

# ***Movement, depth distribution and survival of spinetail devilrays (Mobula japonica) tagged and released from purse-seine catches in New Zealand***

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## ABSTRACT

1. Mobulid rays are protected in New Zealand, but the spinetail devilray *Mobula japonica* is caught as bycatch in skipjack tuna purse seine fisheries.

2. Between 2005 and 2014, rays were recorded in 8.2% of observed purse seine sets. Rays were caught during summer, with a ‘hotspot’ (24.3% of sets) near the shelf edge off North Island over seabed depths of 150–350 m. Rays were usually brailed aboard with the tuna catch from successful sets, but were often entangled in the bunt of the net during unsuccessful sets.

3. Observers tagged nine rays with popup archival tags to obtain preliminary information on their post-release survival, and spatial and vertical movements. Seven of the nine tags reported data, and four of those rays died within 2–4 days of release. All four rays that died had been brought aboard entangled in the bunt. The three surviving rays were all brailed aboard with the tuna catch.

4. One surviving ray remained near New Zealand for 2.7 months during summer, and the other two migrated 1400–1800 km northward to tropical waters near Vanuatu and Fiji at minimum speeds of 47 and 63 km day<sup>-1</sup> at the end of summer.

5. Archive data from one ray showed that it made regular vertical movements of 25–100 m amplitude, but spent most of its time shallower than 50 m, more so during the night (89.6%) than the day (76.6%), and mainly experienced temperatures of 18–22 °C. Dives deeper than 200 m were usually made during the day or twilight.

6. All three surviving rays typically moved between the surface and 200–300 m daily, and reached greatest depths of 649 m, 1000 m and 1112 m, respectively, substantially exceeding the previous depth record for this species of 445 m.

7. Recommendations are made for reducing purse seine mortality of mobulid rays by avoiding areas of high ray abundance, avoiding setting on ray-associated tuna schools, and adopting best-practice methods of returning rays to the sea from the net or vessel.

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Received 20 July 2015; Revised 29 January 2016; Accepted 03 February 2016

KEY WORDS: ocean; tracking; distribution; protected species; fish; fishing

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## INTRODUCTION

Purse seine fisheries catch schools of fish by encircling them with a net, and then hauling the net and catch aboard a fishing vessel. The most important global purse seine fisheries target small tunas, especially skipjack tuna (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*), in tropical and subtropical waters. Purse seine tuna catches are often relatively 'clean' compared with most demersal fishing methods, and bycatch of non-tuna species is generally low (Bailey *et al.*, 1996; Ménard *et al.*, 2000; Romanov, 2002; Hall and Roman, 2013). However, tunas frequently associate with other large animals (or vice versa) and inanimate objects such as floating logs and artificial fish aggregation devices. Consequently animals such as dolphins (Delphinidae), turtles (Chelonia), billfishes (Istiophoridae), jacks (Carangidae), whale sharks (*Rhincodon typus*) and whaler sharks (*Carcharhinus* spp.) are caught by purse seiners and released or discarded (Bailey *et al.*, 1996; Ménard *et al.*, 2000; Romanov, 2002; Molony, 2005; Amandè *et al.*, 2010; Hall and Roman, 2013). Because of increasing concern over the impact of fishing on these species, attempts are being made to avoid catching them, facilitate their return to the sea alive if they are caught, and monitor their post-release survival. Large animals that are seen in the net early in the capture process (e.g. dolphins, whale sharks) can often be released before the net is hauled, thus reducing mortality. Other species, however, may not be seen until hauling begins or even after it has been completed. Species such as the silky shark (*Carcharhinus falciformis*) can suffer high mortality rates, and it has been the subject of recent tag and release studies to quantify the mortality rate (Poisson *et al.*, 2014a; Hutchinson *et al.*, 2015).

One group of purse seine bycatch species that has received virtually no attention is the manta and devil rays, Family Mobulidae, which comprises nine species of *Mobula* and two species of *Manta*. Most mobulid species have been reported caught by purse seine fleets (Paulin *et al.*, 1982; Bailey *et al.*, 1996; Romanov, 2002; Molony, 2005; Couturier *et al.*, 2012; Hall and Roman, 2013), and they are also taken as target species or bycatch by other fishing

methods such as gillnets and tuna longline (Bailey *et al.*, 1996; White *et al.*, 2006a; Couturier *et al.*, 2012; Mas *et al.*, 2015). Mobulid rays have low productivity and are considered vulnerable to overfishing as a result (Couturier *et al.*, 2012). Most species that have been classified by the IUCN Redlist (IUCN, 2014) are listed as Near Threatened or Vulnerable but one species (*Mobula mobular*) is listed as Endangered and three could not be assessed because of insufficient data (Couturier *et al.*, 2012). However, mobulid population sizes are notoriously difficult to quantify so there is little hard information on population trends.

Two species of mobulid rays are known to occur in New Zealand waters – spinetail devilray (*Mobula japanica*) and giant manta ray (*Manta birostris*) (Gilbert and Paul, 1969; Paulin *et al.*, 1982; Stewart, 2002; Duffy and Abbott, 2003). Both species have been protected under the Wildlife Act (1953) since July 2010. Other species of *Mobula* and *Manta* may also occur in New Zealand waters, at least seasonally as migrants from tropical waters, but their presence has not been confirmed (Duffy and Abbott, 2003). *Mobula japanica* and 'manta rays' have been reported caught by the New Zealand skipjack tuna purse seine fishery which operates mainly around northern North Island in summer (January–March) (Paulin *et al.*, 1982; West, 1991; Kendrick, 2006; Langley, 2011). *Mobula japanica* comprises most and possibly all of the mobulid ray bycatch in New Zealand purse seine fisheries (Francis and Lyon, 2012; Jones and Francis, 2012). *Manta birostris* may also be caught occasionally by purse seiners but that has not been confirmed (Francis and Lyon, 2012; Jones and Francis, 2012).

The protected status of mobulid rays in New Zealand means that their capture and mortality should be avoided or minimized. In this study, observer data on the capture of *M. japanica* were analysed with a view to identifying where and how the rays are caught. Electronic tags were placed on *M. japanica* caught and released by purse seine vessels to obtain preliminary information on their post-release survival, and spatial and vertical movements in New Zealand waters. Finally recommendations are made for reducing or avoiding bycatch of *M. japanica*.

## METHODS

The locations of skipjack purse-seine sets recorded by observers during the 2005–2014 summer fishing seasons were extracted from the Ministry for Primary Industries' (MPI) *Central Observer Database (COD)*, along with records of *M. japonica* catches, and seabed depth at the set location. The depth distribution of *M. japonica* sets was compared with the depth distribution of all sets within a north-east coast North Island region where most *M. japonica* were reported caught (34.90–36.45 °S, see Figure 1). Observer coverage during 2005–2014 averaged 11.0% of all sets (Ministry for Primary Industries, 2014).

Data forms were provided to observers from 2012 onwards to document ray captures including when rays were first observed, their behaviour before and during capture, and, if possible, handling and release methods, ray size, sex and their apparent health status on release. This information, supplemented by the trip reports, diaries and photographs provided by

MPI observers from previous years, was used to categorize and assess the type and frequency of ray capture, and the handling and release methods used by the vessels.

Nine *M. japonica* were tagged using pop-up archival transmitting (PAT) tags produced by Wildlife Computers Ltd. (models miniPAT and sPAT; Table 1). Rays were tagged by MPI observers aboard commercial skipjack purse-seine vessels. The intention was to make a preliminary assessment of whether these rays survived after being caught by purse seine, subjected to normal handling practices, and then released. Consequently, observers were instructed not to make any special effort to treat the rays better than the crew would normally have done. Only rays that were lifted on to the deck were tagged, because rays that were released from the purse seine net while still in the water were expected to be in excellent condition and survive (Hutchinson *et al.*, 2015). All tagged rays appeared healthy and lively and had only minimal superficial injuries. Tags were anchored in the central, thick part of the wing musculature using a PIER umbrella anchor with eight plastic barbs, some of which were covered with a dacron sleeve to promote tissue healing around the anchor (Domeier *et al.*, 2005). Anchors were attached to tags by 10–11 cm long monofilament nylon or stainless steel tethers. A plastic, serially numbered, conventional tag was looped around the tether of the PAT tag and its nylon anchor was inserted 50 mm into the wing to provide a secondary attachment point, and to restrict movement of the PAT tag. PAT tags were fitted with a release device designed to sever the tether and release the tags if they sank below 1700–1800 m, to avoid them being crushed. A similar attachment method has been used successfully to track *M. japonica* for up to 188 days in the Gulf of California (Croll *et al.*, 2012).

Tagged rays were sexed (only possible if the pelvic fins were visible), and their disk width (DW), disk length (DL) and weight were measured or estimated. The entire tagging procedure took only a few minutes. The behaviour of the ray following release was recorded, as were the location, sea surface temperature (SST) and sea bed depth at the point of release. A tissue sample was taken from the tip of the tail or a wing margin for subsequent DNA analysis.

