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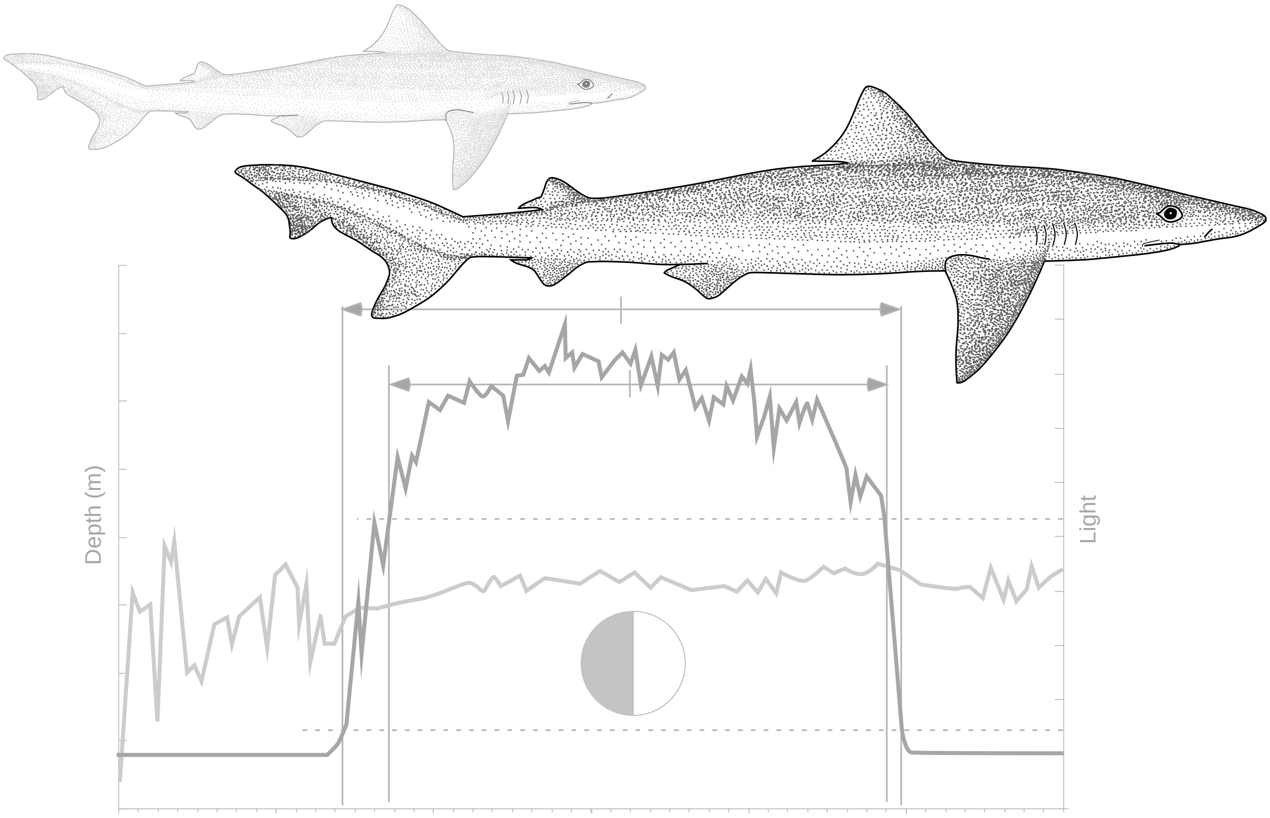
The use of archival tags for studying the movement and swimming behaviour of school sharks

G. J. West and J. D. Stevens



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1. NON-TECHNICAL SUMMARY

96/128 The use of archival tags for studying the movement and swimming behaviour of school sharks

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Objectives:

1. To determine the frequency and extent of movements of individual school sharks within the fishery leading to an improved understanding of spatial structure required for regional assessments of school shark stocks.
2. To determine whether the total population of mature female school sharks migrate to Tasmanian and Victorian waters to pup and consequently whether recruitment is dependent on south-eastern pupping areas.
3. To provide information on the swimming depth of school sharks and to estimate the amount of time they spend off the bottom and unavailable to commercial fishing gear. This information is required in assessing the relative impact of current fishing effort directed at school and gummy shark.

There has been serious concern over the status of the school shark fishery for many years, and it has been the subject of numerous stock assessments (Punt & Walker 1998). It is a well researched species: Olsen (1954) showed that school shark can make extensive migrations, and that females moved to pupping grounds in the south-east of Australia to give birth. However, despite their apparent ability to move freely through the fishery, there are regional differences in size, age and reproductive condition, together with different catch-rate trends in different regions of the fishery. Originally stock assessment models were based on the assumption of a single freely-mixing stock, in light of the ability of the species to move long distances. However, Prince (1992) argued that the biological and catch data was incompatible with the assumption of a single stock, and was instrumental in having spatial structure in the fishery taken into account. Punt et al. (2000) developed a model that takes account of the spatial structure of the population, allows for multiple stocks and which uses catch-rate data and information from tagging studies to derive values for the parameters of the model.

Conventional tagging provides movement information for the point of release and the point of recapture. The path taken by the fish is not known, but general movement trends can be modelled. Archival tags have the advantage of describing directly the actual movement path and revealing movement patterns independently of where the fisheries operate. In addition they provide vital information on the depth distribution, diving behaviour and water temperature. These tags developed from earlier time-depth recorders that were first used on marine mammals to study diving behaviour and physiology. The addition of a light sensor enabled local solar noon to be estimated from the mid-point of the daily light curve, allowing estimation of longitude. While the longitude estimates were not precise, they were satisfactory for use on the highly migratory tunas they were intended for. The original concept for estimating latitude for these pelagic species was based on water temperature data obtained during their dives. An alternative method of deriving latitude is based on estimates of day length from each day's light record. However, day length provides poor estimates of latitude, and none at all around the time of the equinoxes. In addition correcting for the effects of light-attenuation under water, and dealing with the inherent variability caused by weather conditions means that at present this method is not satisfactory. In our study of a demersal species we had the option of estimating latitude from bathymetry. Except around Tasmania the isobaths run approximately east-west, so once a longitude has been established for a particular day, a corresponding latitude can be derived by comparison of the maximum depth reached by the fish with bathymetric data. This method assumes that the fish is on the bottom at the maximum depth, and analysis of the daily depth profiles supported this assumption for much of the time. Around Tasmania where the isobaths run north-south and where similar depths can occur in Bass Strait or off the south coast of Tasmania, this method broke down.

We tagged 46 school shark (125–165 cm total length) with both external and internal archival tags at sites in the Great Australian Bight, eastern South Australia, and NE Tasmania. To date we have had 15 (33%) returned and although the sample sizes are small it indicates a high exploitation rate. The return rate is higher than from conventional tagging and reflects the intense interest in the study shown by fishers.

In this study it was the longitudinal movements of the fish that were of greatest interest, and although daily longitude estimates from the archival tags were highly variable, weekly median estimates appeared reliable. Latitude estimates were based on bathymetry except around Tasmania where none were possible. One fish appeared to move to New Zealand, but the clock in the archival tag was found to be seriously defective when tested upon its return. Although conventional tagging shows movements of school shark between Australia and New Zealand, we conclude that there was no evidence of any movement of archival-tagged fish further east than 149–150° E. No school shark migrated across the entire range of the Australian fishery in the time they were at liberty (<1.5 y), and there was limited mixing between the eastern and western regions of the fishery in this time frame. The restricted movement shown by the archival-tagged sharks provides additional support for the move to spatially-structured stock assessments. Although these results seemed at odds with the impression of wide-ranging movements shown by earlier conventional tagging, re-analysis of tag returns from the 1947–56 tagging program (Olsen 1954) provided support for restricted longitudinal movements. For school sharks ≥ 95 cm total length at release tagged in Victoria and Tasmania, the percentage recaptured in South Australia did not peak until after 4–6 y at liberty for females (~70%) and 12–14 y for males (~40%). These results however depend upon the relative fishing effort in these two areas at the time.

The archival-tagged sharks favoured 4 regions across southern Australia. The outer regions (Great Australian Bight and Tasmanian east coast) were frequented during summer, and in winter the fish in these regions moved to more central regions (Kangaroo Island and the Tasmanian west coast respectively), resulting in a contraction of their longitudinal range.

We found that in Tasmanian waters March–April were times of major movements to the west coast, and October–November were times of major movements to the east coast. In South Australia movements occurred over a wider time period, with elevated movement rates from October to May. Movement rates peaked in November with fish moving both east and west. This is in general agreement with Olsen's conclusions: movements in late summer–winter and October–November.

The second objective of the study was to study the movements of pregnant school sharks, to ascertain whether recruitment was completely dependent upon south-eastern pupping areas. By tagging in South Australia just prior to the pupping season the movements of the females could be followed, knowing that they would give birth within several months. However, this objective was not met, because of the scarcity of pregnant fish in the catch. Only one tagged shark was considered to be pregnant (based on girth measurement) and it was not recaptured. The scarcity of pregnant females in the catch makes it doubtful that archival tagging can address this question.

The final objective of the study was to study the swimming depth of the school sharks, and to estimate the amount of time they spent off the bottom and unavailable to the commercial fishing gear. The school sharks were in depths from the surface down to 660 m. They have previously been reported at depths from the surface (Ripley 1946) to 600 m (Cowper & Downie 1957). One of the most striking dive patterns was seen in deep water when the sharks would make regular descents during daylight hours to depths up to 660 m and return to near the surface at dusk. At other times in deep water, although the fish were deeper during the day, the depth pattern was very irregular. However, the amount of time spent in deep water was minor – school sharks spent 90% of their time on the continental shelf at depths <200 m, where a wide variety of dive patterns was observed. One of the most common was a pattern of nightly ascents, often to near the surface. At the time of the full moon, these ascents were usually, but not always, suppressed. We have yet to estimate the amount of time the fish spent off the bottom because of the complexity of other dive patterns shown by the species, and the uncertainty this introduces as to whether the fish were actually on the bottom.

Keywords

Data storage tags, depth, temperature, light, geo-location, migration, sharks, *Galeorhinus,* tagging.

