Evaluating post-release behaviour modification in large pelagic fish deployed with pop-up satellite archival tags

John P. Hoolihan[1], Jiangang Luo[2]*, Francisco J. Abascal[3], Steven E. Campana[4], Gregorio De Metrio[5], Heidi Dewar[6], Michael L. Domeier[7], Lucy A. Howey[8], Molly E. Lutcavage[9], Michael K. Musyl[10], John D. Neilson[11], Eric S. Orbesen[12], Eric D. Prince[12], and Jay R. Rooker[13]

[1]Cooperative Institute for Marine and Atmospheric Studies, Rosenstiel School for Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, USA
[2]Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, USA
[3]Instituto Español de Oceanografía, Centro Oceanográfico de Canarias, Apartado 1373, 38120 Santa Cruz de Tenerife, Spain
[4]Fisheries and Oceans Canada, Bedford Institute of Oceanography, PO Box 1006, Dartmouth, NS, Canada B2Y 4A2
[5]Department of Animal Health and Welfare, University of Bari, S.P. per Casamassima km 3, 1-70010 Valenzano (BA), Italy
[6]National Marine Fisheries Service, Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, CA 92037, USA
[7]Marine Conservation Science Institute, 2809 S. Mission Road, Fallbrook, CA 92028, USA
[8]Guy Harvey Research Institute, Nova Southeastern University Oceanographic Center, 8000 North Ocean Drive, Dania Beach, FL 33004, USA
[9]Large Pelagic Research Center, University of New Hampshire, Durham, NH 03824, USA
[10]Joint Institute for Marine and Atmospheric Research, Pelagic Fisheries Research Program, University of Hawai'i at Manoa, Kewalo Research Facility, 1125-B Ala Moana Blvd, Honolulu, HI 96814, USA
[11]Fisheries and Oceans Canada, St Andrews Biological Station, St Andrews, New Brunswick, Canada E5B 2L9
[12]National Marine Fisheries Service, Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, FL 33149, USA
[13]Department of Marine Biology, Texas A&M University, 5007 Avenue U, Galveston, TX 77551, USA

*Corresponding Author: tel: +1 305 421 4847; fax: +1 305 421 4925; e-mail: jluo@rsmas.miami.edu.

Post-release behaviour modification, possibly a result of capture and handling stress, was evaluated using empirical eigenfunction analysis to detect changes in vertical movement patterns recorded by 183 pop-up satellite archival tags (PSATs) deployed on large pelagic fish. Argos-transmitted summary, timed interval, and some archival data were included. Scoring of irregular post-release behaviour was based on a separation of plotted eigenfunction coefficient values by their mean, with the transection across the mean reference line denoting the duration of irregular behaviour. In all, 67 (36.6%) individual fish exhibited irregular behaviour, lasting from 3 to 60 d (mean = 15.8, s.d. = 10.4). An additional 27 (14.8%) displayed patterns suggestive of irregular behaviour. Data quality and quantity were important criteria for revealing behaviour patterns. Irregular behaviour was detected in 32.6% of Argos-transmitted dataseries, increasing to 60.6% in the higher-resolution archival series. Decreased vertical movement characterized the irregular behaviour of blue sharks (Prionace glauca) and porbeagles (Lamna nasus), whereas all other species showed increased vertical activity. The approach described provides a useful method of revealing behavioural modification during the post-release recovery period of PSAT-tagged large pelagic fish, although the extent of influence on normal behaviour is not fully understood.

Keywords: billfish, empirical eigenfunction analysis, pop-up satellite archival tagging, sharks, tuna, vertical movement.

Introduction

Some of the greatest advancements in understanding the behaviour of large pelagic fish are a product of electronic tagging technology. In the 1950s, ultrasonic telemetry was introduced to monitor fish movement using real-time tracking (Arnold and Dewar, 2001). Although useful for documenting fine-scale movements, ultrasonic tracks are typically close to shore and short in duration, because of vessel and manpower requirements and weather restrictions (Yuen, 1970; Laurs et al., 1977; Jolley and Irby, 1979). By the early 1990s, archival tags became available to measure and store large quantities of depth and temperature data collected over extended periods (Arnold and Dewar, 2001). One limitation of archival tags is that physical recovery, i.e. fish recapture, is necessary to access stored data. For species with relatively high rates of recovery, such as tropical pelagic tuna (family Scombridae), archival tagging studies have proved effective (Schaefer et al., 2009). However, for species whose recapture may be somewhat rare or dependent on incidental bycatch [e.g. billfish (family Istiophoridae), sharks (superorder Selachimorpha)], the chance of recovering an archival tag can be extremely low. This limitation was resolved in the late 1990s with

the introduction of the pop-up satellite archival tag (PSAT). The PSAT was designed to detach from the fish at a pre-programmed date, whereupon it floats to the surface and transmits stored data back to the user via the Argos satellite system (Block *et al.*, 1998; Lutcavage *et al.*, 1999). As these data are fishery-independent, PSATs are very suitable for studying species with low probabilities of recapture.

PSATs are programmed to measure and record depth (pressure) and ambient water temperature, as well as solar irradiance for estimating geographic location. These features have advanced studies addressing, but not limited to, large pelagic fish movement, distribution, habitat preference, post-release survival, and swimming speed for billfish (Prince and Goodyear, 2006; Hoolihan and Luo, 2007; Kraus and Rooker, 2007), swordfish (*Xiphias gladius*; Neilson et al., 2009), tuna (Block *et al.*, 1998; Lutcavage *et al.*, 1999; De Metrio *et al.*, 2005), and sharks (Domeier and Nasby-Lucas, 2008; Campana *et al.*, 2009). Whereas PSAT and other electronic tagging data have generally been analysed and presented with the assumption that they reflect normal behaviour accurately, *a priori* reasoning suggests some degree of post-release behavioural modification in response to capture and handling. Physiological stress responses, including elevated levels of plasma electrolytes and enzymes, blood metabolites, and haematocrit values, may result in short-term behaviour modification following capture and handling (Wells and Davie, 1985; Wells *et al.*, 1986). Behaviour modification may extend for longer periods following bodily injury from fishing gear, e.g. internal hooking or net abrasion, improper tag-and-release procedures, and acclimatization to carrying the electronic instrument. Although these factors are not in dispute, the severity and duration to which performance and behaviour are influenced is not well understood. This is mostly attributable to the complexities of monitoring large, highly mobile species in a vast aquatic environment. The unfortunate result is that behavioural changes caused by capture, handling, or tag retention may go unnoticed, thereby risking the introduction of bias into the analyses. In situations where electronically tagged animals are more easily observed, such as birds, a variety of post-release competitive impairments have been reported, including reduced flight and swimming speeds, increased duration of foraging trips, and abandonment of nests (Wilson *et al.*, 1986; Phillips *et al.*, 2003).