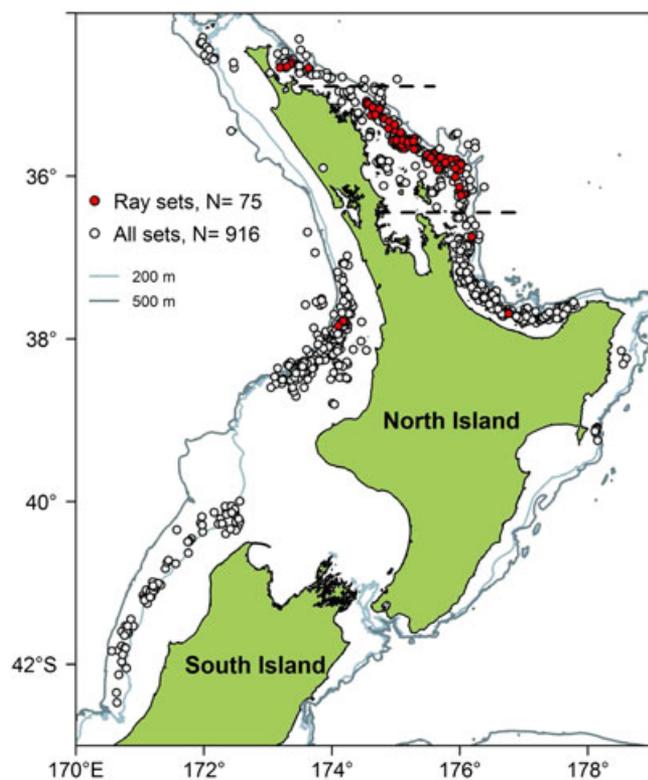


Figure 1. Map of northern New Zealand showing the distribution of skipjack purse seine sets and sets that caught *Mobula japonica* during 2005–2014. Dashed lines indicate the region used for the analysis of depth distributions shown in Figure 2.

Table 1. Tagging details for nine *Mobula japonica* released off north-eastern New Zealand. End status indicates whether the ray was alive or dead at the end of the track

Tag number	Tag type	Tagging location	Tag latitude (°S)	Tag longitude (°E)	Tag date	Disk length (cm)	Disk width (cm)	Sex	Weight (kg)	SST	Depth (m)	Days tracked	End status
115487	miniPAT	NE Great Barrier Is	35.7450	175.5033	10 February 2013	110	215	M	90	22.4	179	4	Dead
115488	miniPAT	NE Great Barrier Is	35.7443	175.4870	10 February 2013	140	240	M	100	22.7	187	4	Dead
115489	miniPAT	NE Great Barrier Is	35.7772	175.5550	11 February 2013	130	260	-	110	22.5	215	2	Dead
115490	miniPAT	E Poor Knights Is	35.3940	174.9862	10 January 2013	140	260	-	130	21.0	300	82	Alive
115491	miniPAT	N Poor Knights Is	35.2898	174.6183	11 January 2013	130	260	F	140	23.0	141	no data	-
115492	miniPAT	NE Great Barrier Is	35.8258	175.6208	12 January 2013	130	265	-	130	22.0	240	no data	-
115490_2*	miniPAT	Gt Exhibition Bay	34.6717	173.1850	7 March 2014	120	260	M	130	21.0	83	1	Dead
142681	sPAT	Gt Exhibition Bay	34.6733	173.3633	9 April 2015	135	250	F	150	-	133	30	Alive
142682	sPAT	Gt Exhibition Bay	34.7150	173.4900	6 April 2015	115	245	M	150	-	145	30	Alive

\* Refurbished tag

MiniPAT tags are designed to monitor approximate geographic location, vertical movements and water temperature. The tags were programmed to record light intensity, depth and temperature at 5 s or 15 s intervals, and archive the data in memory until the tag released itself either on a programmed date, or detached prematurely. Tags also stored time series of depth and temperature measurements at 5 min or 10 min intervals (hereafter called time series data). Released tags floated to the surface and transmitted time series data to orbiting Argos satellites. Time series were not always complete because not all transmitted messages were received by the Argos satellite and decoded correctly. For one tag that was physically recovered (tag 115490), high resolution (15 s) data were downloaded (hereafter called archive data). The recovered tag was subsequently refurbished by Wildlife Computers and re-deployed on a second ray (Table 1).

Daily positions were estimated from ambient light data stored on tag 115490 using proprietary software from Wildlife Computers (WC-GPE: Global Position Estimator Program Suite, www.wildlifecomputers.com). Days with poor dawn/dusk light level curves were excluded from the analyses. Most probable tracks were developed by matching tag-measured SST with remotely-sensed SST data using unscented Kalman filtering (*UKFSST*) (Nielsen *et al.*, 2006; Lam *et al.*, 2008). *UKFSST* models were fitted with or without latitude bias, longitude bias, SST bias, solstice error variance (which accounts for greater error around the equinoxes), and last position not known accurately (fix.last = true or false).

Individual deep dives were identified for tag 115490 using the Instrument Helper module (IH) in Wildlife Computers' Data Analysis Programs software. Deep dives were defined as vertical movements starting and finishing at depths less than 75 m, and having a maximum depth greater than 200 m. IH output estimates of the dive start and finish times, dive duration and maximum depth reached during a dive.

MiniPAT tags 'detect' death by monitoring vertical movements from measurements of depth recorded by its pressure sensor. If no vertical movement is detected by the tag within a pre-programmed period (3 days in the present study),

the tag releases itself by sending a current through the metal pin that connects the tag to its tether, and an electrolytic reaction with seawater dissolves the pin in a few hours. This allows the tag to float to the surface where it begins transmitting data to a satellite. Dead *M. japonica* are expected to sink to the sea bed, thus producing a period of constant depth. If a ray dies over deep water, the tag's depth-activated safety mechanism will release it at about 1800 m depth. Live rays are expected to swim continuously and at various depths, so the constant-depth auto-release will not activate on living rays, and the tag will not pop up until the prescribed end-date for the experiment (or the tag anchor pulls free from the ray prematurely). Depth data from the days before tag pop-up can determine whether the ray survived until that time.

Archive data were classified into Day (dawn to dusk) and Night (dusk to dawn) subsets. Dawn was defined as the start of civil twilight, and dusk was defined as the end of civil twilight, where both reference points occur when the sun is 6° below the horizon. The daily times of dawn and dusk were calculated for a position near the centre of the track of ray 115490 (34.0°S, 174.5°E), using purpose-written R software (R Development Core Team, 2008).

sPAT tags are designed to determine whether an animal survives being caught and released. They are similar to miniPAT tags, but they record and transmit a reduced set of data. These data are analysed by Wildlife Computers who then provide reports giving tag pop-up date and location, daily minimum and maximum depth and temperature, a daily assessment of whether light levels are varying, and a 'reason for release'. The last item is classified into four categories: (1) completed deployment (the animal is assumed to have survived based on daily variation in depth, temperature and light); (2) sinker (the tag sank deeper than 1700 m, presumably attached to a dead animal); (3) floater (the tag was floating at the sea surface, either through animal mortality or premature tag detachment); and (4) sitter (the tag was sitting stationary on the sea bed, presumably attached to a dead animal). For this study, sPAT tags were programmed by the manufacturer to pop up and transmit data if the ray died, or after 30 days, whichever happened first.

Rays with tags in category 1 were interpreted as having survived the 30 day deployment, rays in categories 2 and 4 were interpreted as mortalities, and rays in category 3 were classified as alive or dead at tag detachment by inspecting the associated depth data.

## RESULTS

Skipjack purse-seine sets recorded on the COD database during 2005–2014 were concentrated along the outer half of the continental shelf off the north-eastern and western coasts of North Island (Figure 1). Of 916 observed sets having latitude and longitude coordinates, 75 (8.2%) caught *M. japonica*. Most ray sets (66 out of 75) came from a small part of the area fished, between 34.90°S and 36.45°S off the north-eastern North Island (Figure 1). In that region, observed sets were mostly made over seabed depths of 50–400 m, with a mode at 200–250 m (Figure 2). Ray sets, which comprised 24.3% of all sets in the defined region, were distributed slightly deeper, with 89.1% of ray sets in the depth range 150–350 m, and 75.0% in the range 200–350 m (Figure 2). The ray catch rate peaked at 62.5% of sets at 300–350 m, and exceeded 20% of sets across a broad range of depths (150–450 m).

Additional detailed observer diaries and/or photographs from 11 out of 14 trips between 2005 and 2011, and bycatch forms from six trips in 2012–2015, were reviewed. A total of 141 rays were recorded from 87 sets (average = 1.62 rays per set). Almost half of the ray sets (47.2%) were classed as 'successful' with all or most of the tuna catch being captured, and 30.3% were classed as 'skunked', where all or most of the tuna school evaded the net. There was insufficient information for the remainder of the sets to determine the success or otherwise (Table 2). Before 2012, if more than one ray was caught in a set, it was not possible to determine handling categories for each individual, so data are presented at the set level, assuming that all rays were caught and handled in the same way. From 2012, capture, handling and release data were available for