2. BACKGROUND

2.1 The fishery

School (*Galeorhinus galeus*) and gummy (*Mustelus antarcticus*) shark, captured by bottom-set gillnets and longlines are the target species for the southern shark fishery in Australia. From 1970 to 1998 the catch of school shark declined from 2600 t to 580 t carcass weight (Walker et al. 1999). Tagging studies have shown that school shark make long-distance movements within Australia (Olsen 1954), and between Australia and New Zealand (Hurst et al. 1999). However, genetic studies indicate that the Australian and New Zealand stocks may be distinct – there is evidence of some restriction of gene flow between the two populations (Ward & Gardner 1997). Within Australia the school shark stock is spatially structured by size, age and reproductive condition but because tagging studies showed that the species was capable of long-distance movements stock assessment was based on the assumption of a single stock (Walker 1998). Prince (1992) argued that the catch history in the different regions of the fishery was typical of that resulting from serial over-exploitation of different functional stocks within a single fishery, and that the poor performance of the single-stock assessments was partly the result of ignoring spatial structure in the fishery. Punt et al. (2000), using a spatially-explicit population dynamics model that assumed that there were two "movement types", estimated that pup production in 1997 was 12–18% of pre-exploitation equilibrium levels. Movement probabilities within the 8 regions of the fishery defined by Prince (1992) were estimated in this assessment using tag-recapture data from conventional tagging (Olsen 1954, Walker et al. 1997).

2.2 Archival tag development

The development of miniature time-depth recorders since the 1980s led to fascinating insights into the diving behaviour of air-breathing marine animals (Wilson et al. 1995). These types of tags have also been successfully used in the study of fish movements. Metcalfe and Arnold (1997) estimated movements for a demersal fish by combining information on tidal amplitude from the tag with a very detailed knowledge of the tidal cycles of the North Sea. However, this approach is not possible for most studies of fish movement. In a workshop on new technologies that might be used to investigate tuna movements, Hunter et al. (1986) supported the development of an 'archival' tag that could store information on swimming depth, water temperature and light level. The light data could be used to estimate the time of sunrise and sunset, from which longitude could be estimated, and latitude could be determined by depth-specific seawater temperatures (Smith & Goodman 1986). Wilson et al. (1992) reported the successful development of a 'global location sensor' that used light data to estimate both latitude and longitude to an accuracy of about 150 km. DeLong et al. (1992) studied the movements of northern elephant seals (*Mirounga angustirostris*) using a 'geographic location time-depth recorder' (GLTDR) that measured light when the animal was near the surface. The accuracy of their position estimates was considered to be about ± 1º (Hill 1994). This estimate was supported by the work of Stewart & DeLong (1995), who attached satellite-linked radio transmitters as well as the 'GLTDRs' to northern elephant seals. Stewart & DeLong (1995) found that differences in position between those derived from satellites and those from archival tags increased as the daily distance covered by the seals increased – all current archival tag geo-location software is based on the assumption that the animals do not move between the two twilights used for estimating the day's longitude (Hill 1994). While these errors can be overlooked in many marine species, in sea birds such as albatross, which can travel distances of up to 900 km day^{-1}, it poses particular problems (Tuck et al. 1999).

Gunn et al. (1994) carried out an experiment in which caged southern bluefin tuna (*Thunnus macoyii*) tagged with archival tags were towed a distance of 450 km to a farm site. They found that the position estimates were accurate to within 1º. By 1994, Northwest Marine Technology Inc.,Washington USA, had developed a tag that estimated the time of dawn and dusk on-board, and compensated for the effect of depth on light levels. The tag had the ability to calculate light-extinction coefficients on a daily basis, providing that the fish dived during the day, or used an open-ocean default value. The light-extinction coefficient was used to allow light measured at depth to be corrected to surface intensities. Block et al. (1998) tagged 170 Atlantic bluefin tuna (*Thunnus thynnus thynnus*) ranging in size from 76–234 kg with internal archival tags, 25 of which (9.5%) have been recovered (B. Block, Hopkins Marine Station, Stanford Uni., Pacific Grove CA 93950, pers. comm.) Their tests with tags on moorings at 50 m depth indicated that while longitude could be estimated to within 1º, latitude estimates were less accurate. Their experiment was carried out near the equinox, a period when latitude estimates are known to be very poor (Hill 1994). Welch and Eveson (1999) tested a variety of archival tags using both reference light levels and rate of change in light levels to identify dawn and dusk, and a number of techniques to smooth the light signal. They found that the algorithm used to determine dawn and dusk had more influence on the results than the method used to smooth the data. In practice, however, the differences were not large. The average position error was about 140 km (standard deviations of 0.9º of longitude and 1.2º of latitude). Klimley et al. (1994) reviewed the state of archival tag development and suggested three general research needs: improved estimates of latitude, additional means of data retrieval other than tag recovery, and improved methods of fish handling and tag attachment.

3. NEED

When this research project was planned in 1995 the southern shark fishery was considered as a single unit for assessment purposes, even though the school shark stock was spatially structured by size, age and reproductive condition and catch-rates for different parts of the fishery exhibited clearly different trends (Prince 1992, Walker 1998). The complex structure of the school shark stock accounted for much of the uncertainty produced by spatially aggregated models, but in order to develop spatially structured models information on rates of movement between major areas of the fishery was required (Walker et al. 1997). The tagging carried out in the 1950's (Olsen 1954) showed the extent of movements of adult and juvenile school shark, but because fishing effort at this time was poorly documented, could not be used to quantify movement rates (Xiao 1996). An extensive tagging program using conventional tags was carried out between 1990–96, to provide the information on movement rates. The complex stock assessment model needed to take into account movement, mortality, growth rates and the level, selectivity and spatial distribution of fishing effort. However fish movement, mortality and growth rates cannot be estimated independently of each other (Walker et al. 1997). Archival tagging offered the potential to provide movement information free from these restrictions, although, because of the small number of potential recaptures, could only ever be considered as complementary to conventional tagging.

Another question that archival tagging could address was the long-held view that the entire southern Australian stock of school shark pup in south-eastern waters. This hypothesis is being increasingly questioned by industry and scientists. It has been suggested that some, if not all school sharks caught in South Australia (SA) and Western Australia pup locally. Since most of the historic pupping areas in Tasmania (Tas) and eastern Victoria (Vic) appear to be depleted, and some are environmentally degraded (Walker 1998), the possibility of recruitment being maintained from other areas has important implications for management of the fishery.

Additionally, we know very little about the vertical movements of school shark in the water column. Current fishing methods involve capturing this species on or near the bottom. However, from captures by pelagic longliners in southern Australia and knowledge that they migrate across the Tasman Sea over depths in excess of 5000 m, school sharks spend an unknown proportion of their time in mid-water or near the surface. Information on the depths at which they swim are required to understand both their localised movements and large-scale migrations. Until recently the only method of collecting data on the movement of fish in three dimensions was by acoustic telemetry (tracking individuals fitted with acoustic 'pingers'). The main problem with this technique is that it provides movement information for only a short period, because of constraints on the endurance of the tracking team, and limited battery life of the tag. There is also the problem that the initial behaviour of the animal may be affected by the stress of capture and tagging. Acoustic tracking can also be expensive, a consequence of vessel costs and the labour intensive nature of the work. Data from tracking studies and conventional tag and recapture experiments provide two ends of the spectrum in terms of our understanding of fish movement. A major information gap exists between the short (1–3 day) highly detailed paths of acoustically tracked individuals and the two position points recorded for marked and eventually recaptured fish (Gunn et al. 1994).

4. OBJECTIVES

1. To determine the frequency and extent of movements of individual school sharks within the fishery leading to an improved understanding of spatial structure required for regional assessments of school shark stocks.

2. To determine whether the total population of mature female school sharks migrate to Tasmanian and Victorian waters to pup and consequently whether recruitment is dependent on south-eastern pupping areas.

3. To provide information on the swimming depth of school sharks and to estimate the amount of time they spend off the bottom and unavailable to commercial fishing gear. This information is required in assessing the relative impact of current fishing effort directed at school and gummy shark.

5. METHODS

5.1 Dummy tagging experiment

Prior to application of archival tags on school sharks, we carried out an experiment with 'dummy' tags to ensure that we achieved satisfactory recapture rates. We used three types of tags, two of them external, and one internal. The external tags were cast from epoxy resin, one a rectangular block (52 mm long x 24 mm wide x 12 mm thick), the other a streamlined shape (27 mm maximum diameter and 116 mm long) with fins at the rear. Nylon pins with an expanded arrow head were screwed into the tags, and the tags were pinned through a pre-punched hole in the lower anterior region of the first dorsal fin and secured by the female half of a cattle ear-tag (Daltons Supplies Australia Pty Ltd). The internal tag was simply the rectangular block with a 3 mm diameter plastic-coated copper wire (to simulate the light sensor) projecting 175 mm from the tag. The internal tags were inserted into the coelomic cavity through a 3 cm longitudinal incision made just in front of, and above, the pelvic fin. The incision was closed with sutures (coated Vicryl) or with stainless steel surgical staples, leaving the wire protruding through the body wall. The tags were deployed during 1995 as part of an extensive conventional tagging project (Walker et al. 1997). The stainless steel staples were tested in a tank experiment by L. Brown (MAFRI, Queenscliff, Australia 3225, pers. comm.) when an internal dummy tag was inserted into a gummy shark, *Mustelus antarcticus*. The wound had healed completely when the shark was inspected 12 weeks later, and the staples were still present and not corroded 2.2 y after insertion.

5.2 Tag evaluation

When the proposal to tag school shark with archival tags was submitted to FRDC in 1995, it was intended to use archival tags manufactured by Zelcon Technic Pty Ltd of Hobart, Australia. These tags had been used successfully by CSIRO in trials on southern bluefin tuna (Gunn et al. 1994). These tags had sensors for depth, temperature and light, and stored this data in memory together with a time stamp from the tag's internal clock. Following the success of their first generation tags, Zelcon were encouraged to make them smaller, more sensitive to light, with increased memory (up from 128 to 512 Kb), and to use 'flash RAM' memory that would keep the data even after the batteries (rated for up to 9 y) had run flat. The new '200' series tags were more advanced than the tags available from the two overseas manufacturers Northwest Marine Technologies (NMT) of Washington and Wildlife Computers (WLC) of Seattle, and were deployed on southern bluefin tuna by CSIRO. Unfortunately, the quite significant changes made to the tags rendered them unreliable – they failed after relatively short periods on tuna, and the light signal was not stable. Zelcon chose not to revert to their earlier model but to carry out more development work on their new tags. This delayed the start of our school shark project, but by mid-1997 prototypes of the modified Zelcon tags were supplied. These were tested together with prototypes of a WLC archival tag. Both of these types of tags failed our tests, which involved lowering them to 200 m and inspecting the depth and light traces. The Zelcon tags showed large variations between the two tags tested, a non-linear depth response, and a maximum light penetration of about 70 m. The WLC tags showed an excellent depth response and, for depths down to about 150 m, an excellent light response, but at great depths (lower light levels) the light signal became unstable. Both manufacturers needed to modify their tags. Zelcon did not succeed in this, and as far as we know, have not produced any further archival tags. WLC were able to fix the problem, but not until the following year.