Earlier, short-duration, ultrasonic-tracking studies recognized that several hours of post-release recovery were often apparent based on irregular vertical movement patterns of billfish (Holland *et al.*, 1990; Holts and Bedford, 1990; Block *et al.*, 1992; Pepperell and Davis, 1999; Hoolihan, 2005) and sharks (Klimley *et al.*, 2002; Nakano *et al.*, 2003). More recently, Campana *et al.* (2009) reported that PSAT-tagged blue sharks (*Prionace glauca*) exhibited depth-holding recovery behaviour for periods ranging from 1 to 27 d following release, and Abascal *et al.* (2009) noted that PSAT-tagged swordfish remained at shallow depths for several days following release. Concern for how these irregularities may negatively affect the interpretation of normal behaviour has prompted some authors to exclude early portions of data from their analyses (Hoolihan *et al.*, 2009; Leroy *et al.*, 2009). Depending on the purpose of PSAT analyses, the inclusion of irregular post-release behaviour (IPRB) may not alter the results significantly, particularly for long-term deployments. However, for short-duration deployments, the effects may be more profound. Hence, there is a need to understand better the severity and duration of this phenomenon.

Inspiration for the present study came about during discussions at the second International Tagging and Tracking Symposium held in San Sebastian, Spain (Nielsen *et al.*, 2009). Irregularities in vertical movements following release suggested that the trauma of capture, handling, and tagging may result in behavioural modifications. In response, our objectives were to conduct an exploratory analysis of available data from PSATs deployed on large pelagic fish to determine the feasibility of detecting IPRB from transmitted and archival data and to raise the awareness of IPRB for improving future tagging studies. We purposely included PSAT data from a large and diverse group to determine whether such behaviour was pervasive across species. However, because of species-specific behavioural differences and sample number variability, interspecies comparisons were deemed beyond the scope of our study.

Material and methods

Electronic tagging data were evaluated from 183 large pelagic fish monitored with PSATs in the Atlantic Ocean, Pacific Ocean, Mediterranean Sea, Arabian Gulf, and Coral Sea during the period 2001–2009 (Supplementary material). These included 50 blue marlin (*Makaira nigricans*), four black marlin (*Makaira indica*), 15 white marlin (*Tetrapturus albidus*), seven striped marlin (*Tetrapturus audax*), 21 sailfish (*Istiophorus platypterus*), 16 swordfish, 13 Atlantic bluefin tuna (*Thunnus thynnus*), 27 blue sharks, 19 porbeagles (*Lamna nasus*), four shortfin mako sharks (*Isurus oxyrinchus*), five white sharks (*Carcharodon carcharias*), one oceanic whitetip shark (*Carcharhinus longimanus*), and one silky shark (*Carcharhinus falciformis*; Supplementary material). Days at liberty ranged from 26 to 358 d.

Our study included PSATs manufactured by Microwave Telemetry (MT, Columbia, MD, USA) and Wildlife Computers (WC, Redmond, WA, USA). Readers are referred to the respective manufacturers for individual PSAT model specifications. PSATs were attached by tethering to a plastic or metal anchor inserted into the dorsal musculature, as described by various authors cited earlier. Methods of capture included recreational hook and line, longline, purse-seine, and trap (Supplementary material). In addition, some were harpoon-tagged, as described by Chaprales *et al.* (1998). Each PSAT was pre-programmed to initiate release via a corrosive wire link, allowing it to detach and float to the surface. Stored data were then transmitted through the Argos satellite system and forwarded to the end-users. As the particulars of each capture (e.g. fight time, time on line, hook type, condition at release) were not always available, comparisons between post-release behaviour and gear type were considered beyond the scope of this study.

The methods used to process transmitted PSAT data were managed differently by WC and MT units. The WC units measured and archived depth (pressure), temperature, and irradiance data at intervals ranging from 10 to 60 s. When WC units were recovered, the fully archived data stored in the non-volatile memory were accessible. For satellite transmission, limited battery capacity and satellite coverage precludes the transfer of these large volumes of data. Instead, these WC units summarized the data into three types of message: (i) histogram messages that place the readings for each sensor into 12 or 14 user-specified ranges; the users also set the period (1–24 h) at which the histograms were built; (ii) depth–temperature (PDT) profile messages consisting of minimum and maximum depth and temperature for each period used for the histogram, plus the six most commonly

visited depths generated from equally spaced bins; and (iii) irradiance data, later processed by the user for geolocation estimates. The MT units measured and archived PDT data at timed intervals ranging from 15 min to 1 h. This, coupled with an MT feature that coordinates data transmission with satellite duty cycles, allowed for robust data retrieval through the Argos system. Overall, three different types of PSAT data were available for analyses: (i) archival time-series (10–60 s) data from WC units that were physically recovered; (ii) Argos-transmitted summary data from the WC units; and (iii) Argos-transmitted timed-interval series data from the MT units.

Two-dimensional matrices were constructed for each of the three various data types. The values and sizes of individual matrices varied depending on the data type and deployment duration. For archival data (WC units), the first matrix represents average hourly depth for 2 min, and the second the sum of activity for 10 min. The activity index was based on a binary value determined by the change in depth between consecutive readings, whereby values of zero were assigned to changes <3 m and 1 to changes ≥ 3 m (considering the accuracy of the depth sensor of $\pm 1\%$). For both matrices, days at liberty was placed on the x-dimension, and time of day (hour) on the y-dimension. For the Argos-transmitted summary data (WC units), the first matrix represents the depth histogram and the second the temperature histogram (placing days at liberty on the x-dimension, and depth bin or temperature bin on the y-dimension). For the Argos-transmitted timed-interval series data (MT units), the first matrix represents the depth and the second the temperature (placing days at liberty on the x-dimension, and hour on the y-dimension for both matrices).

Matrices were processed using empirical eigenfunction analysis (EEA), also known as empirical orthogonal function, a technique similar to principal component analysis (PCA) used widely to determine the dominant functions of variation in datasets. The eigenfunctions correspond to a statistically optimal description of the data with respect to how variance is concentrated in the functions, where the explained variance decreases with an increase in function number. As the explained variance typically drops at a high rate with the function number, only a limited number of functions is needed to explain most of the variance in the data. Here, we used the EEA to create a few key functions (first and second) that characterized the variation in the full matrices of depth, activity, and temperature data to determine the most dominant daily behaviour patterns of the data. Detailed descriptions of the method are available in the literature (Jackson, 1991; Wai and Bedford, 1995; Everson et al., 1997; Arendt et al., 2001; Maron et al., 2008). For the purposes of this study, the method was used to discern subtle changes in behaviour patterns across time (days at liberty) and is summarized below.

For a time-series of archival depth data, we constructed an $m \times n$ rectangular matrix of $C_{x,y}$, where $x = 1, 2, \ldots, m$ (number of days in deployment, x-dimension) and $y = 1, 2, \ldots, n$ (number of time bins within a day, y-dimension), with average depth located in each cell of the matrix. To obtain the x-dimension coherent (orthogonal) functions of $C_{x,y}$, the x-dimension autocorrelation matrix, R^x, was constructed from

$$[R] = \frac{1}{n}[C^*][C], \tag{1}$$

where the asterisk represents the matrix transpose. Writing the

relationship between the x-dimension eigenvalues and the corresponding eigenfunctions with R^x, one obtains

$$R^x T = \lambda_x T, \tag{2}$$

where T denotes the x-dimension eigenfunction, which is the function of x only, and λ_x denotes the corresponding x-dimension eigenvalue. Note that the y-dimension arrangement of depth in the matrix $[C]$ does not affect the x-dimension autocorrelation function R^x. Hence, it does not necessarily require a y-dimension distribution of depth to determine the x-dimension eigenfunctions.