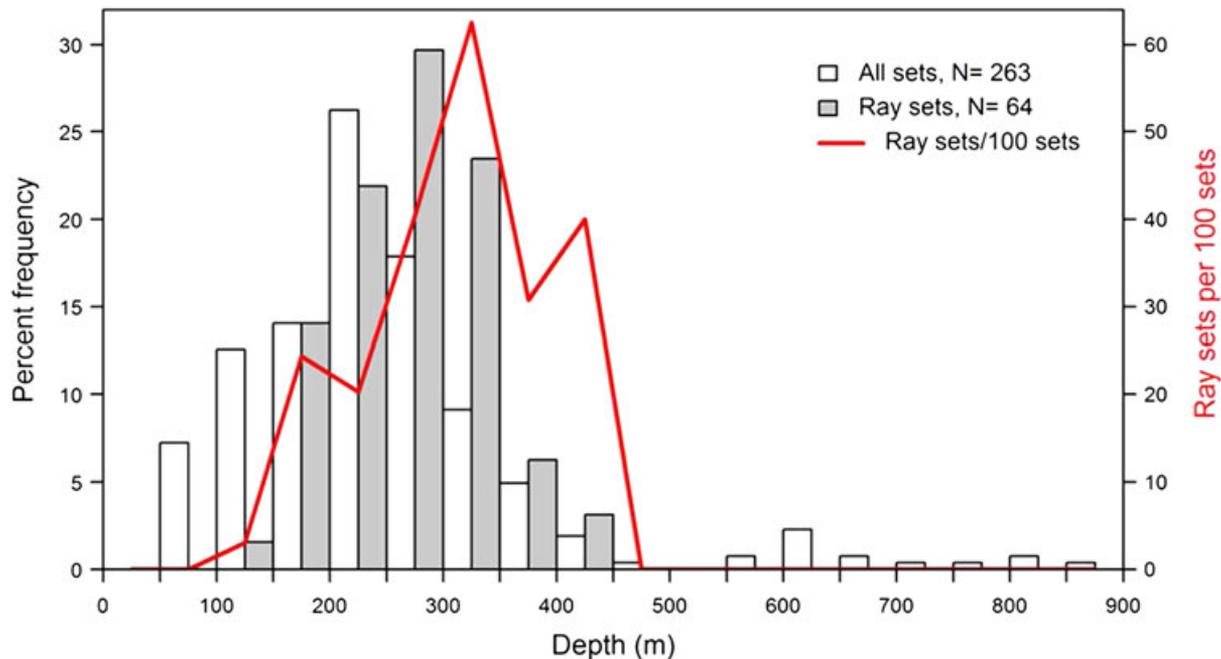


Figure 2. Depth distribution of skipjack purse seine sets and sets that caught *Mobula japonica* in the region indicated in Figure 1 during 2005–2014. The line graph shows the catch rate (number of ray sets per 100 sets) by 50 m depth class.

Table 2. Occurrence of different handling and release methods for devilray bycatch inferred from collated observer information for trips between 2005 and 2015. ‘Skunked’ sets were those in which all or most of the tuna catch escaped

Handling category	Outcome of set			Total
	Skunked	Successful	Unknown	
Released in water; swam out of net	3	1	0	4
Brailled onboard with catch	8	29	0	37
Tangled in bunt, brought on deck with net	10	4	0	14
Tangled but released while still in water	0	0	1	1
Handling unknown	6	8	19	33
Total	27	42	20	89

each individual ray, and in the case of two sets with multiple rays, different handling categories were assigned. Hence Table 2 presents 89 ‘events’ from 87 sets. Rays were brought out of the water and onto the deck in at least 57% of events. In only four events did rays swim free from the net. Where a small, skunked tuna catch was made, the rays were mainly brought aboard in the brail net or in the bunt of the net as it was hauled aboard. When the tuna school was successfully captured, rays were usually brought aboard with the catch in the brail net (at least 69% of events), with few devilrays being tangled in the netting.

Nine *M. japonica* were tagged off north-eastern North Island, New Zealand, during summer (January–April) 2013–2015 (Table 1). All rays were caught and released near the edge of the continental shelf (approximately defined by the 200 m isobath) (Figure 3). The rays were measured or estimated to be 110–140 cm DL and 215–265 cm DW. Six of the rays were sexed, and they comprised four males and two females. Male *M. japonica* mature at about 200–210 cm DW, with females maturing at perhaps a slightly larger size (Notarbartolo-di-Sciara, 1988; White *et al.*, 2006a), so all the tagged rays were probably mature.

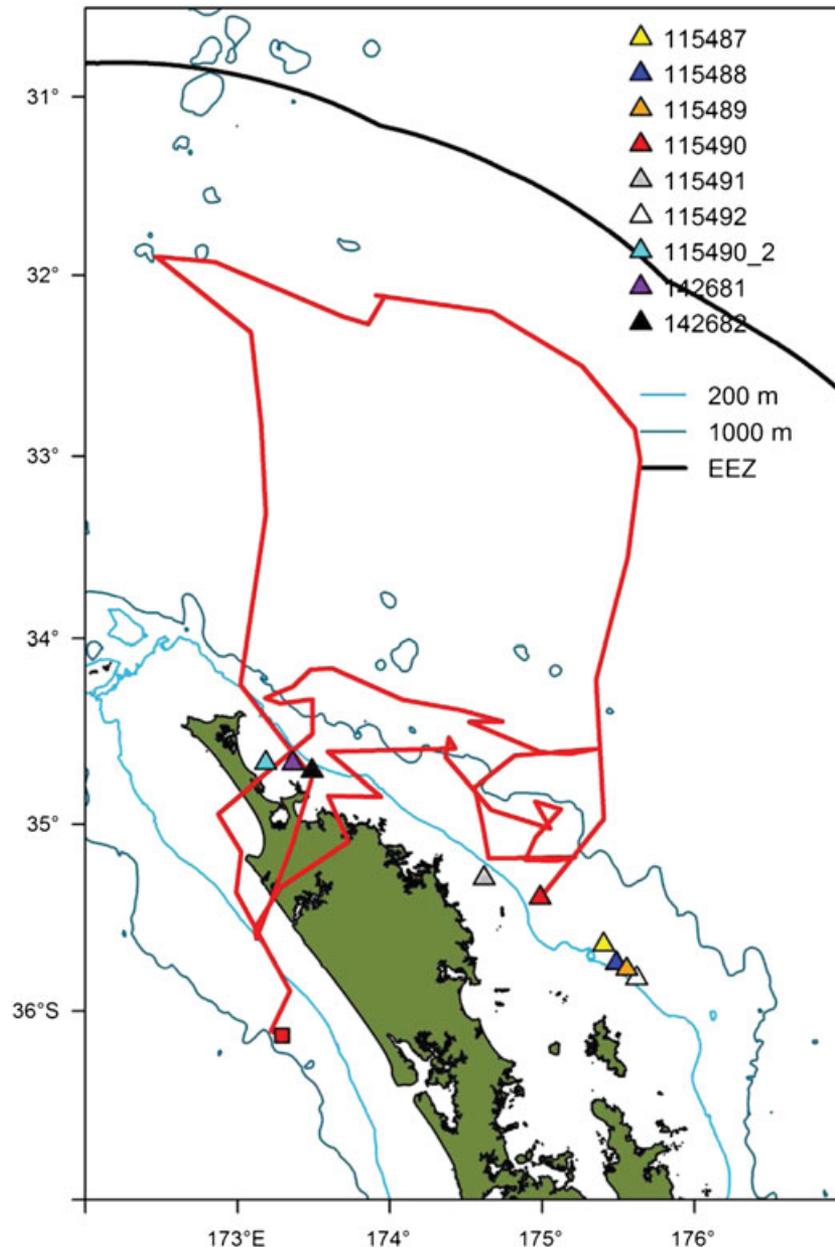


Figure 3. Tag release locations (triangles) of all tagged *Mobula japonica*. Also shown are the fitted track and popup location (square) of ray 115490. EEZ, New Zealand Exclusive Economic Zone.

Seven of the nine PAT tags reported data (Table 1). Four of those seven rays died within 1–4 days of release, as indicated by their rapid descents to ~1800 m (Figure 4). For two of those rays, the depth-activated release mechanism allowed the tag to return rapidly to the surface and begin transmitting. For the other two rays, the tags did not return to the surface for about 3–4 weeks. This probably resulted from the rays landing on their

backs on the sea bed, thus trapping the tags underneath their bodies. The tags eventually surfaced, presumably after the rays had decomposed sufficiently to release the tags. Three of the four rays that died were caught in skunked sets, and all four rays became entangled in the netting and were hauled aboard in the bunt.

Three of the tagged rays survived. These rays were all brought aboard in the brail net, tagged,

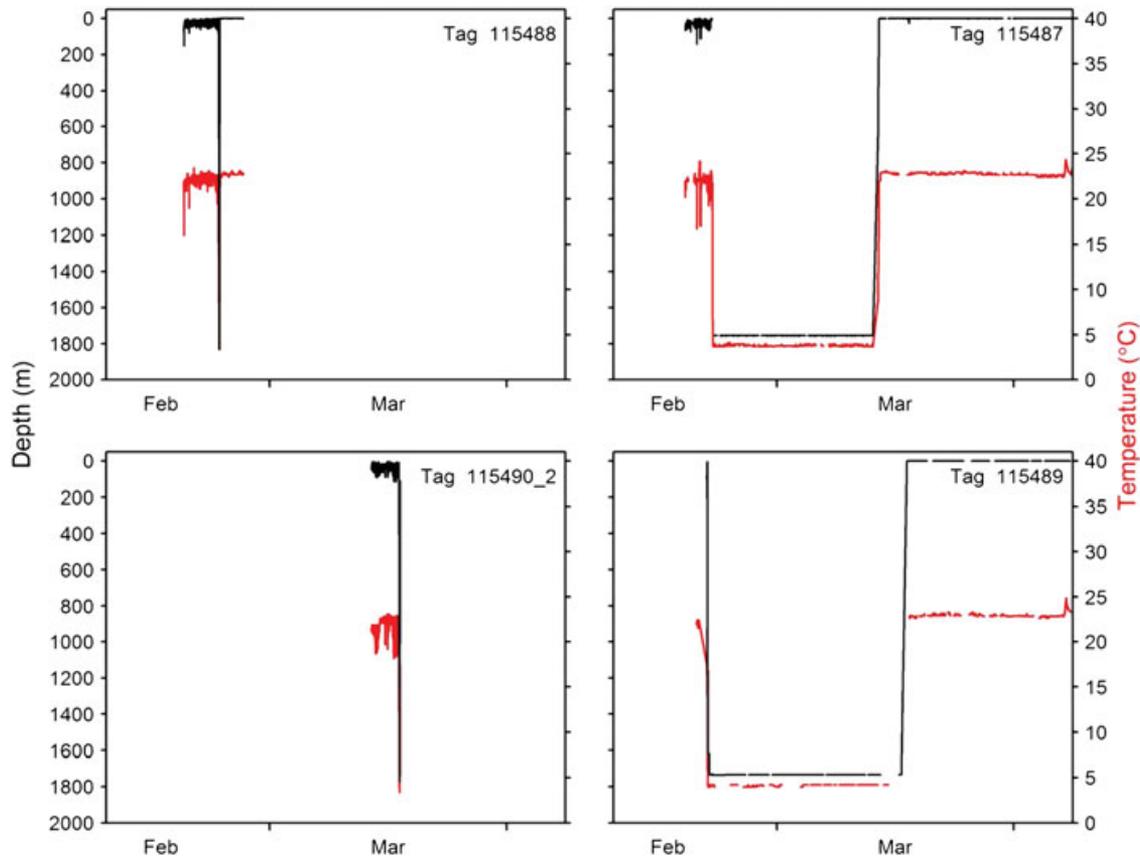


Figure 4. Depth and temperature profiles of *Mobula japonica* that died after tagging.

and released either directly from the brailer, or lifted using a rope and winch. Two of the three rays were caught in successful sets, while the third was captured in a skunked set, with only a small proportion of the tuna school retained.