To avoid further delays to the project, we re-considered using the NMT tags. These tags were a very advanced design for their time, and are still the only ones yet made that carry out the estimation of times of sunrise and sunset on board. They can store this information for the full life expectancy of the batteries – stated to be >7 y in their specifications, and also store individual records of depth, temperature and light measured at 4.2 minute intervals, for about 160 days. The reservations we had about these tags were that battery failure led to complete loss of data, we wanted to store individual records for at least 2–3 y, and the method they used to estimate the time of dawn and dusk, and correct the light data for the effects of depth, were secret.

In 1997 Lotek Marine Technologies, of St. John's, Newfoundland commenced manufacture of an archival tag designed by the Centre for Environment, Fisheries and Aquaculture Science in Lowestoft, UK. We had tested prototypes in late 1996, but, although they performed well, were at that stage only rated to 100 m depth. However, Lotek were able to supply tags in housings rated to 1000 m by our tagging deadline of November 1997. Like the NMT tags, the electronics in the Lotek tags were housed in a cylinder – made from transparent polycarbonate for Lotek, stainless steel for NMT[1] (the Zelcon and WLC tags were embedded in epoxy resin). The end of the case was sealed with a removable end cap fitted with an O-ring. In case of flooding of the cylinder, Lotek were confident that the data could still be retrieved from the non-volatile RAM. The 1 Mb of memory was sufficient for 1.9 y of data collected at 4 minute intervals, which, though not as much as we would have liked, was still acceptable. Unlike the other three tag designs that had the light sensor on the end of a stalk, the light sensor in the Lotek tag was inside the polycarbonate cylinder, and hence was only suitable for external application. The tags supplied by overseas manufacturers were more than twice as expensive (~ A$2500 each) as the original Zelcon tags. This limited the number of tags we could buy to less than 50 (we had planned to deploy 100). The experience of the tuna team, and our own testing of tags, made us reluctant to use only one type of tag, so we purchased only 30 Lotek tags. The tag housing was attached to a polycarbonate baseplate using 1 mm diameter titanium wire. The baseplate incorporated a nylon pin that was secured through the first dorsal fin in the same way as the external dummy tags. The tags carried a return address label, and notice of a A$200 reward. The following year, after successful testing of the modified WLC tags, we purchased the remaining tags (Mk 7's) from them. These tags were

[1] The electronics in the NMT tag are embedded in epoxy resin, then housed in the stainless steel cylinder. NMT have been aware for some time of the problems of moisture penetration through epoxy resin or polycarbonate that may occur during deployment in the ocean (K. Stoodley, Lotek Marine Technologies, pers. comm.)

inserted in the same way as the internal dummy tags. The specifications for the two types of tags used are given in Table 1.

Table 1. Specifications for Lotek (1997) and Wildlife Computers (1998) archival tags

	Lotek			Wildlife Computers		
Sensor	Range	Resolution	Accuracy	Range	Resolution	Accuracy
Depth	1000 m	<0.5 m	±5 m	0–800 m	0<55 m: 0.5 m[a] 55<165 m: 2 m 165<385 m: 4 m 385<825 m: 8 m	Not stated
Temperature	2–30° C	0.03° C	± 0.06° C	-20–50° C	0.2° C[b]	0.1–0.2° C
Memory	1 Mb			2 Mb		
Clock accuracy			not stated			± 30 secs y^{-1}

a: For a sensor rated to 1000 m the actual resolution is 0.5 m, but because the tag only stores 250 depth values, the user must tailor the resolution regime to suit individual needs.

b: The actual measured range is -20 to +50°C with 0.05°C resolution. However, as with the depth sensor, only 250 individual values can be stored, resulting in an effective 0.2° resolution in our case.

5.3 Geo-location methodology

Smith & Goodman (1986) discussed the estimation of longitude based on determining the time of sunrise and sunset (and hence the time of local solar noon) from light data collected by archival tags, and the feasibility of estimating latitude from water temperature and depth. Wilson et al. (1992) produced estimates of longitude based on the time of solar noon, but also estimated latitude based on day length. They used as a 'reference light level' the average light intensity when the sun was 5° below the horizon – the time when light intensity is changing most rapidly at the earth's surface. Hill (1994) used a similar method, although the reference light levels used were relative to light intensity at noon, and he considered the time at which light intensity changed most rapidly to be when the sun was 6° below the horizon. The method developed at CSIRO was similar to that of Wilson et al. (1992) and used the same astronomical formulae referred to by Hill (1994) and Klimley et al. (1994). The astronomical formulae predict the time of sunrise and sunset (or any specified zenith angle of the sun) for a given date and location; to derive position from the time of sunrise and sunset for a given day requires an iterative solution.

The geo-location software (GLS) required values for a number of parameters, which were specific to the type of tag used. We carried out a series of experiments to derive these estimates and to establish the accuracy of the method (Appendix B).

5.3.1 Longitude estimation based on light

Longitude is based on estimating the time of solar noon, the mid-point between dawn and dusk on the daily light curve. The time of local solar noon relative to Greenwich provides the longitude estimate. Every hour of difference is equivalent to 15° (360°/ 24 hours) of longitude. The time of dawn and dusk is based on average light levels at the time when light is changing most rapidly, as large changes in light are associated with only small changes in time. Mariners navigating above water can observe the times of sunrise and sunset directly, and use the mid-point of these times to estimate local solar noon. However, this estimate is inherently less reliable than observing the time of local solar noon directly (using a sextant) because the time at which we see the sun reach the horizon is more heavily influenced by variations in the earth's atmosphere. Because the light rays from the sun are bent as they enter the atmosphere, we see the sun reach the horizon at dawn before it is actually there. The extent of this refraction varies with temperature and pressure and limits the accuracy of observing sunrise and sunset to ± 2 minutes (Hill 1994). This problem becomes worse at high (>70°) latitudes. Since an error of 1 minute equates to 0.25° of longitude, it is unlikely that daily longitude estimates based on observing the time of sunrise and sunset (assuming that there is no cloud obscuring the horizon) above the surface can ever be better than ± 0.25–0.5° (approximately 20–40 km at 35° latitude). Below the surface of the ocean, where the altitude of the sun must be inferred from the intensity of light, the time at which light reaches the pre-determined level will also be influenced by depth, cloud cover and water clarity, and the resulting errors in longitude will be greater.

5.3.2 Latitude estimation based on light

The difficulties of estimating latitude based on day length have been long recognised (Klimley et al. (1994), and are the reason why with pelagic fish such as tunas that spend time at the surface, latitude is estimated by comparison of water temperatures measured by the tag and sea-surface temperatures measured by satellites. The problem with light-based latitude estimates is that the time at which the sun rises or sets is based on pre-determined average light levels, and is subject to the vagaries of weather. Relatively small differences in day length can, depending on the time of year and the latitude of the fish, blow out to errors of many degrees. At times near the equinoxes, where there is very little variation in day length with latitude, it is not possible to derive meaningful latitude estimates based on day length.

There have been recent promising developments – software developed by WLC uses the slopes of the dawn/dusk light curves, rather than day length, but it has not yet progressed beyond the developmental stage.

5.3.3 Dive-based estimation of longitude

At times the sharks were diving to 500–600 m each day and ascending at night, so there was no response from the light sensor. Boggs et al. (1999), faced with similar problems in deep-diving pelagic fish used dive behaviour as a substitute for light data, on the assumption that the fish was responding to changes in light intensity. For one fish we derived the time at which the sharks reached a particular depth – 250 m (instead of the time at which they reached a particular light level) in the morning and evening and estimated local solar noon (and midnight) from the mid-points.

5.3.4 Latitude estimation based on maximum daily depth

For much of the Australian south coast we have, fortuitously, an alternative method of estimating latitude. Along this coast, except in the east around Tas, the isobaths run roughly east-west. If we could be confident that the sharks were close to the bottom, we could use the maximum daily depth in conjunction with the estimate of longitude to search a bathymetric data set for matching depths along the given line of longitude. Examination of depth plots from the recovered tags indicate that for much of the time when the sharks are in shallow water (<200 m), there is often a pattern of nightly ascents from a relatively constant baseline. When they are in deeper water the baseline disappears, but the depth still provides an estimate of the most northerly latitude consistent with the longitude. A digital data set was available for southern Australia from the Australian Government Survey Organisation, with representative depths on a 0.5 minute (approximately half-mile) grid. Software was developed that searched along the estimated longitude for depths (and hence latitudes) that matched the deepest daily depth reached by the shark. If more than one position matched the depth, the program attempted to locate the latitude closest to the estimate for the previous day, but variation in the latitude estimates defeated it, and as a result many points were located on the coastline. Our remedy was simply to have the software choose the most southerly position, although this is recognised as only a temporary solution.

5.3.5 Position outliers

Dealing with position outliers is a problem. Visual inspection of the light data for suspicious days will often reveal the reason for unusual position estimates, but simply rejecting unusual estimates without an objective basis was justifiably criticised by Welch & Eveson (1999). We tried two approaches: curve fitting through longitude and latitude estimates to reject points lying outside confidence bands, and calculating weekly median positions.

5.3.6. Tagging protocol

Sharks were captured during commercial fishing trips using longlines and gillnets set on the bottom. Only specimens that were in a lively condition were tagged. If there was doubt about the condition of the shark, it was kept under observation either in a tank with flowing water, or towed gently behind the boat. Sharks were measured (total length, TL and girth at the origin of the first dorsal fin), sexed, tagged and released.