Similarly, to obtain y-dimension eigenfunctions and their eigenvalues, the y-dimension autocorrelation matrix R^y is constructed as

$$[R^y] = \frac{1}{m}[C][C^*]. \tag{3}$$

Here, the y-dimension eigenvalues and the corresponding eigenfunctions associated with R^y are given as

$$R^y Z = \lambda_y Z, \tag{4}$$

where Z is the y-dimension eigenfunction, which is the function of y only, and λ_y is the corresponding eigenvalue. Also, note that R^y is not affected by the arrangement of the x-dimension distribution of depth. It is important to realize that the x-dimension and y-dimension eigensystems share the same non-zero eigenvalues:

$$\lambda = \lambda_x = \lambda_y. \tag{5}$$

Hence, the original depth matrix $C(x, y)$ can be reconstructed as

$$C(x, y) = \sum_{j=1}^{p} \lambda_j^{1/2} T_j(x) Z_j(y), \tag{6}$$

where $x = 1, 2, \ldots, m$, $y = 1, 2, \ldots, n$, and p is the number of non-zero eigenvalues. A zero eigenvalue means that the variation in the n column dataset can be expressed with one less $(n - 1)$ eigenfunction, and if one has k zero eigenvalues, then one only needs $n - k$ eigenfunctions to express the data. Interactive Data Language software (IDL from ITTvis.com) was used to estimate the eigenvalues and the x-dimension eigenfunction $T_j(x)$ to evaluate depth distribution patterns resulting from fish behaviour from the time of release to the time of pop-up or recapture. The empirical eigenfunction $T_j(x)$ expressed the observed data in terms of superposition of fixed daily patterns (eigenfunction) corresponding to increased subtle features of the data. The first eigenfunction $T_{j=1}(x)$, which is the same as the coefficients of first component in PCA, was representative of the combined structure of those forcing functions that generate the greatest variation in the data. The second eigenfunction $T_{j=2}(x)$, which is orthogonal to the first, was representative of the forcing functions that are uncorrelated with the first group of forcing functions and are responsible for generating the residual variance in the dataset. Similarly, the depth data were substituted for temperature or activity data, as described above, to obtain their respective eigenvalues and x-dimension eigenfunctions.

To describe the level of apparent IPRB, a behaviour score was created by determining if the initial post-release coefficient values were separated from later values by the mean reference line (Figure 1). The results from examining the four plots from each individual were then used to determine their behaviour score as follows: 0, none of the four coefficients displayed separation; 1, only one of the four coefficients displayed separation; 2, at least two of the four coefficients displayed separation (Supplementary material). Therefore, scores of 2 were assumed to be positive displays of IPRB, scores of 1 suggested such behaviour, but were not as definitive, and 0 indicated no behavioural modification.

Data types were further evaluated for their efficacy to demonstrate IPRB by simulating summary data from the archival data (WC-AMP software, WC), then comparing and scoring the EEA plots as described above. In addition, for blue marlin, because of their size range and large sample number, we were able to split them into two groups approximately equal in number (≤90 vs. >90 kg) to determine whether there was a statistical difference between fish size and the occurrence of IPRB. We used the two-tailed Fisher exact test (Zar, 1984) to analyse a 2 × 2 contingency table that compared the frequency of blue marlin behaviour scores (either 0 or 1 and 2) with each size group.

Results

Electronic tagging data were examined from 183 large pelagic fish deployed with PSATs for periods ranging from 26 to 358 d (Supplementary material) using EEA. The analyses revealed patterns in PDT distribution data that may reflect IPRB activity. In all, 67 individual fish (36.6%) exhibited behaviour assessments (score = 2) consistent with our definition of IPRB (Figure 2; Supplementary material). Of these, the duration of IPRB ranged from 3 to 60 d (mean = 15.8, s.d. = 10.4; Supplementary material). An additional 27 (14.8%) fish exhibited behaviour scores of 1, suggesting the possible presence of IPRB (Figure 2; Supplementary material). Example plots of the multiaxis contour plots and eigenfunction coefficients are illustrated for the WC archival data and Argos-transmitted summary data (Figure 3), and MT timed-interval data (Figure 4).

For individual species, six (85.7%) of the striped marlin exhibited behaviour scores of 2 (Figure 2). For blue marlin, 24 (48.0%) scored 2 for IPRB (Figure 2). Three black marlin (75.0%) exhibited a score of 2, and one (25.0%) scored 1 (Figure 2). Three (20.0%) white marlin, five (23.8%) sailfish, and four (25.0%) swordfish scored 2 (Figure 2). For bluefin tuna, none of the 11 fish monitored in the Mediterranean indicated IPRB, but the two monitored in the western North Atlantic displayed scores of 1 (Figure 2). None of the five white sharks or single oceanic whitetip shark exhibited IPRB (Figure 2). However, behaviour scores of 2 were displayed by the single silky shark and 17 (63.0%) blue sharks (Figure 2). Two (50.0%) shortfin mako sharks had behaviour scores of 1 (Figure 2). For porbeagles, six (31.6%) scored 2, and one (5.2%) scored 1.

When comparing the three data types from all individuals (Supplementary material), 60.6% of archival datasets ($n = 33$) displayed behaviour scores of 2, compared with 35.3% for transmitted timed-interval data ($n = 17$), and 32.3% for transmitted summary data ($n = 133$). A further comparison of archival and simulated summary data suggested that the archival data were superior in revealing patterns of IPRB when using EEA. This is illustrated in the archival and transmitted summary data plots

from blue marlin PTT 27825 and PTT 23439 (Figure 3). Further support was provided by comparing simulated summary data with the archival data from the seven striped marlin, of which six scored 2, and one fish scored 1 for IPRB (Supplementary material). During simulation, WC-AMP used the identical bin size assigned during the initial setup for each PSAT. Bin sizes varied among these striped marlin (1, 6, 8, and 24 h), and visual examination of the EEA plots from the simulated summary data (not shown) indicated that the resolution of activity decreased with increasing bin size. From all seven striped marlin, only the simulated data with the 1-h bin size supported the IPRB evident in the archival data EEA plots.

Fish size may have factored into the IPRB scores of blue marlin (Figure 5). For small blue marlin (≤90 kg), 6 (22.2%) exhibited no change in behaviour (score 0) and 21 (77.8%) scored 1 or 2, whereas for large blue marlin (>90 kg), 13 (59.1%) showed no change (score 0) and 9 (40.9%) scored 1 or 2. The Fisher exact test (two-tailed) indicated a significant difference ($p = 0.017$) in the proportion of post-release behaviour between small and large blue marlin (Figure 5).