Two of the surviving rays had track lengths of 30 days as scheduled (sPAT tags 142681 and 142682) and one a track length of 82 days followed by premature tag detachment (miniPAT tag 115490) (Table 1, Figure 3). Tag 115490 washed ashore at Taemaro Bay (34.945°S, 173.574°E) near Mangonui and was recovered, enabling the archived data to be downloaded. No satellite fixes were obtained on that tag at pop-up on 2 April 2013 (that date was determined from the archived depth data that showed it was floating at the surface) because the tag did not begin transmitting until it washed ashore two weeks later on 16 April. The best fit track had parameters for latitude bias, solstice error variance (to account for greater error

around the equinoxes), and inaccurately known last fix (because of premature tag pop-up). Inspection of observed and fitted values for tracks fitted using various parameter options indicated a conflict between latitude and SST: when SST was fitted well, latitude was fitted poorly, and vice versa. Longitude was well fitted in all models. Thus latitude may have been poorly estimated, particularly during the last one-third of the track which occurred near the equinox. The fitted track indicated that this ray immediately headed north after tagging, away from New Zealand and into the open ocean, and did a large loop before returning to the continental shelf after 2.5 weeks (Figure 3). This is supported by temperature data that showed an increase in SST to about 22 °C soon after tagging as the ray moved offshore into the warm East Auckland Current, and a sharp drop of about 2 °C when it moved back near the shelf on 26 January. Positions near the end of the track suggest the ray

moved to the west coast of North Island, but this may be erroneous because the tag subsequently washed ashore on the north-east coast, and the last estimated track position was on 21 March, one day after the equinox when light-based geolocation is subject to large errors (Teo *et al.*, 2004).

The two *M. japonica* tagged with sPAT tags (142681 and 142682) showed major northward movements to near Vanuatu and south of Fiji, respectively (Figure 5). sPAT tags do not provide

dawn and dusk light data, so no tracks could be reconstructed for them. However, the shortest direct routes between tagging and popup locations involved minimum distances travelled of 1878 km and 1404 km respectively in 30 days, with minimum average speeds of 62.6 and 46.8 km. day<sup>-1</sup>, respectively.

Time series data for the two 30-day sPATs showed that both rays experienced minimum depths of 0 m on every day except one day for

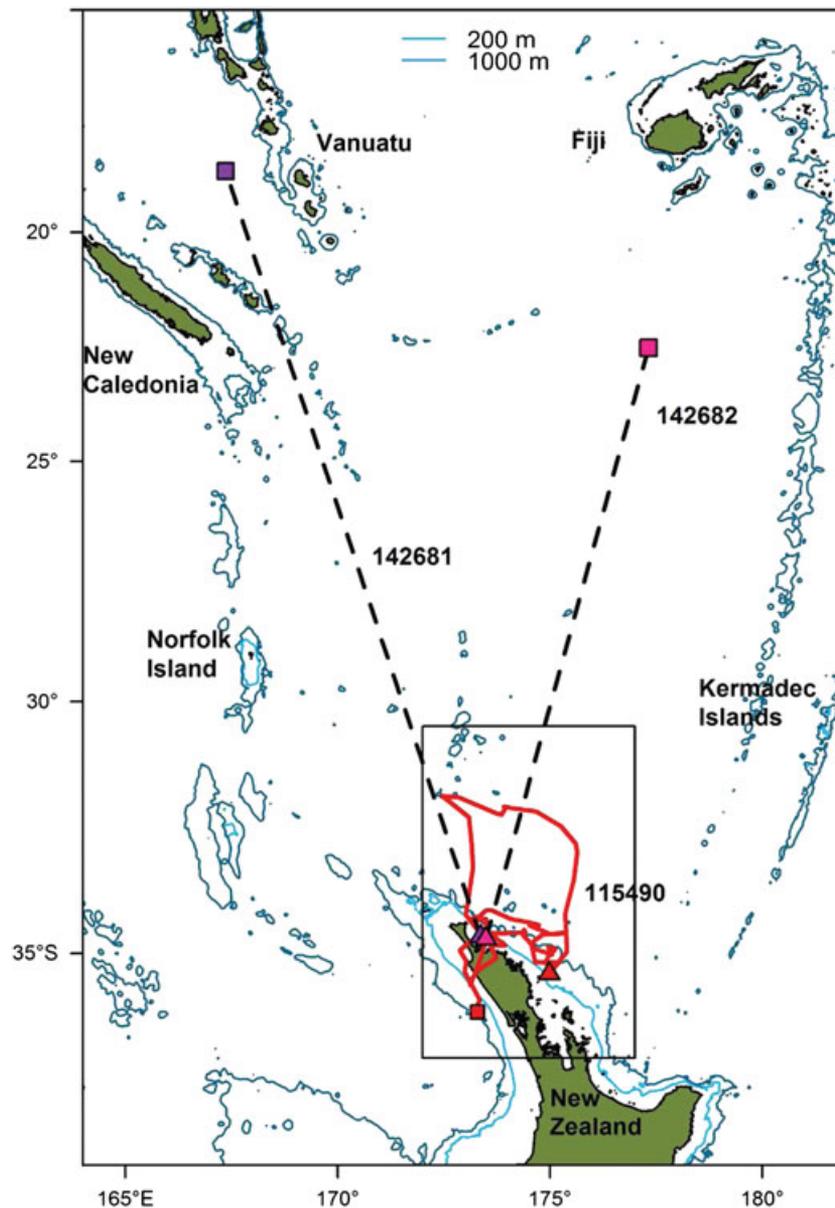


Figure 5. Tag release (triangles) and pop-up (squares) locations of *Mobula japonica* that survived. Dashed lines indicate shortest distances between tag release and pop-up for two survival PAT tags. The area inside the inset box is enlarged in Figure 3.

ray 142681, when the minimum was 6 m. Maximum daily depths for both rays were typically around 200–300 m, but with occasional deeper dives: ray 142681 reached 1112 m, and ray 142682 reached 808 and 1000 m on separate days (Figure 6). Maximum daily temperatures climbed steadily from 21–22 °C for both rays to 26–27 °C for ray 142681 and 24–25 °C for ray 142682 as they moved north (Figure 6). Minimum temperatures increased from about 15–17 °C to about 20 °C as the rays moved north, except for days when they were making deep dives, when minima dropped to 5–7 °C.

High resolution depth and temperature data were available from miniPAT tag 115490. Over the 82-day period, the ray spent most of its time shallower than 50 m (Figures 7, 8). More time was spent in shallow water during the night than during the day: the proportions of time spent in 0–25 m, 25–50 m, and greater than 50 m were 62.8%, 26.8% and 10.4%, respectively, by night, and 40.8%, 35.8% and 23.4%, respectively, by day (Figure 8). Time spent deeper than 200 m was very low (0.2% by night and 2.5% by day). The median night time depth was 17 m and the median day depth was 30 m. The distribution of

temperatures experienced was similar by night and day (Figure 8) because most of the water column traversed by the ray was well mixed and isothermal; median temperatures were 20.6 °C at night and 20.5 °C by day. Dives deeper than 200 m were mostly (92.1%) made during the day or twilight (0500–1900 New Zealand Standard Time) (Figure 9). These dives lasted 8–76 min, but the median was 24 min and only one dive exceeded 1 h. The ray made three dives deeper than 500 m, and reached a maximum depth of 649 m (Figure 7).