6. RESULTS

6.1 Dummy tagging

A total of 243 school shark were tagged in the dummy tagging experiment (Table 2). By mid-1997, the overall recapture rate was 16%, well above the 10% we had set as a minimum criterion to proceed with the use of real archival tags. The recapture rate for the internal tags was higher (21.7%) than for the external streamlined and block tags (16.3% and 11.4%, respectively). Although the results favoured internal tags, at the time of purchase there were none of these available that we considered suitable for our application. By August 1999, the overall recapture rate had risen to 19.3% (Table 2), with 27.5% of internal tags being returned. Differences in return rates between the two tag types were not significant at the 5% level (χ^2= 4.35, 2 df, p = 0.114), but indicated that internal tags were preferable to external ones.

Table 2. Results of the dummy-archival tagging experiment on school shark, *Galeorhinus galeus,* up to August 1999.

Tag type	Number released	Number recaptured	Percent recaptured
Internal	69	19	27.5
External streamlined	86	15	17.4
External block	88	13	14.8
Total	243	47	19.3

6.2 Archival tag releases and recaptures

6.2.1 South Australian releases

While it had been intended to concentrate the archival tagging on pregnant sharks, the realities of fishing dictated otherwise. Catches of school shark were small, and very few were pregnant. In SA in October-November 1997, 23 females (125–165 cm TL) and 7 males (131–141 cm TL) were tagged with Lotek external tags. The first 15 releases, caught in gillnets, were made in shallow water (40–100 m) in the Great Australian Bight (GAB) (Fig. 1). The fifteen longline releases were made at the edge of the shelf, in water 200–350 m deep, off Beachport, SA.

In the 2.5 y following the releases, there have been nine recaptures (30% recapture rate). Six of them were from longline releases and three from gillnet releases. Two fish were at liberty for only 8 and 23 days, another three for 4 months, two for 10 months and two for 17 months (Fig. 1). In addition one shark was recaptured with the tag base plate still attached to the dorsal fin, but missing the archival tag.

Fig. 1. Release and recapture positions for school shark tagged with Lotek external tags.

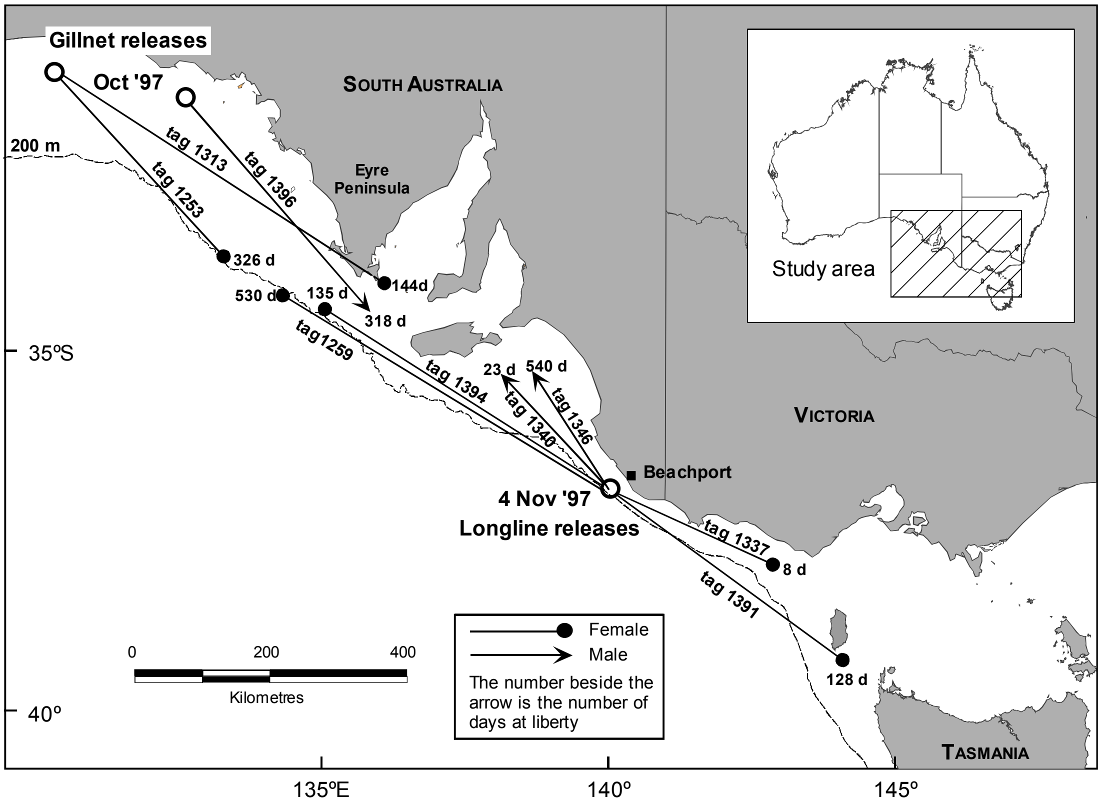
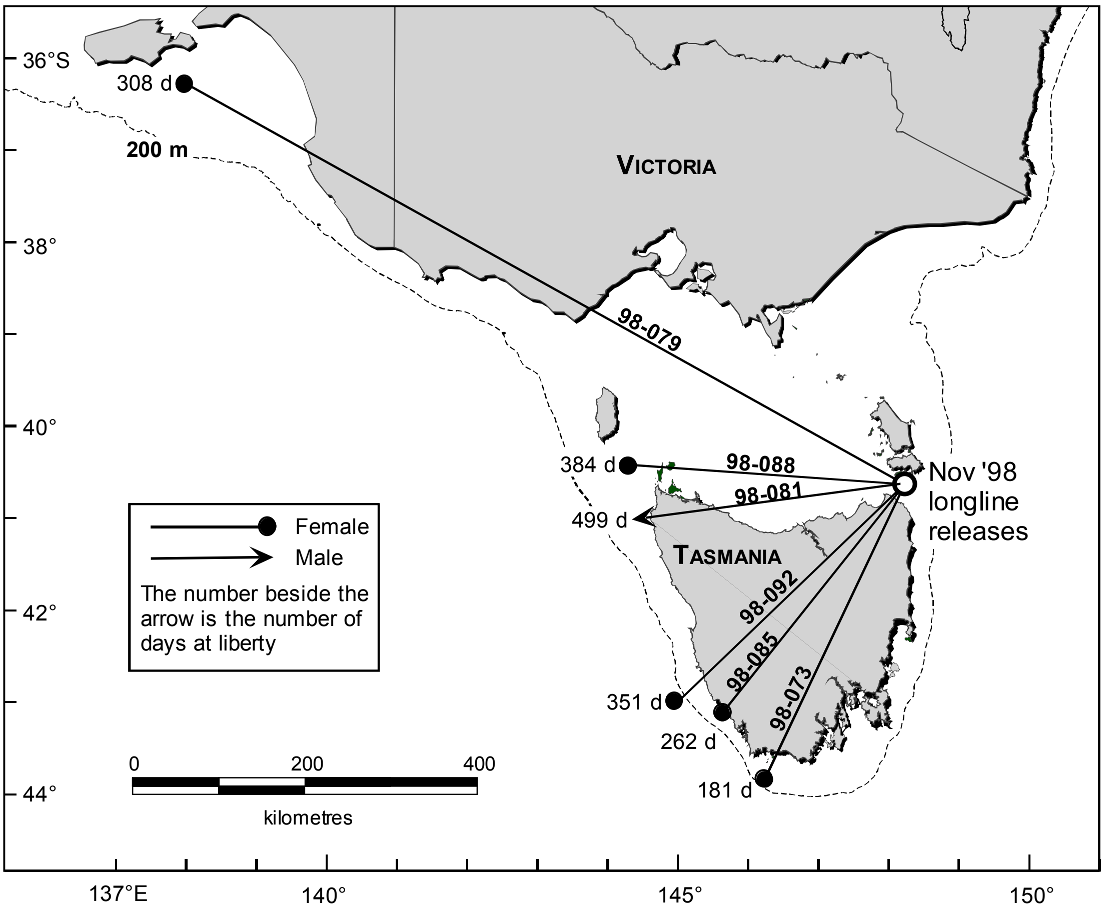


Fig. 2. Release and recapture positions of school shark tagged with Wildlife Computer internal archival tags.



6.2.2 Tasmanian releases

In November 1998, 16 school sharks (10 females 126–148 cm, 6 males 126–153 cm TL) caught on a longline, were tagged with Wildlife Computers internal tags in Banks Strait, Tas. To date (May 2000) 6 of them, at liberty from 6 to 16 months, have been returned – 37.5 % (Fig. 2).

A summary of the recapture data is shown in Table 3.