Discussion

The behaviour of pelagic fish is largely influenced by environmental conditions, life-history phase, and species-specific preferences. Our analyses of both summarized and archival data derived from PSAT analyses suggest that the trauma and stress associated with capture and handling may influence the behaviour of some species. The fish in the present study were tagged using a variety of methods, which is likely to contribute to the performance and behavioural variation portrayed in the EEA (Supplementary material). For example, sublethal injuries may result from extensive jumping while on recreational hook and line (e.g. billfish), hook damage (depending on hook type and hook location), external abrasions from contacting purse-seines and cages, inadequate handling when lifting fish from or replacing fish back in the water, and poor PSAT anchor placement that impedes function or results in excessive bleeding or infection. As our analyses consisted of existing datasets collected from multiple species, countries, and oceans over the past decade, specific information detailing the variability of these attributes and condition at release were often unavailable. Therefore, it was impossible to compare behavioural patterns and gear type.

The behavioural changes observed may be related to the physiological and biochemical effects of exhaustive exercise associated with capture and handling (Wells *et al.*, 1986; Skomal and Chase, 2002). Blood acidosis and high blood lactate levels have been reported for tuna, sharks, and billfish subjected to capture and handling (Wells and Davie, 1985; Skomal, 2007). Lengthy capture periods may lead to hypoxia, particularly for obligate ram-ventilating species that demand high levels of oxygen. The fact that a significantly greater proportion of smaller (≤90 kg) blue marlin in the present study exhibited IPRB, compared with those >90 kg, suggests that size may also factor into the ability of a fish to withstand the rigours of capture, handling, and carrying a PSAT, at least for that particular species. In addition to the impacts from capture and handling, other reasons could contribute to the behavioural modifications we defined as irregular. Behaviour may be influenced by species-specific adaptation to factors such as temperature, foraging, spawning, predator evasion, bathymetry, and seasonality. The possibility that the behavioural modifications displayed by our study animals were affected by these factors
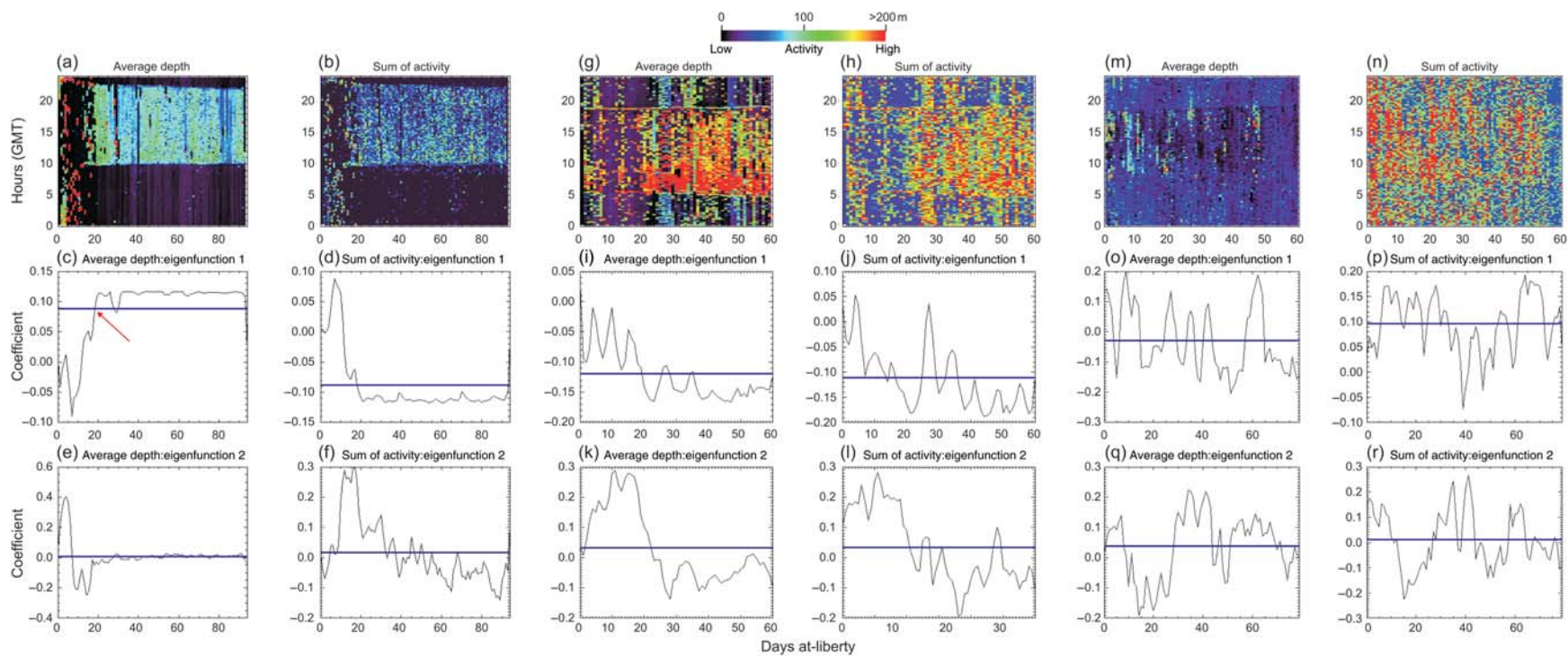
Figure 1. Examples illustrating the behaviour score system used to determine IPRB in large pelagic fish using EEA. Multiaxis contour plots and corresponding plots for the first and the second eigenfunctions for both average depth and sum of activity are presented for high-resolution pop-up archival data from blue marlin PTT 42724 (a–f), black marlin PTT 23590 (g–l), and white shark PTT 23764 (m–r; Supplementary material). The level of apparent IPRB was scored by the number of plots that showed clear separation by the mean (blue lines) between the initial post-release coefficient values and later values (0, none of the four plots showed separation; 1, one of the four plots showed separation; 2, at least two of the four plots showed separation). For these examples, the blue marlin scored 2 for IPRB with clear separation for three plots (c, d, e), the black marlin scored 1, suggesting possible irregular behaviour, with clear separation in only one plot (k), and the white shark scored 0, with no clear separation for any of the four plots. The point at which the eigenfunction coefficient transected the mean reference line was used to estimate the duration of IPRB, e.g. the red arrow in (c).
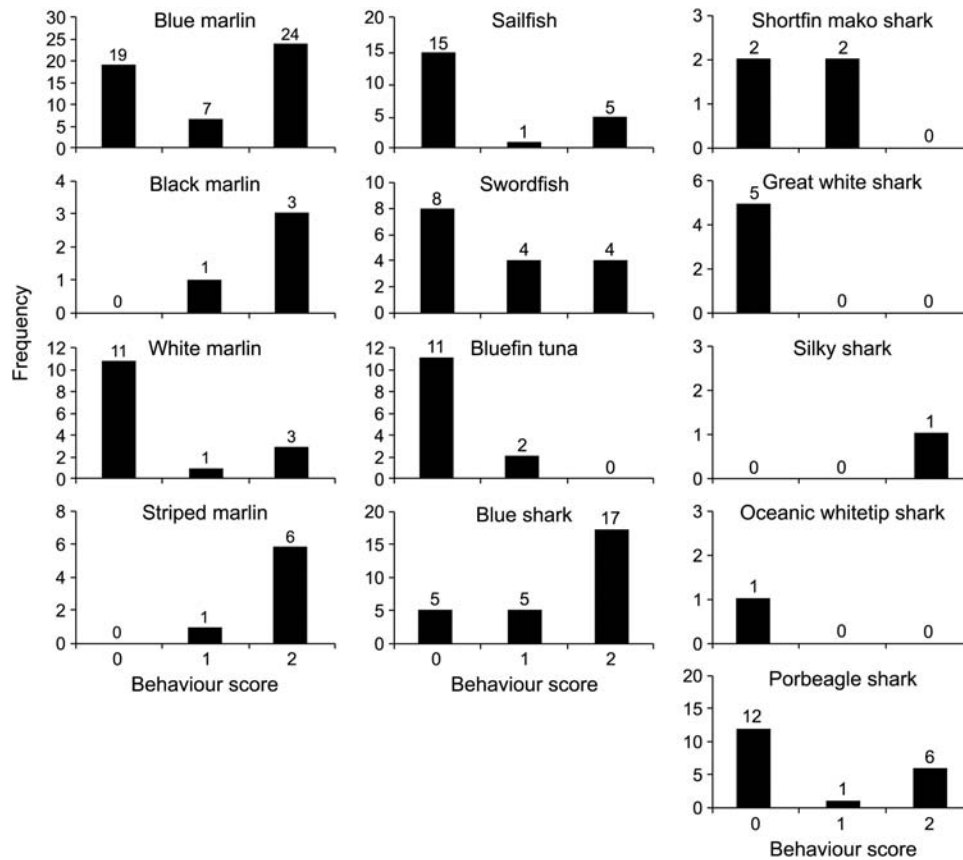
Figure 2. Frequency histograms for the occurrence of IPRB indicated by EEA of 183 large pelagic fish deployed with PSATs. Irregular behaviour was scored as follows: 0, no apparent change in behaviour; 1, possible presence of irregular behaviour; 2, irregular behaviour apparent.