Ray 115490 was very active, making almost continuous vertical movements of at least 30–40 m amplitude (Figure 7). However, its vertical behaviour varied considerably through a diel cycle and over the full deployment period. Most days showed movement between the surface and about 40 m, but deeper dives were irregular with some periods having few dives deeper than 200 m (e.g. mid January) and others having many dives deeper than 300 m (e.g. mid March). Depth and light traces during six selected 24 h periods are shown in Figure 10 to illustrate various vertical behaviour patterns. They included:

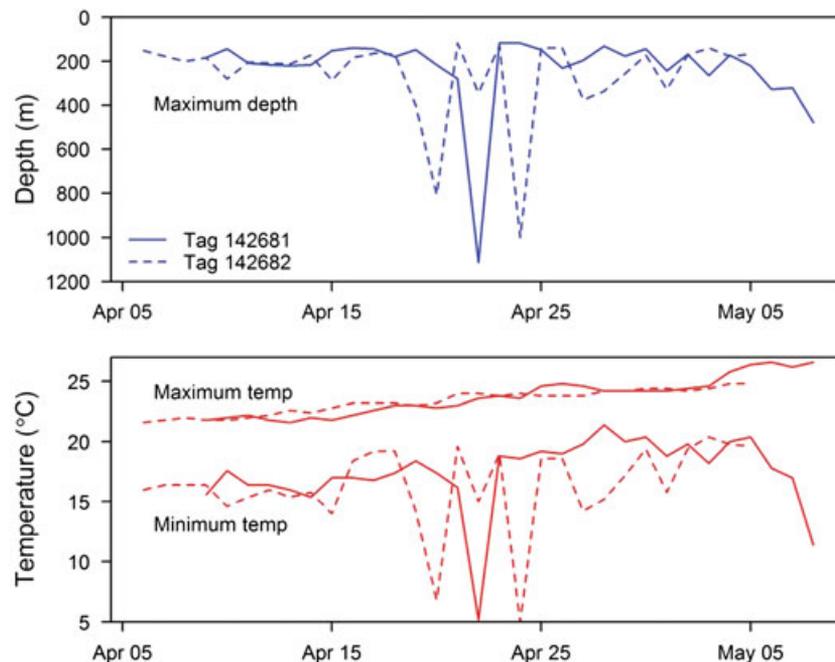


Figure 6. Daily maximum depths, and maximum and minimum temperatures, for two *Mobula japonica* recorded by sPAT tags.

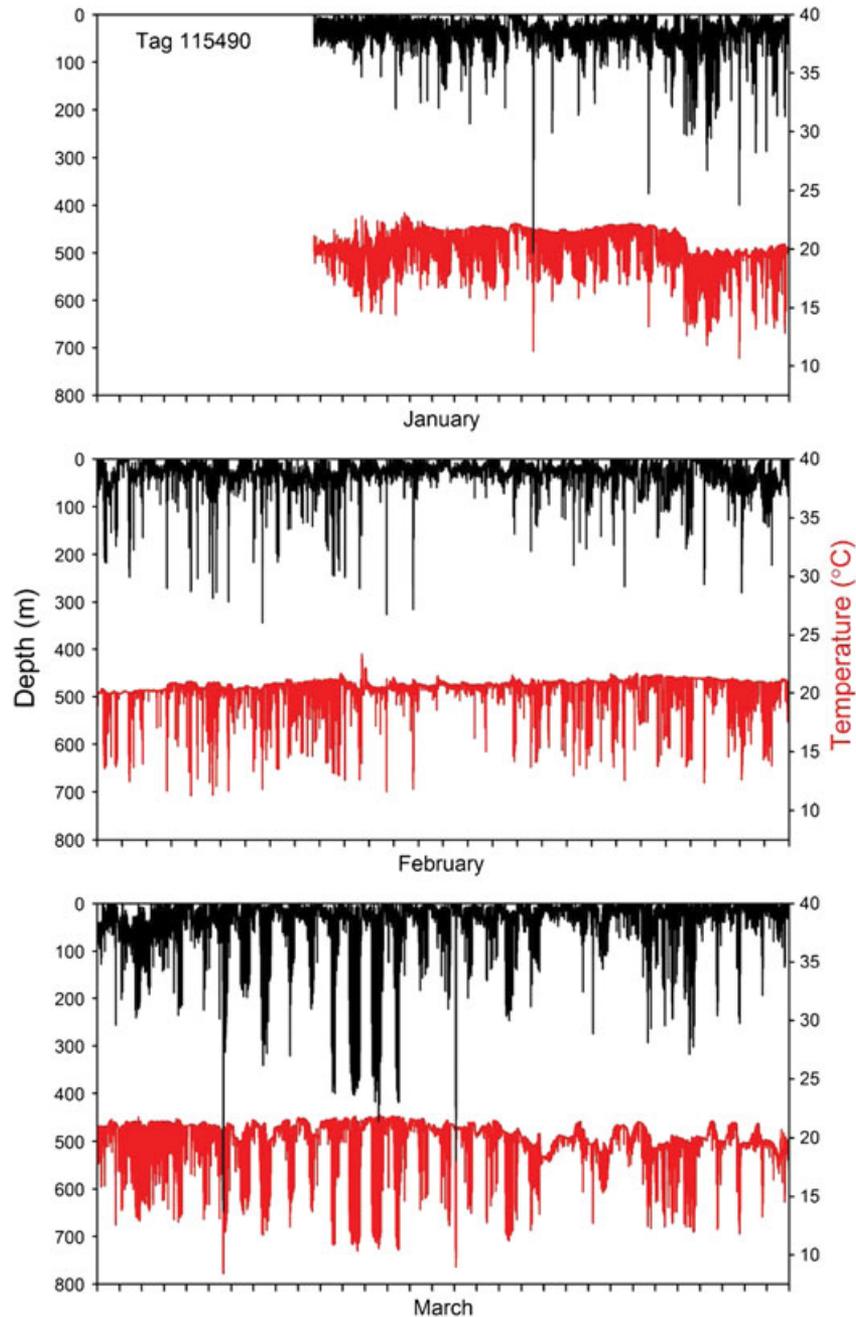


Figure 7. Depth and temperature profiles at 15 s intervals for ray 115490. The last two days of the track in early April are not shown.

- A Continuous, low amplitude, vertical movement with little difference between day and night. This was only two days following tagging and may represent unnatural behaviour during recovery of the ray from the capture and tagging process.
- B Continuous vertical movement with greater amplitude during the day than at night.
- C Highly variable vertical behaviour including periods of negligible movement at depths of 25–50 m and at the surface, and abrupt changes.
- D Small vertical movements at night, and larger amplitude movements by day including periodic deeper dives to more than 200 m.

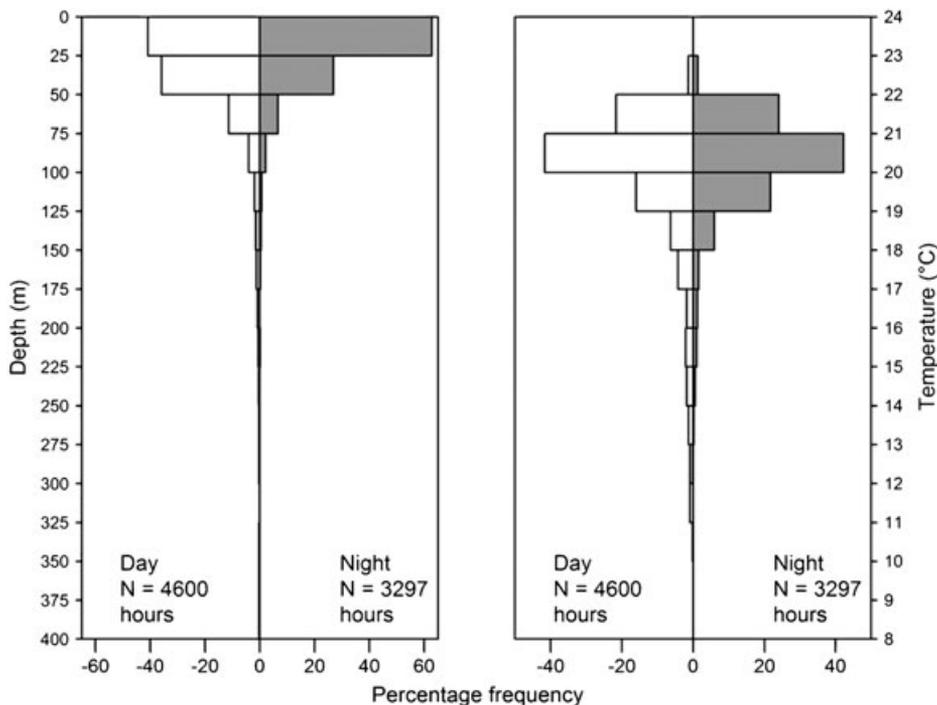


Figure 8. Depth and temperature histograms classified by day and night for ray 115490.

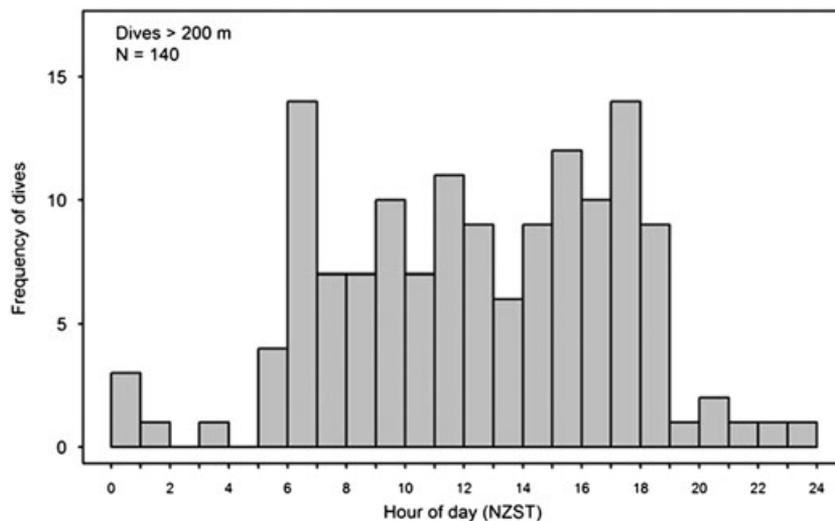


Figure 9. Diel distribution of start times for dives deeper than 200 m by ray 115490. NZST, New Zealand Standard Time.

- E Low amplitude vertical movement by day, with deeper and sometimes lengthy dives from late afternoon to midnight.
- F Negligible vertical movement at night and highly regular deep dives between the upper 50 m and about 350 m during the day.