Table 3. School shark recapture data

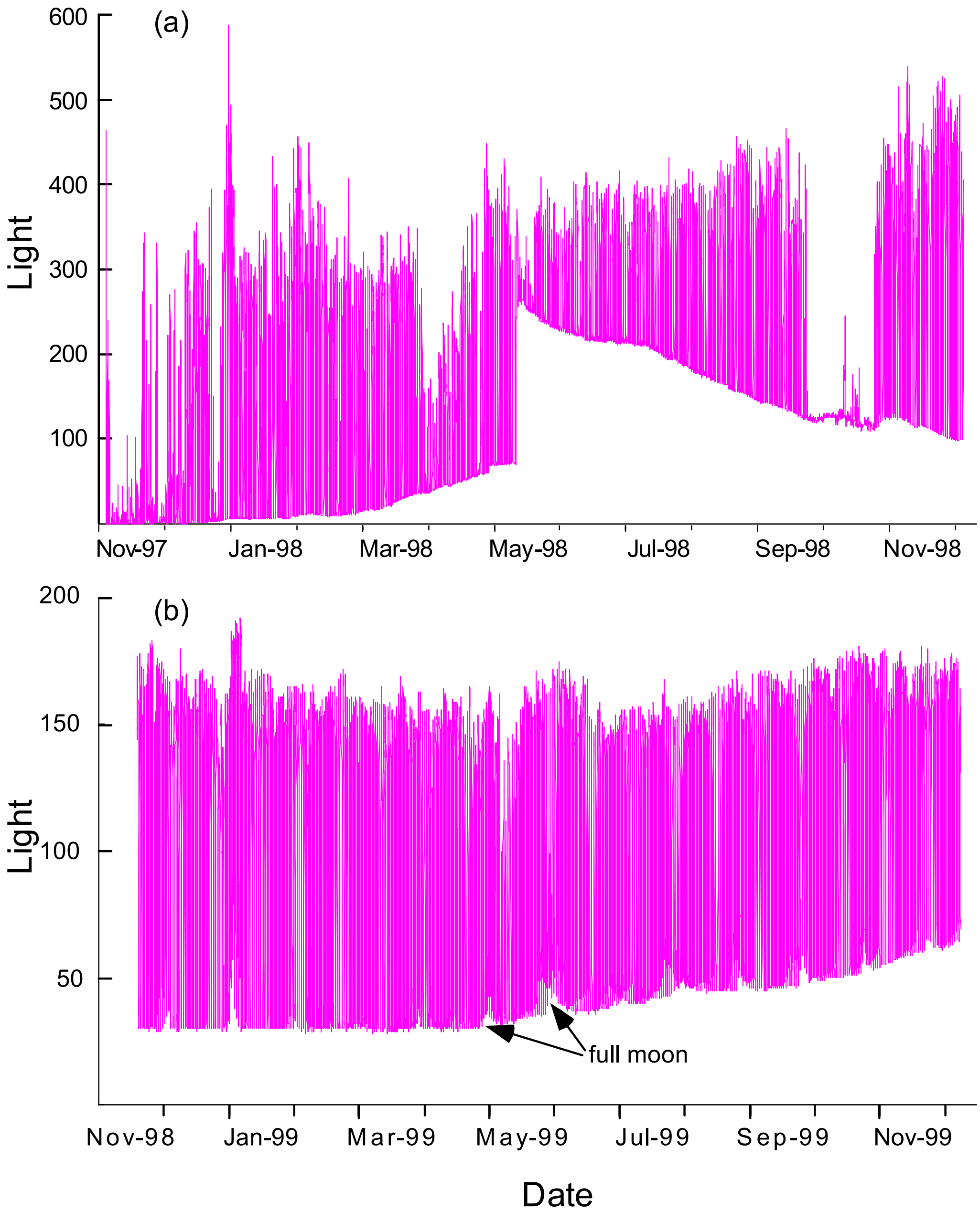
Tag no.	Tag type	Release locality	Sex	TL (cm) at release	Release date	Recapture date	No. months at liberty	No. months of data
1337	Lotek	Beachport SA	female	153.5	4-Nov-97	12-Nov-97	0.3	0.3
1340	Lotek	Beachport SA	male	131.0	4-Nov-97	27-Nov-97	0.8	0.8
1313	Lotek	GAB	female	146.0	18-Oct-97	11-Mar-98	4.7	4.7
1391	Lotek	Beachport SA	female	128.6	4-Nov-97	12-Mar-98	4.2	4.2
1394	Lotek	Beachport SA	female	150.7	4-Nov-97	19-Mar-98	4.4	4.4
1396	Lotek	GAB	male	138.3	25-Oct-97	8-Sep-98	10.4	8.4
1253	Lotek	GAB	female	136.1	18-Oct-97	10-Sep-98	10.7	10.7
1259	Lotek	Beachport SA	female	128.3	4-Nov-97	18-Apr-99	17.4	14.3
1346	Lotek	Beachport SA	male	130.5	4-Nov-97	28-Apr-99	17.7	13.0
?	Lotek		female			31-Mar-00		
98-073	WLC	Banks Strait	female	132.0	19-Nov-98	19-May-99	5.9	5.9
98-085	WLC	Banks Strait	female	140.0	19-Nov-98	8-Aug-99	8.6	8.6
98-079	WLC	Banks Strait	female	128.0	19-Nov-98	23-Sep-99	10.1	10.1
98-092	WLC	Banks Strait	female	153.0	19-Nov-98	5-Nov-99	11.5	11.5
98-088	WLC	Banks Strait	female	151.3	19-Nov-98	8-Dec-99	12.6	12.6
98-081	WLC	Banks Strait	male	143.0	17-Nov-98	30-Mar-00	16.4	16.4
						Total	11.3y	10.5y

6.2.3 Performance of recovered tags

Three of the Lotek tags failed after periods of 255–436 d, presumably as a result of a voltage leak observed in the high impedance light circuit, which resulted in the light signal failing to return to zero at night, effectively erasing any low light signals. This problem emerged after periods of 1–7 weeks, and usually became progressively worse, although occasionally it was more erratic (e.g. tag 1346, Fig. 3a). Entry of minute amounts of water vapour, apparently not through the O-ring seals, is thought to be the cause of the voltage leak. Lotek tags now incorporate a conformal coating to the circuit board, and the voltage leak problem appears to be solved (K. Stoodley, Lotek Marine Technologies, St. John's Newfoundland, pers. comm.). Curiously, most of the WLC tags, which are fully embedded in epoxy, also showed signs of the same problem, but to a lesser extent and only after 5–9 months of deployment (Fig. 3b). In addition, it did not result in premature failure of any of the WLC tags. Providing that the artificially raised light threshold was less than the reference light levels used, it caused no problems with the GLS. However, it did cause problems if the fish were deep, so that during the day the light signal increased very little, or not at all, above the raised threshold value. WLC are phasing out the MK 7 tag, and a new model is under development.

Some of the WLC tags had a problem with drift in the pressure sensors, being in error by as much as 16 m by the end of the deployment (in air, after recovery the depth should be close to zero). This was corrected for but relied upon the assumption that the drift was progressive through the deployment. This problem is presumably caused by curing of the flexible sealant, although reaction with body fluids may also be involved. In school sharks the translucent sealant over the pressure transducer developed a white appearance in places, and in southern bluefin tuna the sealant around the base of the umbilical stalk has been observed to soften. Another correction that was required was to account for drift in the tag's clock. No accuracy was specified for the Lotek tag: the clock error ranged from 38 sec fast (in 182 d) to 11 min 48 sec slow (576 d), and in one tag (1396, see section 6.8.1) the clock had stopped prior to recovery. This was particularly disappointing, as the longitudes generated for tag 1396 meant either that the fish was in New Zealand, or that the clock had gained several hours. The accuracy of the WLC clocks was much better: they ranged from 22 sec (407 d) to 1 min 55 sec (516 d) slow c.f. specified value of ±30 sec y^{-1}. The WLC tags incorporate correction within the tag to account for the effect of temperature on clock speed. However, occasional problems with clock accuracy in WLC tags have been experienced by other investigators. In a mooring experiment from August 1998 to August 1999 (353 d) off Hawaii one WLC tag was 2 h 22.4 min fast, although two companion tags were only 2.3 to 2.6 min slow. Two NMT tags on the same mooring were 5 secs slow and 59 secs fast (M. Musyl, Uni. Hawaii at Manoa, 2570 Dole St Honolulu, HI 96822, pers. comm.).

Fig. 3. Voltage drift in light sensor circuits: a – Lotek tag 1346; b – WLC tag 98-088.

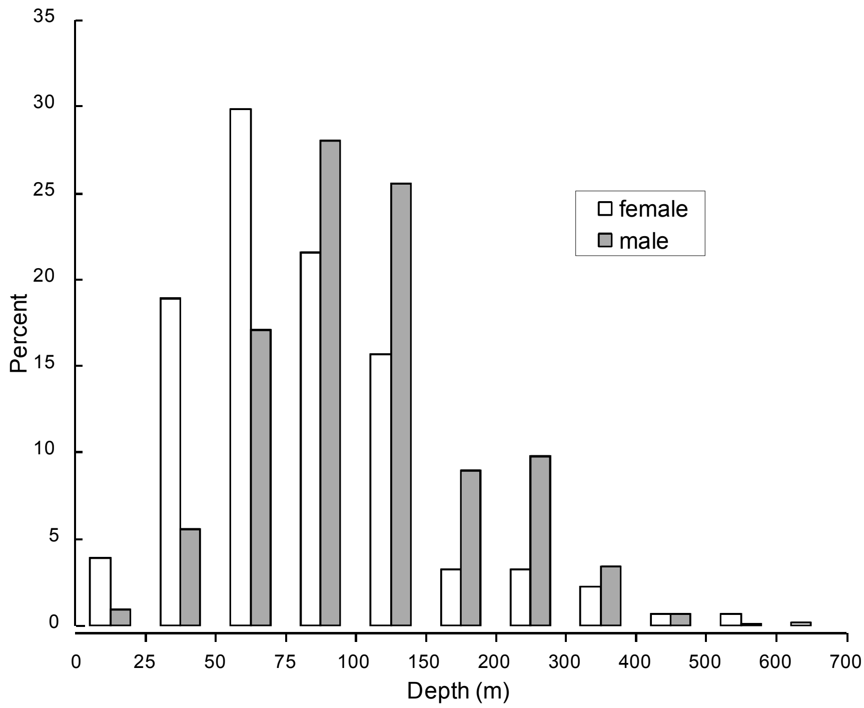


The temperature data used in this report was the raw output from the tags, as no re-calibration of the temperature sensors has yet been carried out. In the WLC tags that were set up to measure internal as well as external temperature, there was generally no difference between the two, except for slight lag effects when water temperature changed rapidly. However, in one tag there was a progressive drift in the difference between the two temperatures, amounting to 0.6°C after 6 months. This emphasises the need to have the sensors re-calibrated after the deployment, and to have a method of correcting the temperature data if necessary. Recovered tags can be returned to the factory for re-calibration and replacement of the batteries. The construction of the Lotek tags makes it simpler to replace the batteries (in the WLC tags the battery embedded in epoxy resin at the end of the tag has to be sawn off and the connection exposed), although Lotek now offer the option of embedding the batteries because of breakage of the connecting wires during severe deployments on moorings (P. Eveson, CSIRO Marine Research, Hobart Tas 7000, pers. comm.) or on seabirds (A. Terauds, Nature Conservation Branch, DPIWE, PO Box 44a Hobart Tas 7001, pers. comm.). The cost of the refurbishment is currently US$250 –260 (WLC and Lotek respectively.

6.3 Depth distribution

Overall, school sharks spent 91% of their time at depths <200 m. However, there appeared to be a difference between the sexes, with females spending 93% and males 86 % at depths <200 m. (Fig. 4). The modal depth for females was 50–75 m, for males 75–100 m. The tendency for the males to spend more time at depths below 150–200 m was not reflected in the maximum depth (657 m) which was reached by a female

Fig. 4. Depth distribution by sex of archival tagged school sharks.