cannot be excluded, but there were no observed trends for any particular species, area, or season that would implicate any of them as the primary cause of IPRB. In terms of the effect of bathymetry on behaviour, we scrutinized vertical activity vs. bathymetry for the 27 blue sharks tagged in the western North Atlantic, of which 22 had behaviour scores of 1 or 2 (Supplementary material). Most of those sharks were released over the continental shelf where the depth is relatively shallow (<200 m). Subsequent horizontal movement away from the shelf into the deeper, warmer waters of the Gulf Stream was clearly discernible in the EEA activity plots (not shown). Interestingly, the IPRB modifications displayed by blue sharks and porbeagles were characterized by their holding at depth (i.e. decreased vertical activity), whereas all other species displaying IPRB increased their vertical movement. For the blue sharks not displaying IPRB, the patterns for vertical movement were similar while on and off the continental shelf, even though the maximum depth of suitable habitat was limited on the shelf.

The effectiveness of using EEA to distinguish changes in behaviour activity from PSAT data was largely dependent on the quality and duration of the data. Overall, the higher-resolution WC archival data were superior in revealing IPRB than the MT Argos-transmitted timed-interval data, whereas the WC Argos-transmitted summary data were the least likely to show IPRB. For summary data, the number of periods per day assigned in the setup procedure greatly influenced the perceived depth activity. For example, vertical-movement behaviour modification reflected in summary data eigenfunction coefficients 1