## DISCUSSION

### Distribution and occurrence in New Zealand

*Mobula japonica* has a worldwide distribution in tropical and subtropical waters (Last and Stevens,

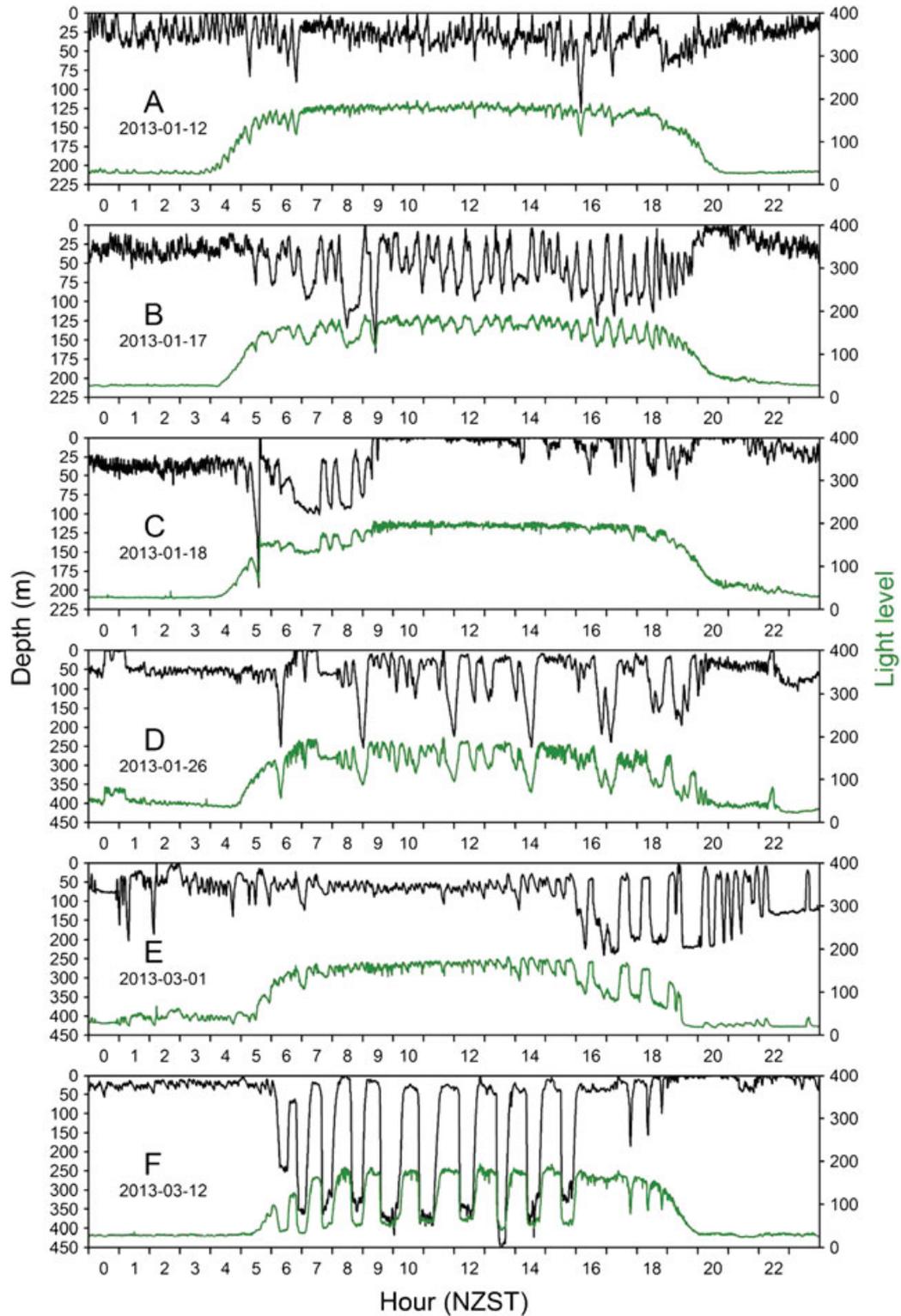


Figure 10. Depth (black) and light (green) profiles for six selected days for ray 115490. Note that panels A–C and D–F have different depth ranges (left axes). NZST, New Zealand Standard Time.

2009; Poortvliet *et al.*, 2015), though its occurrence is patchy; for example it has been reported from Queensland and New South Wales in Australia, but not from other Australian states (Townsend and Kyne, 2010; Couturier *et al.*, 2012). However, field identification difficulties and the offshore occurrence of the species in some regions suggest that some apparent gaps may not be true absences. A recent study found no genetic differentiation among *M. japanica* populations in the north-west Pacific, north-east Pacific, Indian and east Atlantic oceans (Poortvliet *et al.*, 2015). However, in the north-east Pacific, the species does not exceed 2.5 m DW (Notarbartolo-di-Sciara, 1987; Croll *et al.*, 2012; Cuevas-Zimbrón *et al.*, 2013), whereas it grows to at least 3.1 m DW in New Zealand (Paulin *et al.*, 1982) and 2.84 m DW in Indonesia (White *et al.*, 2006a). This suggests that there may be geographically isolated populations of *M. japanica* in the the north-east and south-west Pacific.

In New Zealand, *M. japanica* is restricted to the northern North Island (Francis and Lyon, 2012). Rays recorded by observers aboard tuna purse seiners were spatially and temporally localized compared with the distribution of the fishery: most rays were caught during January–March near the shelf edge off north-east North Island between Great Barrier Island and Cape Brett (~35.0–36.5° S) in water depths of 150–350 m, with catch rates peaking at 300–350 m (Paulin *et al.*, 1982; Francis and Lyon, 2012; Jones and Francis, 2012; present study). The southernmost known record was at 38.36°S (Paulin *et al.*, 1982). New Zealand is at the southern limit of the world range of *M. japanica* (Couturier *et al.*, 2012; Poortvliet *et al.*, 2015), and rays are rarely seen there outside summer, suggesting that they may migrate seasonally into New Zealand waters from subtropical or tropical areas to the north. This hypothesis is supported by the movements of three tagged rays in the present study. Ray 115490 was tagged in early summer (January) and remained near the New Zealand continental shelf for 2.7 months apart from a brief offshore movement up to ~580 km away from the tagging site soon after release. Rays 142681 and 142682 were tagged in late summer (early April) and they travelled

rapidly (averaging at least 47 and 63 km.day<sup>-1</sup> over 30 days, respectively) for distances of ~1400–1800 km to tropical waters north of New Zealand within one month of tagging. In the Sea of Cortez, Mexico, tagged *M. japanica* made straight line movements of more than 1000 km, covering up to 55 km in 24 h (Freund *et al.*, 2000; Croll *et al.*, 2012). *Mobula tarapacana* has been tracked over distances as large as 3800 km in the central North Atlantic Ocean, with a greatest minimum daily speed of 49 km. day<sup>-1</sup> (Thorrold *et al.*, 2014).

Although the sample size of tagged rays in the present study was very small and strong conclusions are not justified, it appears that some *M. japanica* at least spend several months near the New Zealand continental shelf during summer before migrating to tropical waters where they presumably spend the rest of the year. Information to date indicates that in the south-west Pacific *M. japanica* rarely occur over the continental shelf, and mostly inhabit the open ocean.

### Vertical behaviour

*Mobula japanica* is a filter feeder that strains plankton from the water with its gill plates. In Mexico, *M. japanica* feeds almost exclusively on the euphausiid *Nyctiphanes simplex* (Notarbartolo-di-Sciara, 1988; Sampson *et al.*, 2010; Croll *et al.*, 2012) but its diet in New Zealand waters is unknown. The vertical and horizontal movements of this species probably reflect its attempts to find and exploit concentrations of prey (Croll *et al.*, 2012; Poortvliet *et al.*, 2015). The north-east coast of North Island, New Zealand, is subject to wind-driven upwelling during spring and early summer that pushes nutrient-rich water up on to the continental shelf (Zeldis, 2004), presumably boosting zooplankton abundance. *Mobula japanica* may migrate to north-eastern New Zealand during summer to exploit this food source, along with a range of other large planktivores such as the giant manta (*Manta birostris*), whale shark (*Rhincodon typus*) and skipjack tuna that also feed in this area (West, 1991; Duffy, 2002; Duffy and Abbott, 2003). Croll *et al.* (2012) concluded that in the Sea of Cortez ‘the large-scale movement patterns of *Mobula*

*japanica* are likely best explained by seasonal patterns in euphausiid availability combined, perhaps, with limitations imposed by water temperature in the upper 5 to 10 m of the water column'. A similar conclusion may apply to *M. japonica* in the south-west Pacific Ocean.

Ray 115490 spent most of its time shallower than 50 m, more so during the night (89.6%) than the day (76.6%). The only previous study to investigate vertical movements in *M. japonica* found similar behaviour: in the Sea of Cortez most time was spent in water shallower than 50 m, with a higher proportion during the night (97%) than the day (90%) (Croll *et al.*, 2012). *Mobula mobular*, which is genetically and morphologically very similar to and possibly conspecific with *M. japonica* (Poortvliet *et al.*, 2015), also preferred shallow depths, averaging 88% of their time shallower than 50 m at night and 75% by day in the Mediterranean Sea (Canese *et al.*, 2011). SSTs for *M. japonica* in the Sea of Cortez were mostly 20–30 °C (Croll *et al.*, 2012), and for *M. mobular* in the Mediterranean were mostly 20–30 °C (Canese *et al.*, 2011), which are considerably warmer than recorded by tag 115490 in New Zealand in this study (mainly 18–22 °C, modally 20–21 °C), but comparable with temperatures recorded by rays 142681 and 142682 after they had migrated to tropical waters north of New Zealand.