The daily minimum and maximum depths are plotted in Fig. 5 for the SA releases, and Fig. 6 for the Tas releases. There were few similarities between fish in the timing of their movement into deep water. In sharks 1346 and 1259 released in deep water (Fig. 5), there was some indication of an annual pattern in that the fish were also in deep water at the same time the following year.

Fig. 5. Daily depth-range for seven school sharks at liberty for more than one month released in the GAB and at Beachport, SA.

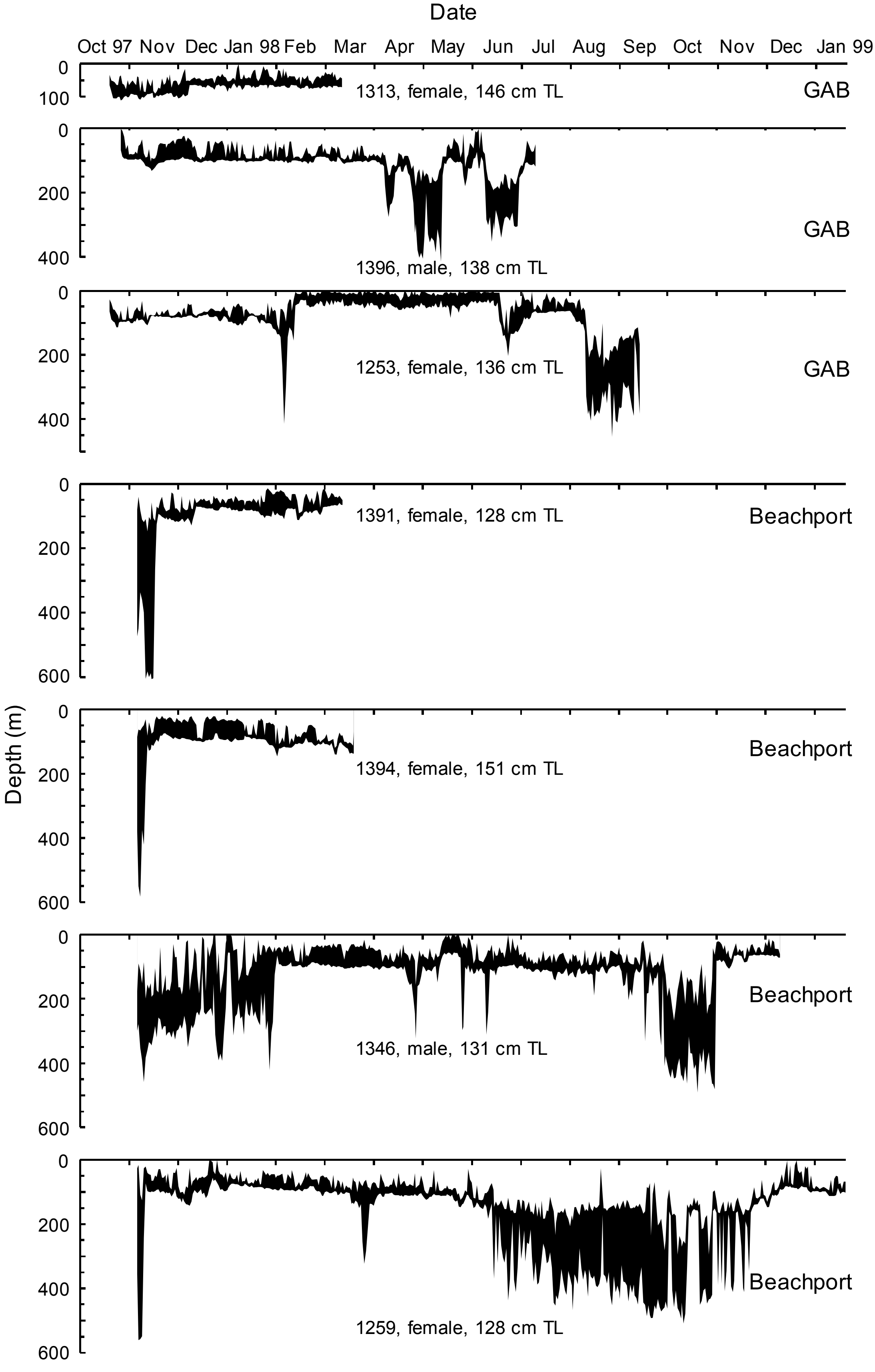
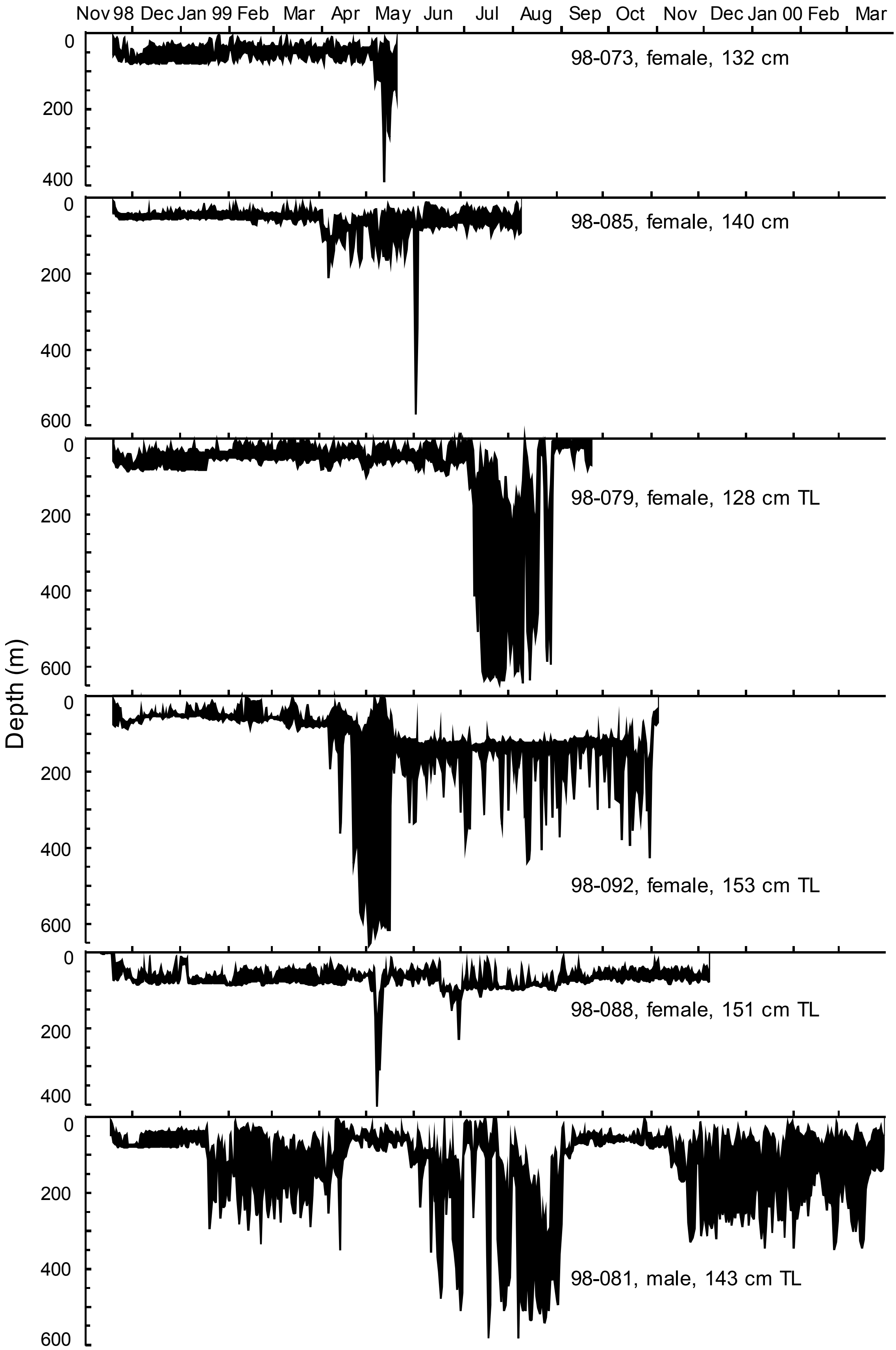


Fig. 6. Daily depth-range for six school sharks released in Banks Strait, Tas.



6.4 Diving behaviour immediately after tagging.

The diving behaviour of many of the tagged sharks was atypical after release, particularly for those caught by gillnet. The condition of the tagged sharks was least certain for many of the gillnet releases and several of them were towed behind the boat or placed in a tank with flowing water to revive them. One fish that caused the tagger considerable dismay appeared to be lively, but when released floated away upside down. It (shark 1396) was subsequently recaptured. This fish had atypical diving behaviour for more than a day after release, staying near the surface for much of the time during the day (Fig. C4a). Shark 1253 (Fig. C5a) which was swimming slowly at the surface when released, spent the next 5 hours during the middle of the day near the surface, interspersed with dives to about 60 m. Shark 1313 also spent some time near the surface after tagging, (Fig. C1) but it was in a lively condition when released. Some sharks caught on longlines also showed unusual diving behaviour for up to 1–2 days after release (e.g. shark 98-073 Fig. C8, shark 98-081 Fig. C13a).