and 2 decreased as PDT bin sizes increased or histogram sizes (h) increased. In contrast, the 10–60-s recordings and greater depth precision of the WC archival data improved our ability to detect changes in vertical movement patterns, suggesting the possibility that IPRB activity may have gone undetected in some lower-resolution summary datasets. The range of depths utilized by an individual fish also affected the detection of IPRB from summary data. For example, fish that remained near the surface generally encountered only a few of the PDT bins defined in the PSAT setup. If the individual bin-size ranges were relatively large, the ability to detect behavioural modifications effectively was diminished. Evidence for this is given by the comparison of the EEA for archival and corresponding simulated summary dataplots (6-h histograms) from blue marlin PTTs 27825 and 23439 (Figure 3). For PTT 27825, the archival data (Figure 3a–f) clearly indicated a score of 2 for IPRB (duration ∼12 d). The corresponding summary data (Figure 3g–l) provided a similar conclusion. In contrast, the archival data from PTT 23439 (Figure 3m–r) also clearly indicated a score of 2 (duration ∼23 d), whereas the summary data (Figure 3s–x) failed to support the same conclusion. The reason for the disparity between the summary data results from PTTs 27825 and 23439 was largely attributable to the fact that PTT 23439 remained near the surface, with data confined to a few bins. This suggests that non-detection of IPRB in summary data using the methods described does not necessarily reflect the actual behaviour.
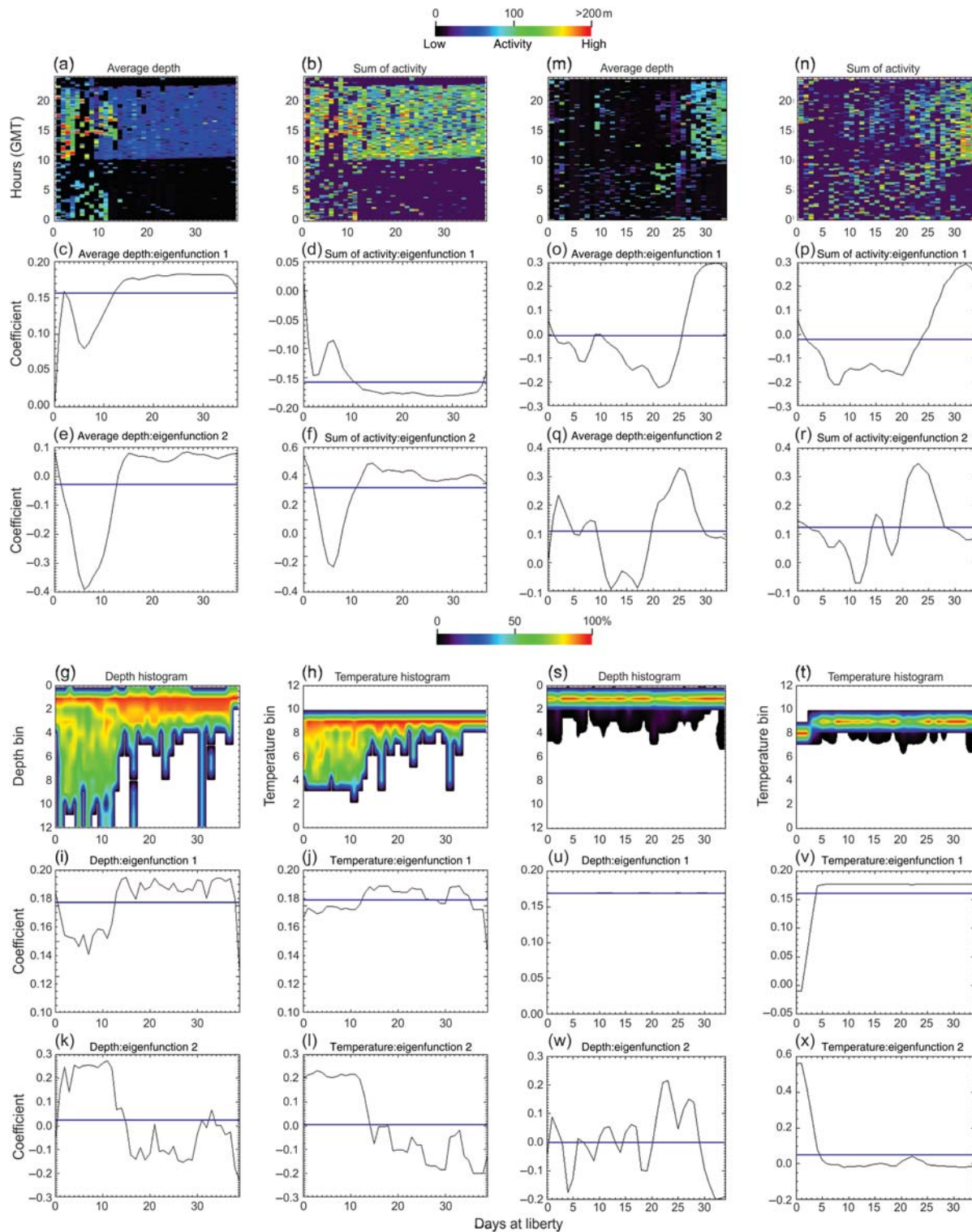
Figure 3. Comparison of EEA plots derived from archival and Argos-transmitted data from blue marlin PTT 27825. Plots (a)–(f) show the graphic matrices for average depth, sum of activity, and their corresponding first and second eigenfunctions. Plots (g)–(l) represent comparative data from the same individual for depth and temperature histograms derived from Argos-transmitted summary data. Similarly, plots (m)–(r) depict archival data from blue marlin PTT 23439, and plots (s)–(x) show Argos-transmitted summary data from the same individual. The archival plots (c–f, o–r) show distinct separation of eigenfunction coefficients from their means for two or more plots, suggesting IPRB for ~12 d (PTT 27825) and 23 d (PTT 23439). The Argos-transmitted summary data (g–l) for PTT 27825 were simulated from the archival data. Here, patterns of behaviour are similar between the two data types, but less distinct for the summary data (g–l). For PTT 23439, the summary dataset originated from actual Argos transmissions. In this case, data were incomplete and failed to reveal the extent of irregular behaviour suggested in the corresponding archival data (m–r).
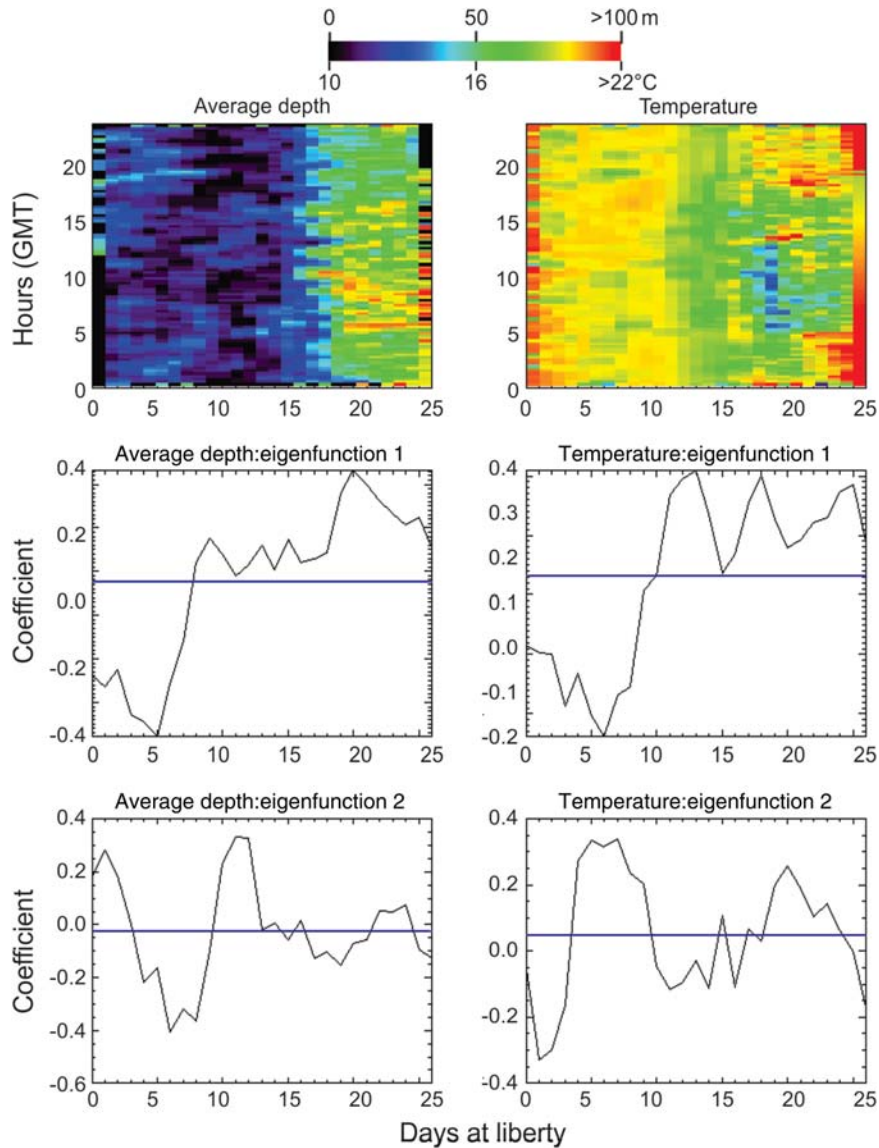
Figure 4. EEA plots of blue shark PTT 44061 for average depth (left column) and temperature (right column) derived from MT Argos-transmitted timed-interval PSAT data. The colour patterns and distinct separation of eigenfunction coefficients from their means for two of the plots suggests IPRB (score 2) lasting ∼10 d from release.

Although a large proportion (85.7%) of the striped marlin had behaviour scores of 2 (Figure 1), this does not imply that they are more prone to IPRB than the other species tested. Given what we learned from the simulations described above, additional samples using the lower-resolution, Argos-transmitted summary data would probably reduce the proportion of positive behaviour scores for striped marlin. Moreover, it suggests that IPRB may have been present, but undetectable, in a proportion of the Argos-transmitted summary datasets of the other individuals examined, and that detection of IPRB would increase overall if high-resolution archival data were available from all study animals.