In the Sea of Cortez, *N. simplex* lives deeper than 50 m during the day, but undergoes a nocturnal vertical migration that brings it near the surface. This suggests that *M. japonica* feeds mainly at night in surface waters (Croll *et al.*, 2012). One New Zealand *M. japonica* made regular, short, day-time excursions into much deeper water, suggesting that at times they also feed on deepwater plankton that has not migrated to the surface. The greatest depths recorded by three rays in this study were 649 m, 1000 m and 1112 m, all of which substantially exceed the previous depth record of 445 m for *M. japonica* reported by Freund *et al.* (2000), although *M. mobular* makes occasional deep dives to more than 600 m (Canese *et al.*, 2011). Nevertheless, *M. japonica* spends very little time deeper than 200 m, and the routine deep diving by ray 115490 to 350 m (Figure 10(F)) was

exceptional. This contrasts with another large, oceanic mobulid, *M. tarapacana*, which routinely dives to depths greater than 800 m, often dives deeper than 1500 m, and reaches maximum depths of 1800–1900 m (Thorrold *et al.*, 2014).

Regular up-down movements were frequently observed in ray 115490 and varied in amplitude from about 25 m to 75–100 m, and rarely as high as 350 m (Figure 10). Such behaviour, also reported by Freund *et al.* (2000), is often termed oscillatory or 'yo-yo' diving, and presumably represents the ray traversing the water column while searching for prey and/or feeding.

### Survival

Devilrays caught in successful purse seine sets were mainly brailled aboard with the tuna catch, removed onto the deck and either winched or dragged off the deck using hooks or rope trusses. When devilrays were caught in skunked sets (more than 30% of ray sets), they were more likely to become entangled in the bunt and be hauled on deck with the net and cut free, than to be set free from the net in the water. Both brailing and becoming entangled in the bunt result in the rays being brought out of the water and subjected to significant handling. However, rays were usually lively, swam away from the vessel, and were judged by observers as likely to survive.

PAT tags have been used frequently to estimate post-release mortality in other large marine species (Domeier *et al.*, 2003; Moyes *et al.*, 2006; Campana *et al.*, 2009a, b). *Mobula japonica* tagged in the Sea of Cortez carried popup tags for 14–188 days (the second shortest period was 44 days), suggesting good survival. However, the rays were mostly smaller (142–238 cm DW, mean 200 cm DW) than those tagged in the present study and they were not removed from the water for tagging (Croll *et al.*, 2012). With a sample of only seven tagged rays, it is premature to draw conclusions about survival rates of *M. japonica* returned to the sea from the deck of New Zealand purse seine vessels. Nevertheless, the four deaths observed out of seven rays indicate that mortality may be significant. Those four had all become entangled in the bunt netting, while those that

were brailled aboard survived. These initial results warrant further investigation to ascertain whether such differences in handling do affect the chances of survival. All tagged rays were reported to have swum away vigorously when released, showing that post-release behaviour is not necessarily a good indicator of survival.

Factors affecting survival of mobulid rays in purse seine nets are unknown but may include whether, and for how long, they are held in the pursed and sacked net or brail net, whether they are entrapped with large numbers of other fish such as skipjack which can rapidly deoxygenate the water, and whether they can continue to move or become entangled. Juvenile silky sharks (*Carcharhinus falciformis*) tagged from purse seine catches in the western central Pacific Ocean suffered 84% overall post-release mortality, with mortality increasing rapidly if the sharks had been confined to the sacked portion of the net or brailled aboard (Hutchinson *et al.*, 2015). A similar study on silky sharks in the Indian Ocean found an overall mortality rate of 81%, including 85% for sharks that had been brailled aboard (Poisson *et al.*, 2014a). MPI observers are now collecting data on the New Zealand purse seine sets that capture rays to determine the duration of each event in the hauling sequence and the ray handling techniques employed by vessel crew. The same data will be collected on ray tagging trips planned for 2016 so that mortality of tagged rays can be related to these factors, and important factors affecting survival rates identified.

### Implications for management

*Mobula japonica* has been classified on the IUCN Redlist as 'Near Threatened' globally, but 'Vulnerable' to extinction throughout south-east Asia where catches and demand are increasing (White *et al.*, 2006b). This classification reflects the low productivity of the species, which produces only a single, large young per litter after an unknown gestation period and reproductive cycle duration (White *et al.*, 2006b; Couturier *et al.*, 2012). Size at birth is about 90 cm DW (Paulin *et al.*, 1982; White *et al.*, 2006a; Couturier *et al.*, 2012), although a 56 cm DW neonate (possibly an aborted embryo) has been caught in New Zealand

(Stewart, 2002). Age estimates for *M. japonica* from Mexico indicate that they grow fairly quickly to reach 2 m DW by an age of 5 years, and live for at least 14 years (Cuevas-Zimbrón *et al.*, 2013). These preliminary estimates suggest that maturity may be reached (for males at least) by about 5–6 years, but the ageing method still needs to be validated, and applied to south-west Pacific rays of both sexes to confirm this. Uncertainties about the biological parameters of *M. japonica*, and a lack of knowledge of the geographic range of the stock and the size of catches being taken from it, mean that management measures should be precautionary.

Between 2005 and 2014, *M. japonica* were caught in 8.2% of all observed skipjack purse seine sets in New Zealand waters. Exactly the same catch rate was reported from the same fishery between 1976 and 1982 (74 sets out of 904 observed with an average of 2.2 rays per set) (Bailey *et al.*, 1996). This suggests there has been little change in the ray encounter rate over three decades. However, it is not known if the distribution of sets in 1976–1982 was similar to that in the present study; any difference in the proportion of sets made in the 'hotspot' area identified here (i.e. ~35.0–36.5° S off the north-eastern coast of North Island in the 150–450 m depth range) would probably bias the comparison among studies.

The *M. japonica* hotspot produced a much higher catch rate (24.3% of sets) than did the overall fishery, and is clearly the area on which to focus research and management in order to reduce incidental bycatch of this protected species. A reduction in fishing effort within the hotspot region would undoubtedly reduce the bycatch of *M. japonica*. So too would restricting purse seine sets to waters over the continental shelf (seabed depths less than 200 m) because ray abundance is greatest beyond the edge of the continental shelf. However, the hotspot region is one of several favoured by purse seiners (West, 1991; Langley, 2011), presumably because the high ocean productivity in the area that attracts *M. japonica* also attracts skipjack tuna. Ray captures could also be reduced by not setting on skipjack schools if mobulid rays are sighted, as they often are by pilots of spotter planes working in conjunction

with the purse seine vessel (Jones and Francis, 2012). Vessels prefer to avoid catching skipjack schools that are associated with *M. japonica*, because they often result in skunked sets, from which the tuna escape (Jones and Francis, 2012).

*Mobula japonica* is also rarely caught on surface longlines and trolled lures in New Zealand (Duffy and Abbott, 2003; Francis and Lyon, 2012), but those methods are unimportant compared with purse seines. However, tuna longlines may be a more important source of bycatch elsewhere in the tropical Pacific (Molony, 2005), and drift nets are used to target mobulids including *M. japonica* in Indonesia (White *et al.*, 2006a).

Purse seine crews should be encouraged to maximize the chances of ray survival by developing techniques to release them from the net while it is still in the water, particularly for skunked sets. If rays are brought aboard in the brail net or entangled in the purse seine, vessels should adopt 'best-practice' handling techniques for elasmobranchs (Poisson *et al.*, 2014b). The common practice of dragging rays off the deck into the water by inserting large hooks or ropes into the gills or into holes cut in the wings, or trussing them up in twine which can cut into the wings (Jones and Francis, 2012; Hall and Roman, 2013), should obviously be discouraged. One particularly promising handling technique is to spread a large mesh 'cargo' net over the fish hold to 'sieve' the rays from a brail load of skipjack, and to facilitate the rapid and humane return of rays to the sea (Jones and Francis, 2012; Hall and Roman, 2013). Such cargo nets should be constructed from soft straps or webbing, or perhaps non-tear PVC rather than thin twine to protect the heavy, soft-bodied rays from being sliced by the net as they are lifted off the deck. Use of a cargo net also has strong benefits for the vessel, because it can substantially reduce the handling time for large bycatch species that are discarded, such as devilrays, sunfish (*Mola mola*) and sharks.

#### ACKNOWLEDGEMENTS

Special thanks are due to Matt Saunders and Leon Berard (MPI) for tagging the rays aboard commercial purse seiners, and to other observers

who collected data. We also thank the fishing industry for their support of this work aboard their vessels. MPI and David Fisher (NIWA) provided observer database extracts. This study was funded by the New Zealand Department of Conservation under research project MIT2011–01, and we thank Kris Ramm for his management and support of the project.