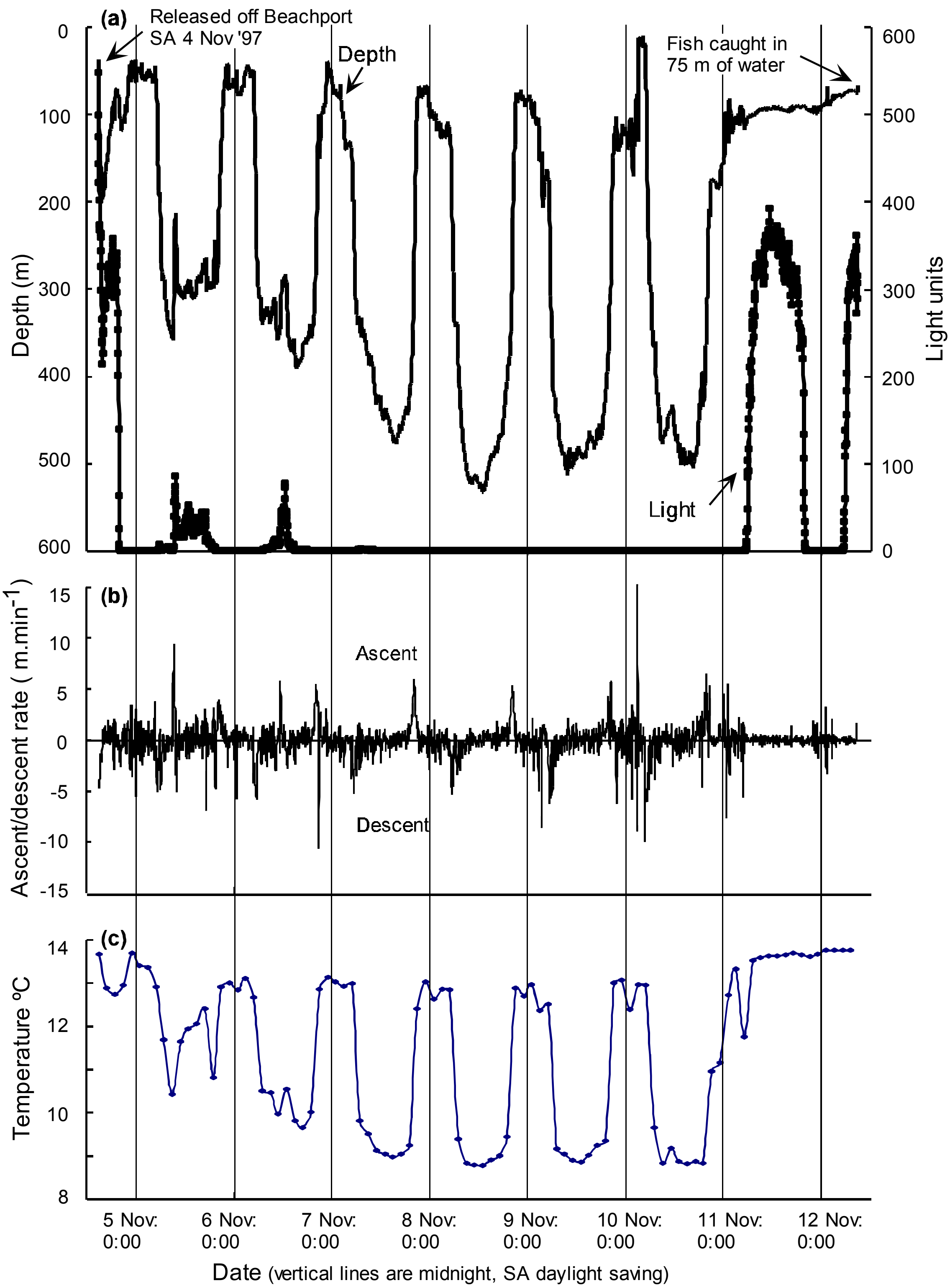
6.5 Patterns of daily diving behaviour

The monthly depth plots for all recaptures except sharks 1337 and 1340 are shown in Appendix C, Figs. C1–C13. They show a wide variety of depth patterns.

The first recapture, that of tag 1337, released in deep water off Beachport, occurred only 8 days after it was released. The depth record showed a dramatic pattern of diving behaviour (Fig. 7a). The light sensor readings for the first two days showed that it was diving during the day but as the depth increased for the next four days the light signal disappeared. It reached depths of up to 530 m during the day, and at night rose to within 37 m of the surface, except for one night when it rose to 6 m. For the last 2 days the depth was 75–100 m, and it was apparently on the bottom since it was caught in 75 m.

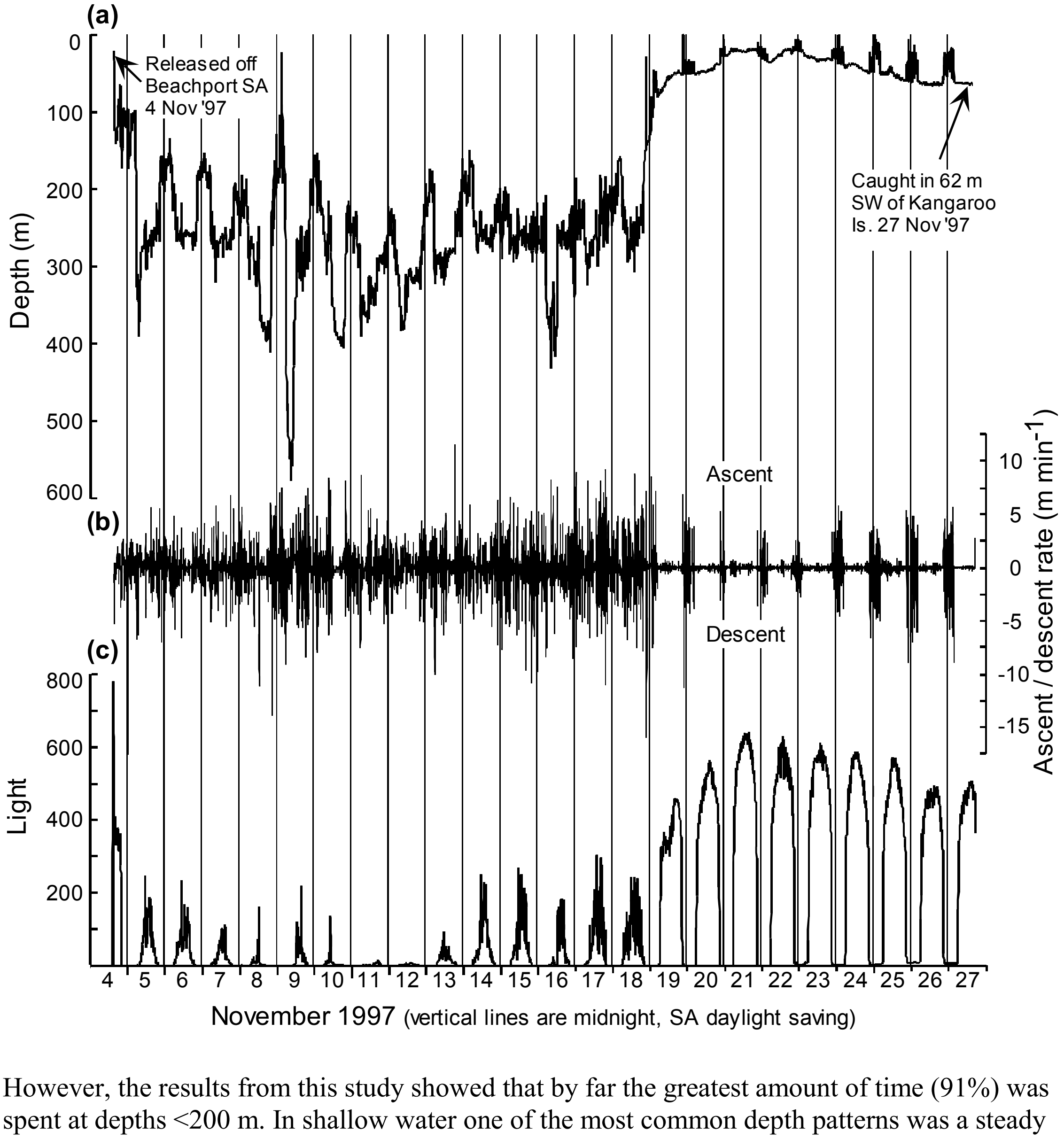
Subsequent recaptures that showed this type of regular deep-diving extended the maximum depth reached to 657 m but also showed that this diving pattern was relatively uncommon – only 6 of the recaptures showed this behaviour and the duration was generally short. Four of them, tagged off Beachport (sharks 1337, 1391, 1394 and 1259, Figs. 7, Appendix C Figs. C2, C3 & C7a) showed this pattern for only 2–11 days after release in November 1997. Shark 98-092 showed this diving pattern from 27 April–16 May 1999, reaching depths of up to 657 m (Fig. C11a). Shark 98-079 showed this diving pattern for a longer period: from 15 July–10 August 1999 and from 13–19 and 25–28 August 1999 (Fig. C10b). At the time of the full moon, in late July, this shark did not ascend as far towards the surface. Whether the fish reach the bottom during their daytime descents is unknown, although in one case it appeared that the depth may have been limited by the bottom (shark 1391, early November 1997, Fig. C2).

Fig. 7. School shark tag 1337: a – depth and light profiles (4 minute intervals); b – vertical movement rates; c – temperature profile (2 h intervals).



The second recapture, tag 1340, at liberty for 23 days, showed an erratic diving pattern (Fig. 8a) that subsequent recaptures proved to be more common than the regular deep-diving. For the first two weeks this shark was generally deeper during the day, reaching depths of 280–575 m, except on the first day when it descended to only 175 m. At night it was in depths of 100–220 m, except for one night when it rose to 20 m. Examples of similar depth patterns are shown by shark 1396 in June 1998 (Fig. C4b), shark 1253 in August–September 1998 (Fig. C5b) and shark 1346 for extended periods from November–December 1997 (Fig. C6a).

Fig. 8. School shark tag 1340: a – depth; b – vertical movement rates; c – light.



However, the results from this study showed that by far the greatest amount of time (91%) was spent at depths <200 m. In shallow water one of the most common depth patterns was a steady depth during the day with ascents at night. Shark 1340 showed this for the last week (Fig. 8a), and most of the recaptures showed it at some stage during their time at liberty e.g shark 1394 (Fig. C3), shark 1396 (Fig. C4a) and shark 98-073 from December 1998 to January 1999 (Fig. C8). We think this depth pattern is convincing evidence that the sharks were swimming near the bottom, and ascending into the water column at night. The recapture depths given by the fishers support this.