Another factor supporting the efficacy of archival data is that recovered series are usually comprehensive. In contrast, MT Argos-transmitted timed-interval and WC Argos summary series are more prone to having gaps resulting from transmission problems or corrupt data (Teo *et al.*, 2007). Any disparity in the data may compromise the detection of IPRB. For example, high
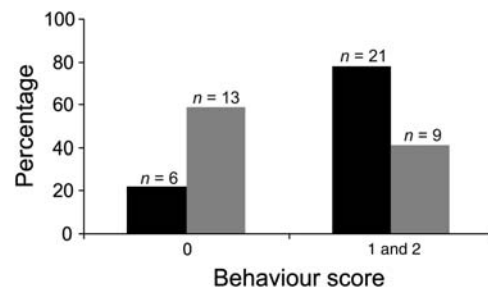
Figure 5. Size vs. post-release behaviour score of 0 or 1 and 2 for 49 PSAT-tagged blue marlin. Black bars denote small blue marlin (≤90 kg) and grey bars large blue marlin (>90 kg).

levels of background noise in the Mediterranean Sea interfere with Argos frequencies, often preventing the complete transmission of data (De Metrio *et al.*, 2005). Poor-quality data

resulting from Argos frequency interference may have hindered detection of IPRB in the 11 Mediterranean bluefin tuna PSAT samples examined. Other factors may also contribute to the low occurrence of IPRB in bluefin tuna. For example, the schooling tendency of this species might cause released individuals to return and resume group behaviour as soon as possible, so eliminating IPRB or at least minimizing it to a degree that it is nondetectable by the methods used here. The duration of PSAT deployment can also influence the detection of IPRB. Our analyses indicated that the duration of detectable IPRB averaged 15.6 d, but extended to as much as 60 d. In comparison, Campana *et al.* (2009) reported PSAT-tagged blue shark recovery times (based on depth-holding behaviour) ranging from 4 to 20 d. Hence, the possibility that short-duration PSAT deployments may not extend beyond their recovery periods suggests that caution is warranted when interpreting these data, because they may not portray normal behaviour in some species.

Although our results indicated that higher-resolution data were more likely to reveal IPRB activity, archival data are rarely available because PSATs are not typically recovered. In addition, programming PSATs to monitor at higher resolution may be unwarranted given specific research objectives.

Despite PSAT archival data being better suited to EEA, none of the archival data from the five white sharks exhibited IPRB, suggesting that that species may be less traumatized by capture, handling, and tagging. In fact, those sharks were lured to the tagging vessel and harpoon-tagged while free-swimming. Therefore, they were not subjected to hooking or handling procedures. In addition, the large size of those sharks may have limited any behavioural modifications associated with carrying the PSAT units, as was also noted for the lower proportion of IPRB displayed by large blue marlin ($>$90 kg).

Given that the present study included multiple species, areas, and seasons, we feel that the results offer compelling evidence to support the idea that IPRB (as defined in this study) is a response to the trauma and stress of capture, handling, and carrying the PSAT. The notion that fishing and tagging activities produce sublethal trauma and stress affecting post-release behaviour is not new, being alluded to in earlier ultrasonic-tracking studies of billfish (Holland *et al.*, 1990; Holts and Bedford, 1990; Block *et al.*, 1992; Pepperell and Davis, 1999; Hoolihan, 2005) and sharks (Klimley *et al.*, 2002; Nakano *et al.*, 2003). What is novel here is the application of EEA to detect subtle changes in post-release behaviour. Caution is warranted, however, considering that variable environmental conditions and species-specific behaviours were not fully comprehended or integrated into the present study and may have been contributing to IPRB. These caveats aside, the unfortunate reality is that the inherent inability to monitor non-captured and nontagged large pelagic fish renders it impossible to differentiate between normal and abnormal behaviour. However, we maintain that the stress response to handling and tagging likely produced post-release behavioural changes in many of the large pelagic fish included in our analyses. Similar consequences could be expected from other types of tagging studies, e.g. conventional, archival, and acoustic. The IPRB results described here are consistent with stress-induced behavioural change, in that they were present immediately after release and diminished over time. To what extent these sublethal modifications affect day-to-day activities, e.g. foraging and spawning, is not fully understood, but deserves further investigation.

We view these results as a preliminary step towards understanding how handling and tagging affect fish behaviour. Additional studies seem to be warranted to refine techniques that differentiate between normal and abnormal behaviour further and to improve methods of capture, handling, and tagging to reduce stress and injury to study animals.

Supplementary material

Supplementary material is available at the online version of this manuscript in *ICESJMS* in the form of tabular summary information for 183 pop-up satellite archival tags included in the eigenanalyses.

Acknowledgements

References

Abascal, F. J., Mejuto, J., Quintans, M., and Ramos-Cartelle, A. 2009. Horizontal and vertical movements of swordfish in the southeast Pacific. ICES Journal of Marine Science, 67: 466–474.

Arendt, M. D., Lucy, J. A., and Evans, D. A. 2001. Diel and seasonal activity patterns of adult tautog, *Tautoga onitis*, in lower Chesapeake Bay, inferred from ultrasonic telemetry. Environmental Biology of Fishes, 62: 379–391.

Arnold, G., and Dewar, H. 2001. Electronic tags in marine fisheries research. *In* Proceedings of the Symposium on Tagging and Tracking Marine Fish with Electronic Devices, 7–11 February 2000, East–West Center, University of Hawaii, Honolulu, pp. 7–64. Ed. by J. R. Sibert, and J. L. Nielsen. Kluwer Academic, Dordrecht. 468 pp.

Block, B. A., Booth, D. T., and Carey, F. G. 1992. Depth and temperature of the blue marlin, *Makaira nigricans*, observed by acoustic telemetry. Marine Biology, 114: 175–183.

Block, B. A., Dewar, H., Farwell, C., and Prince, E. D. 1998. A new satellite technology for tracking the movements of Atlantic bluefin tuna. Proceedings of the National Academy of Sciences of the USA, 95: 9384–9389.

Campana, S. E., Joyce, W., and Manning, M. J. 2009. Bycatch and discard mortality in commercially caught blue sharks *Prionace glauca* assessed using archival satellite pop-up tags. Marine Ecology Progress Series, 387: 241–253.

Chaprales, W., Lutcavage, M., Brill, R., Chase, B., and Skomal, G. 1998. Harpoon method for attaching ultrasonic and "pop-up" satellite

tags to giant bluefin tuna and large pelagic fishes. Marine Technology Society Journal, 32: 104–105.

De Metrio, G., Arnold, G. P., De la Serna, J. M., Megalofonou, P., Sylos Labini, G., Deflorio, M., Buckley, A., *et al.* 2005. Movements and migrations of North Atlantic bluefin tuna tagged with pop-up satellite tags. *In* Aquatic Telemetry: Advances and Applications. Fifth Conference on Fish Telemetry, 9–13 June 2003, Ustica, Italy, pp. 161–168. Ed. by M. T. Spedicato, G. Lembo, and G. Marmulla. FAO/COISPA, Rome. 295 pp.

Domeier, M. L., and Nasby-Lucas, N. 2008. Migration patterns of white sharks *Carcharodon carcharias* tagged at Guadalupe Island, Mexico, and identification of an eastern Pacific shared offshore foraging area. Marine Ecology Progress Series, 370: 221–237.

Everson, E., Cornillon, P., Sirovich, L., and Webber, A. 1997. An empirical eigenfunction analysis of sea surface temperatures in the western North Atlantic. Journal of Physical Oceanography, 27: 468–479.

Holland, K., Brill, R. W., and Chang, R. K. C. 1990. Horizontal and vertical movements of Pacific blue marlin captured and released using sportfishing gear. Fishery Bulletin US, 88: 397–402.

Holts, D., and Bedford, D. 1990. Activity patterns of striped marlin in the southern California Bight. *In* Proceedings of the Second International Billfish Symposium, Kailua-Kona, Hawaii, 1–5 August 1988, pp. 81–93. Ed. by R. H. Stroud. National Coalition for Marine Conservation, Inc. Savannah, GA. 321 pp.