#### REFERENCES

- Amandè MJ, Ariz J, Chassot E, Delgado de Molina A, Gaertner D, Murua H, Pianet R, Ruiz J, Chavance P. 2010. Bycatch of the European purse seine tuna fishery in the Atlantic Ocean for the 2003–2007 period. *Aquatic Living Resources* **23**: 353–362.
- Bailey K, Williams PG, Itano D. 1996. By-catch and discards in Western Pacific tuna fisheries: a review of SPC data holdings and literature. *Oceanic Fisheries Programme Technical Report* **34**.
- Campana SE, Joyce W, Manning MJ. 2009a. 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.
- Campana SE, Joyce W, Francis MP, Manning MJ. 2009b. Comparability of blue shark mortality estimates for the Atlantic and Pacific longline fisheries. *Marine Ecology Progress Series* **396**: 161–164.
- Canese S, Cardinali A, Romeo T, Giusti M, Salvati E, Angiolillo M, Greco S. 2011. Diving behavior of the giant devil ray in the Mediterranean Sea. *Endangered Species Research* **14**: 171–176.
- Couturier LIE, Marshall AD, Jaine FRA, Kashiwagi T, Pierce SJ, Townsend KA, Weeks SJ, Bennett MB, Richardson AJ. 2012. Biology, ecology and conservation of the Mobulidae. *Journal of Fish Biology* **80**: 1075–1119.
- Croll DA, Newton KM, Weng K, Galván-Magaña F, O'Sullivan J, Dewar H. 2012. Movement and habitat use by the spine-tail devil ray in the Eastern Pacific Ocean. *Marine Ecology Progress Series* **465**: 193–200.
- Cuevas-Zimbrón E, Sosa-Nishizaki O, Pérez-Jiménez JC, O'Sullivan JB. 2013. An analysis of the feasibility of using caudal vertebrae for ageing the spinetail devilray, *Mobula japonica* (Müller and Henle, 1841). *Environmental Biology of Fishes* **96**: 907–914.
- Domeier ML, Dewar H, Nasby-Lucas N. 2003. Mortality rate of striped marlin (*Tetrapturus audax*) caught with recreational tackle. *Marine and Freshwater Research* **54**: 435–445.
- Domeier ML, Kiefer D, Nasby-Lucas N, Wagschal A, O'Brien F. 2005. Tracking Pacific bluefin tuna (*Thunnus thynnus orientalis*) in the northeastern Pacific with an automated algorithm that estimates latitude by matching sea-surface-temperature data from satellites with temperature data from tags on fish. *Fishery Bulletin* **103**: 292–306.
- Duffy CAJ. 2002. Distribution, seasonality, lengths, and feeding behaviour of whale sharks (*Rhincodon typus*) observed in New Zealand waters. *New Zealand Journal of Marine and Freshwater Research* **36**: 565–570.
- Duffy CAJ, Abbott D. 2003. Sightings of mobulid rays from northern New Zealand, with confirmation of the occurrence of *Manta birostris* in New Zealand waters. *New Zealand Journal of Marine and Freshwater Research* **37**: 715–721.

- Francis MP, Lyon WS. 2012. Review of commercial fishery interactions and population information for eight New Zealand protected fish species. NIWA client report WL2012-64. Available from <http://www.doc.govt.nz/Documents/conservation/marine-and-coastal/marine-conservation-services/pop2011-03-protected-fish-review.pdf> (accessed 1 July 2015).
- Freund EV, Dewar H, Croll DA. 2000. Locomotor tracking of the spine-tailed devil ray, *Mobula japanica* (Abstract). *American Zoologist* **40**: 1020.
- Gilbert HH, Paul LJ. 1969. First record of manta rays off New Zealand. *New Zealand Journal of Marine and Freshwater Research* **3**: 339–342.
- Hall M, Roman M. 2013. Bycatch and non-tuna catch in the tropical tuna purse seine fisheries of the world. FAO Fisheries and Aquaculture Technical Paper 568.
- Hutchinson MR, Itano DG, Muir JA, Holland KN. 2015. Post-release survival of juvenile silky sharks captured in a tropical tuna purse seine fishery. *Marine Ecology Progress Series* **521**: 143–154.
- IUCN. 2014. *The IUCN Red List of threatened species*. Version 2014.3.
- Jones E, Francis MP. 2012. Protected rays – occurrence and development of mitigation methods in the New Zealand tuna purse seine fishery. NIWA client report prepared for the Department of Conservation. WL2012-49. Available from <http://www.doc.govt.nz/Documents/conservation/marine-and-coastal/marine-conservation-services/mit2011-01-protected-rays-final-report.pdf> (accessed 1 July 2015).
- Kendrick TH. 2006. Characterisation of the New Zealand tuna fisheries in 2002–2003 and 2003–2004. *New Zealand Fisheries Assessment Report* 2006/28.
- Lam CH, Nielsen A, Sibert JR. 2008. Improving light and temperature based geolocation by unscented Kalman filtering. *Fisheries Research* **91**: 15–25.
- Langley AD. 2011. Characterisation of the New Zealand fisheries for skipjack tuna *Katsuwonus pelamis* from 2000 to 2009. *New Zealand Fisheries Assessment Report* 2011/43.
- Last PR, Stevens JD. 2009. *Sharks and Rays of Australia*, 2nd edn. CSIRO: Hobart.
- Mas F, Forselledo R, Domingo A. 2015. Mobulid ray by-catch in longline fisheries in the south-western Atlantic Ocean. *Marine and Freshwater Research* **66**: 767–777.
- Ménard F, Fonteneau A, Gaertner D, Nordstrom V, Stéquert B, Marchal E. 2000. Exploitation of small tunas by a purse-seine fishery with fish aggregating devices and their feeding ecology in an eastern tropical Atlantic ecosystem. *ICES Journal of Marine Science* **57**: 525–530.
- Ministry for Primary Industries. 2014. [New Zealand] Annual report to the commission Part 1: information on fisheries, research, and statistics. Western Central Pacific Fisheries Commission Scientific Committee Tenth Regular Session WCPFC-SC10-AR/CCM-16 Rev. 1.
- Molony B. 2005. Estimates of the mortality of non-target species with an initial focus on seabirds, turtles and sharks. Western Central Pacific Fisheries Commission Scientific Committee First Regular Session WCPFC-SC1-EB-WP-1.
- Moyes CD, Fragoso N, Brill RW, Musyl MK. 2006. Predicting postrelease survival in large pelagic fish. *Transactions of the American Fisheries Society* **135**: 1389–1397.
- Nielsen A, Bigelow KA, Musyl MK, Sibert JR. 2006. Improving light-based geolocation by including sea surface temperature. *Fisheries Oceanography* **15**: 314–325.
- Notarbartolo-di-Sciara G. 1987. A revisionary study of the genus *Mobula* Rafinesque, 1810 (Chondrichthyes: Mobulidae) with the description of a new species. *Zoological Journal of the Linnean Society* **91**: 1–91.
- Notarbartolo-di-Sciara G. 1988. Natural history of the rays of the genus *Mobula* in the Gulf of California. *Fishery Bulletin* **86**: 45–66.
- Paulin CD, Habib G, Carey CL, Swanson PM, Voss GJ. 1982. New records of *Mobula japanica* and *Masturus lanceolatus*, and further records of *Luvaris imperialis* (Pisces: Mobulidae, Molidae, Louvaridae) from New Zealand. *New Zealand Journal of Marine and Freshwater Research* **16**: 11–17.
- Poisson F, Filmlalter JD, Vernet A-L, Dagorn L. 2014a. Mortality rate of silky sharks (*Carcharhinus falciformis*) caught in the tropical tuna purse seine fishery in the Indian Ocean. *Canadian Journal of Fisheries and Aquatic Sciences* **71**: 795–798.
- Poisson F, Séret B, Vernet A-L, Goujon M, Dagorn L. 2014b. Collaborative research: development of a manual on elasmobranch handling and release best practices in tropical tuna purse-seine fisheries. *Marine Policy* **44**: 312–320.
- Poortvliet M, Olsen JL, Croll DA, Bernardi G, Newton K, Kollias S, O'Sullivan J, Fernando D, Stevens G, Galván Magaña F, et al. 2015. A dated molecular phylogeny of manta and devil rays (Mobulidae) based on mitogenome and nuclear sequences. *Molecular Phylogenetics and Evolution* **83**: 72–85.
- R Development Core Team. 2008. *R: A Language and Environment for Statistical Computing*. <http://www.R-project.org>. R Foundation for Statistical Computing: Vienna, Austria.
- Romanov EV. 2002. Bycatch in the tuna purse-seine fisheries of the western Indian Ocean. *Fishery Bulletin* **100**: 90–105.
- Sampson L, Galván-Magaña F, De Silva-Dávila R, Aguiñiga-García S, O'Sullivan JB. 2010. Diet and trophic position of the devil rays *Mobula thurstoni* and *Mobula japanica* as inferred from stable isotope analysis. *Journal of the Marine Biological Association of the United Kingdom* **90**: 969–976.
- Stewart A. 2002. Mantas and devilrays. *Seafood New Zealand* April: 65–68.
- Teo SLH, Boustany A, Blackwell S, Walli A, Weng KC, Block BA. 2004. Validation of geolocation estimates based on light level and sea surface temperature from electronic tags. *Marine Ecology Progress Series* **283**: 81–98.
- Thorrold SR, Afonso P, Fontes J, Braun CD, Santos RS, Skomal GB, Berumen ML. 2014. Extreme diving behaviour in devil rays links surface waters and the deep ocean. *Nature Communications* **5**(4274): 1–7.
- Townsend KA, Kyne PM. 2010. New records of the Japanese devilray *Mobula japanica* (Müller and Henle 1841) for Australian waters. *Memoirs of the Queensland Museum* **55**: 225–230.
- West IF. 1991. A review of the purseseine fishery for skipjack tuna, *Katsuwonus pelamis*, in New Zealand waters, 1975–1986. *New Zealand Fisheries Technical Report* **29**.
- White WT, Giles J, Dharmadi, Potter IC. 2006a. Data on the bycatch fishery and reproductive biology of mobulid rays (Myliobatiformes) in Indonesia. *Fisheries Research* **82**: 65–73.
- White WT, Clark TB, Smith WD, Bizzarro JJ. 2006b. *Mobula japanica*. In *IUCN Red List of Threatened Species*. Version 2013.2, IUCN: Gland: Switzerland.
- Zeldis JR. 2004. New and remineralised nutrient supply and ecosystem metabolism on the northeastern New Zealand continental shelf. *Continental Shelf Research* **24**: 563–581.