <https://doi.org/10.1111/j.1365-2400.2007.00528.x>.
- Stokesbury, M.J.W., Neilson, J.D., Susko, E., et al., 2011. Estimating mortality of Atlantic bluefin tuna (*Thunnus thynnus*) in an experimental recreational catch-and-release fishery. *Biol. Conserv.* 144 (11), 2684–2691. <https://doi.org/10.1016/j.biocon.2011.07.029>.
- Whitney, N., Taquet, M., Brill, R.W., et al., 2016. Swimming depth of dolphinfish (*Coryphaena hippurus*) associated and unassociated with fish aggregating devices. *Fish. Bull.* 114 (4), 426–434. <https://doi.org/10.7755/fb.114.4.5>.
- Whitney, N.M., Lear, K.O., Morris, J.J., et al., 2021. Connecting post-release mortality to the physiological stress response of large coastal sharks in a commercial longline fishery. *PLOS ONE* 16 (9), e0255673. <https://doi.org/10.1371/journal.pone.0255673>.
- Wood, C.M., 1991. Acid-Base and ion Balance, Metabolism, and Their Interactions, After Exhaustive Exercise in Fish. *J. Exp. Biol.* 160 (1), 285–308. <https://doi.org/10.1242/jeb.160.1.285>.
- Wosnick, N., Leite, R.D., Balanin, S., et al., 2023. Behavioral and visual stress-induced proxies in elasmobranchs. *Rev. Fish. Biol. Fish.* 33 (1), 175–199. <https://doi.org/10.1007/s11160-023-09757-8>.
- Wyrtki, K., 1973. Physical Oceanography of the Indian Ocean. In: Zeitzschel, B., Gerlach, S.A. (Eds.), *The Biology of the Indian Ocean*. Springer, Berlin, Heidelberg, pp. 18–36. https://doi.org/10.1007/978-3-642-65468-8_3.