Hoolihan, J. P. 2005. Horizontal and vertical movements of sailfish (*Istiophorus platypterus*) in the Arabian Gulf, determined by ultrasonic and pop-up satellite tagging. Marine Biology, 146: 1015–1029.

Hoolihan, J. P., and Luo, J. 2007. Determining summer residence status and vertical habitat use of sailfish (*Istiophorus platypterus*) in the Arabian Gulf. ICES Journal of Marine Science, 64: 1791–1799.

Hoolihan, J. P., Luo, J., Richardson, D. E., Snodgrass, D., Orbesen, E. S., and Prince, E. D. 2009. Vertical movement rate estimates for Atlantic istiophorid billfishes derived from high resolution pop-up satellite archival data. Bulletin of Marine Science, 83: 257–264.

Jackson, J. E. 1991. A User's Guide to Principal Components. Wiley, New York. 592 pp.

Jolley, J. W., and Irby, E. W. 1979. Survival of tagged and released Atlantic sailfish (*Istiophorus platypterus*: Istiophoridae) determined with acoustical telemetry. Bulletin of Marine Science, 29: 155–169.

Klimley, A. P., Beavers, S. C., Curtis, T. H., and Jorgensen, S. J. 2002. Movements and swimming behavior of three species of sharks in La Jolla Canyon, California. Environmental Biology of Fishes, 63: 117–135.

Kraus, R. T., and Rooker, J. R. 2007. Patterns of vertical habitat use by Atlantic blue marlin (*Makaira nigricans*) in the Gulf of Mexico. Gulf and Caribbean Research, 19: 89–97.

Laurs, R. M., Yuen, H. S. H., and Johnson, J. H. 1977. Small-scale movements of albacore, *Thunnus alalunga*, in relation to ocean features as indicated by ultrasonic tracking and oceanographic sampling. Fishery Bulletin US, 75: 347–355.

Leroy, B., Itano, D. G., Usu, T., Nicol, S. J., Holland, K. N., and Hampton, J. 2009. Vertical behavior and the observation of FAD effects on tropical tuna in the warm-pool of the western Pacific Ocean. *In* Tagging and Tracking of Marine Animals with Electronic Devices, pp. 161–179. Ed. by J. L. Nielsen, H. Arrizabalaga, N. Fragoso, A. Hobday, M. Lutcavage, and J. Sibert. Springer, London. 400 pp.

Lutcavage, M. E., Brill, R. W., Skomal, G. B., Chase, B. C., and Howey, P. W. 1999. Results of pop-up satellite tagging of spawning size class fish in the Gulf of Maine: do North Atlantic bluefin tuna spawn in the mid-Atlantic? Canadian Journal of Fisheries and Aquatic Sciences, 56: 173–177.

Maron, P. P., Reeve, D. E., Rihouey, D., and Dubranna, J. 2008. Transverse and longitudinal eigenfunction analysis of a navigation channel subject to regular dredgings: the Adour River Mouth, France. Journal of Coastal Research, 24: 206–215.

Nakano, H., Matsunaga, H., Okamoto, H., and Okazaki, M. 2003. Acoustic tracking of bigeye thresher shark *Alopias superciliosus* in the eastern Pacific Ocean. Marine Ecology Progress Series, 265: 255–261.

Neilson, J. D., Smith, S., Roter, F., Paul, S. D., Porter, J. M., and Lutcavage, M. 2009. Investigations of horizontal movements of Atlantic swordfish using pop-up satellite archival tags. *In* Tagging and Tracking of Marine Animals with Electronic Devices, pp. 145–159. Ed. by J. L. Nielsen, H. Arrizabalaga, N. Fragoso, A. Hobday, M. Lutcavage, and J. Sibert. Springer, London. 400 pp.

Nielsen, J. L., Arrizabalaga, H., Frangoso, N., Hobday, A., Lutcavage, M., and Sibert, J. 2009. Tagging and Tracking of Marine Animals with Electronic Devices. Springer, London. 400 pp.

Pepperell, J. G., and Davis, T. L. O. 1999. Post-release behaviour of black marlin, *Makaira indica*, caught off the Great Barrier Reef with sportfishing gear. Marine Biology, 135: 369–380.

Phillips, R. A., Xavier, J. C., and Croxall, J. P. 2003. Effects of satellite transmitters on albatrosses and petrels. Auk, 120: 1082–1090.

Prince, E. D., and Goodyear, C. P. 2006. Hypoxia-based habitat compression of tropical pelagic fishes. Fisheries Oceanography, 15: 451–464.

Schaefer, K. M., Fuller, D. W., and Block, B. A. 2009. Vertical movements and habitat utilization of skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*), and bigeye (*Thunnus obesus*) tunas in the equatorial eastern Pacific Ocean, ascertained through archival tag data. *In* Tagging and Tracking of Marine Animals with Electronic Devices, pp. 121–144. Ed. by J. L. Nielsen, H. Arrizabalaga, N. Fragoso, A. Hobday, M. Lutcavage, and J. Sibert. Springer, London. 400 pp.

Skomal, G. B. 2007. Evaluating the physiological and physical consequences of capture on post-release survivorship in large pelagic fishes. Fisheries Management and Ecology, 14: 81–89.

Skomal, G. B., and Chase, B. C. 2002. The physiological effects of angling on post-release survivorship in tunas, sharks, and marlin. *In* Catch and Release in Marine Recreational Fisheries, 5–8 December 1999, Virginia Beach, pp. 135–138. Ed. by J. A. Lucy, and A. L. Studholme. American Fisheries Society Symposium, 30.

Teo, S. L., Boustany, A., Dewar, H., Stokesbury, M., Weng, K. C., Beemer, S., Seitz, A., *et al.* 2007. Annual migrations, diving behavior, and thermal biology of Atlantic bluefin tuna, *Thunnus thynnus*, on their Gulf of Mexico breeding grounds. Marine Biology, 151: 1–18.

Wai, O. W. H., and Bedford, K. W. 1995. Empirical orthogonal function analysis of sediment concentration profiles subjected to wave and currents. Marine and Freshwater Research, 46: 373–382.

Wells, R. M. G., and Davie, P. S. 1985. Oxygen binding by the blood and hematological effects of capture stress in two big gamefish: mako shark and striped marlin. Comparative Biochemistry and Physiology, 81A: 643–646.

Wells, R. M. G., McIntyre, R. H., Morgan, A. K., and Davie, P. S. 1986. Physiological stress responses in big gamefish after capture: observations on plasma chemistry and blood factors. Comparative Biochemistry and Physiology, 84A: 565–571.

Wilson, R. P., Grant, W. S., and Duffy, D. C. 1986. Recording devices on free-ranging marine animals: does measurement affect foraging performance? Ecology, 67: 1091–1093.

Yuen, H. S. H. 1970. Behavior of skipjack tuna, *Katsuwonus pelamis*, as determined by tracking with ultrasonic devices. Journal of the Fisheries Research Board of Canada, 27: 2071–2079.

Zar, J. 1984. Biostatistical Analysis. Prentice-Hall, Inc., Englewood Cliffs, NJ. 620 pp.