The nightly ascents when the fish are on the shelf may be subject to lunar influence. Shark 1394 (Fig. C3) shows suppression of the ascents during the full moon from November 1997 to February 1998. Shark 1396 (Fig. C4) shows a similar effect. In contrast, during Jan 1998 shark

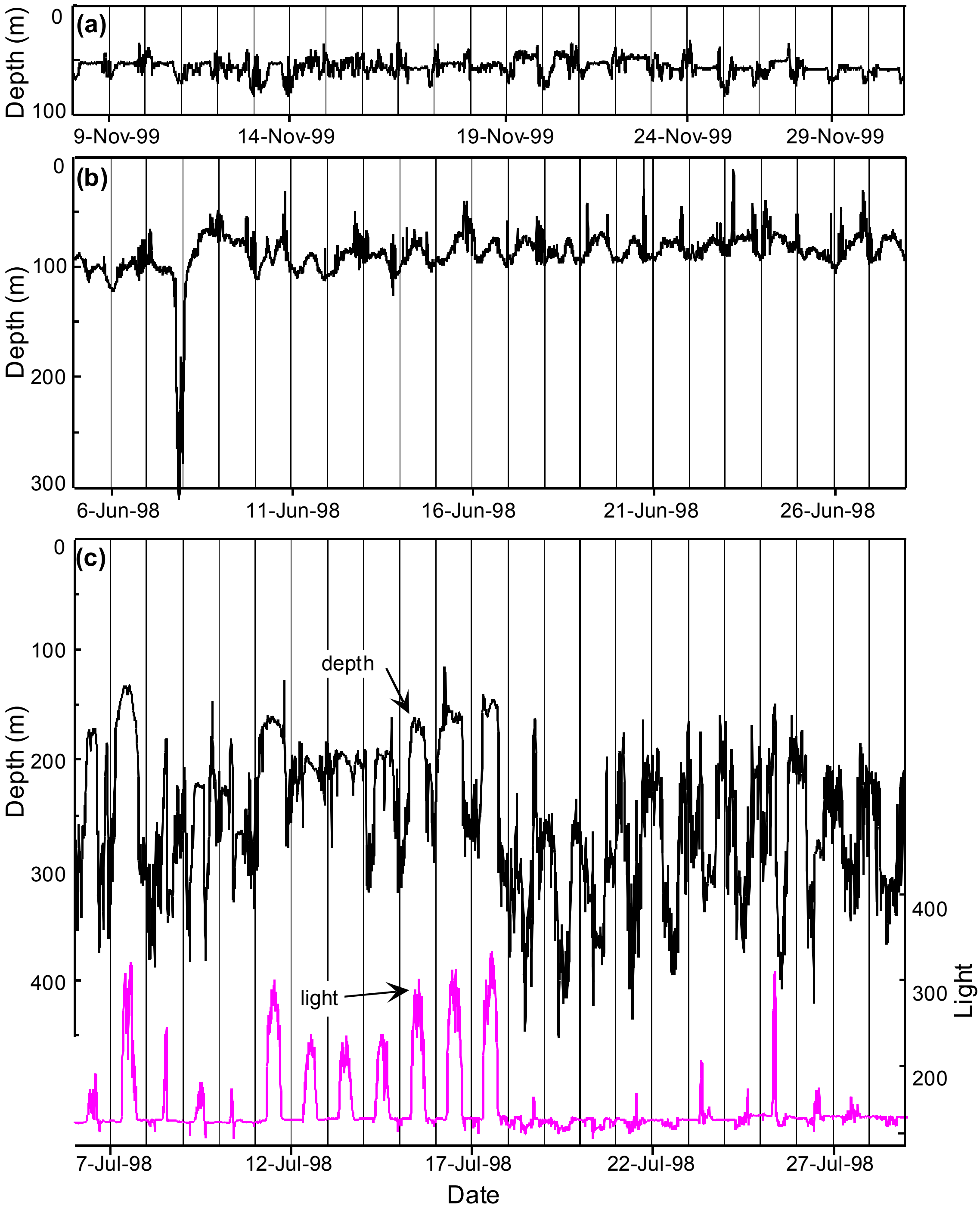
98-073 (Fig. C8) showed no suppression of the nightly ascents (from bottom depths of about 80 m), nor did shark 98-079 during this month (Fig. C10a). In deeper water, shark 1259 in August–September 1998 (Fig. C7b) also showed no suppression of the nightly ascents during full moon. However, in this case it appeared that the ascents were not into mid-water, but back to daytime bottom depths of ~ 150 m (notably on 16–17 August).

An alternative pattern in shallow water, of frequent but brief descents from a steady depth is shown by shark 98-092 from mid-May to September 1998 (Fig. C11a & b). The constancy of the depth at about 110–120 m for this entire period indicates to us that the fish was on the bottom, occasionally following the terrain down into depths of over 400 m. Most of the descents were made at dusk (42%) or at night (33%), with only 16% during the day and 9% at dawn. This fish made occasional brief ascents, nearly all at night. Another example of this type of behaviour, but this time with more frequent and much more prolonged descents, is shown by shark 1259 from August–November 1998 (Fig. C7b). This shark maintained a steady depth of ~150 m throughout this period, and descended during the day to depths of up to 500 m. There were periods, notably in October and November when the descents ceased, and sometimes the odd brief ascent (e.g. August 15–16, September 26–27). Both of these fish, although residing mostly on the shelf had access to deep water, implying that they were in areas near the shelf edge or near to canyons.

Another depth pattern seen in yet shallower water (~50–60 m) was where the fish spent the day on a 'plateau' before descending (but often only for ~10–30 m) at night. e.g. shark 98-088 in October–November 1999 (Fig. 9a and Fig. C12b) and shark 1313 in December 1997–March 1998 (Fig. C1). At times the depth during the day was remarkably constant (Fig. 9a, November 28–30), suggesting that the animal was inactive. Periods of constant depths were normally seen only on the day that fish were caught, when they were presumably dead in the net (e.g. shark 1253 Fig. C5b, shark 98-073 Fig. C8 and shark 98-085 Fig. C9). However, at depths over 55 m the resolution of the WLC depth sensor changed from 1 to 2 m (Table 1), so that minor changes in depth (or a tidal signal over a stationary animal) would not be detected. A variation on this pattern of being shallower during the day was shown by shark 1346 in June 1998 when it showed an almost sinusoidal pattern (Fig. 9b & C6). The spiky ascents indicate that it was following the bottom. There were also numerous periods in shallow water during which there was almost no vertical activity (e.g. shark 1394 March 1998, Fig. C3; shark 1259 January 1999, Fig. C7b; shark 98-092 December 1998, Fig. C11a and shark 98-081 September–October 1999, Fig. C13b).

Occasionally in deep water there were times when the sharks ascended during the day, rather than at night. Shark 1259 showed this pattern for several weeks in early July 1998 (Fig. 9c, C7b). However, the relatively regular depths occupied during the daytime in this initial period suggest the fish was following the terrain when it was more shallow (~150 m) during the day. In late July the fish ascended at night, but the irregular depths at both night and day suggest it was in mid-water.

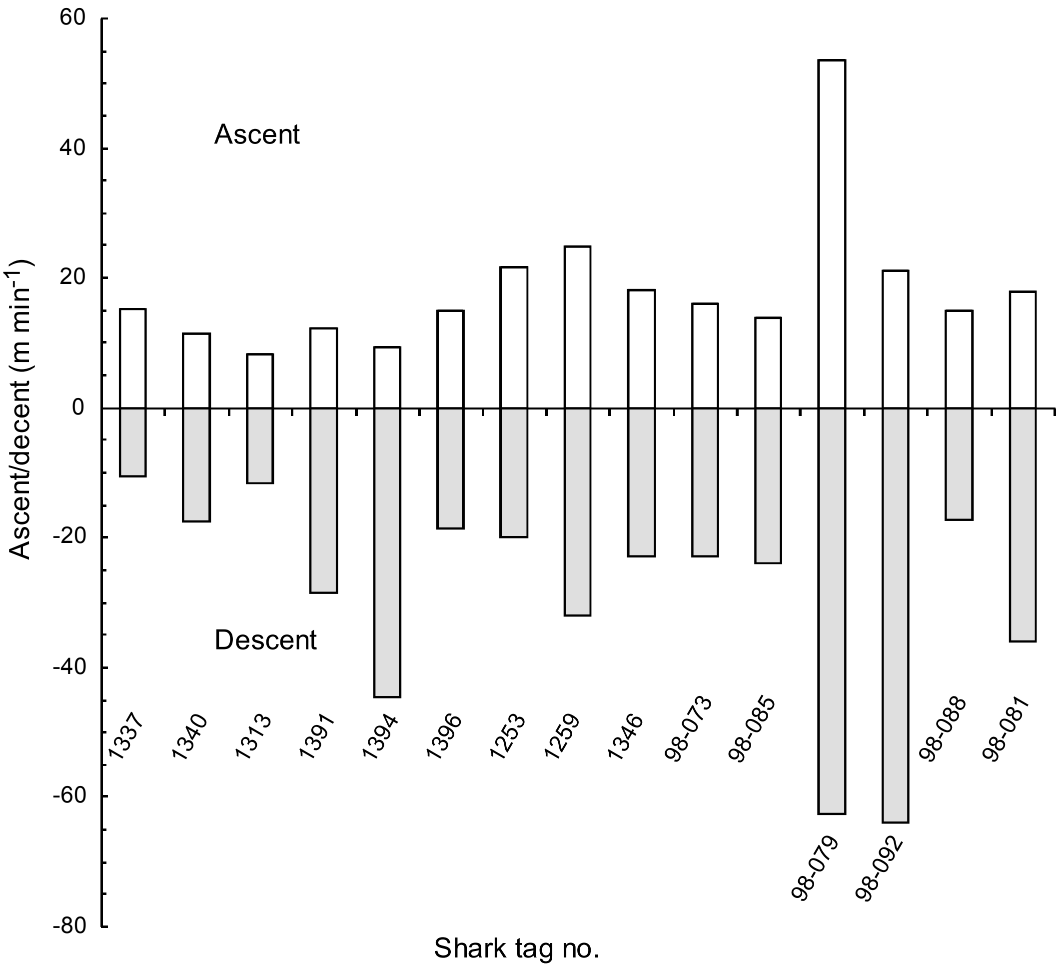
Fig. 9. Depth patterns for school sharks: a – shark 98-088 (vertical lines are midnight Eastern Standard Time); b – shark 1346; c – shark 1259 (vertical lines in b and c are midnight Central Time).



6.6 Vertical movement rates

For shark 1337 the rate of vertical movement was elevated at the times of ascent and descent in deep water, although there were also higher movement rates (up to 15 m min $^{-1}$) at other times (Fig. 7b). Shark 1340 showed a more irregular pattern in deep water, as would be expected from the depth profile, but in shallow water the vertical activity was restricted to the nightly ascents (Fig. 8b). The maximum vertical ascent and descent rates (depth difference between consecutive 4 minute readings / 4) for each shark are shown in Fig. 10. The greatest ascent rate was 53.5 m min $^{-1}$ (368–154 m), and the greatest descent rate was 64.0 m min $^{-1}$ (101–357 m).

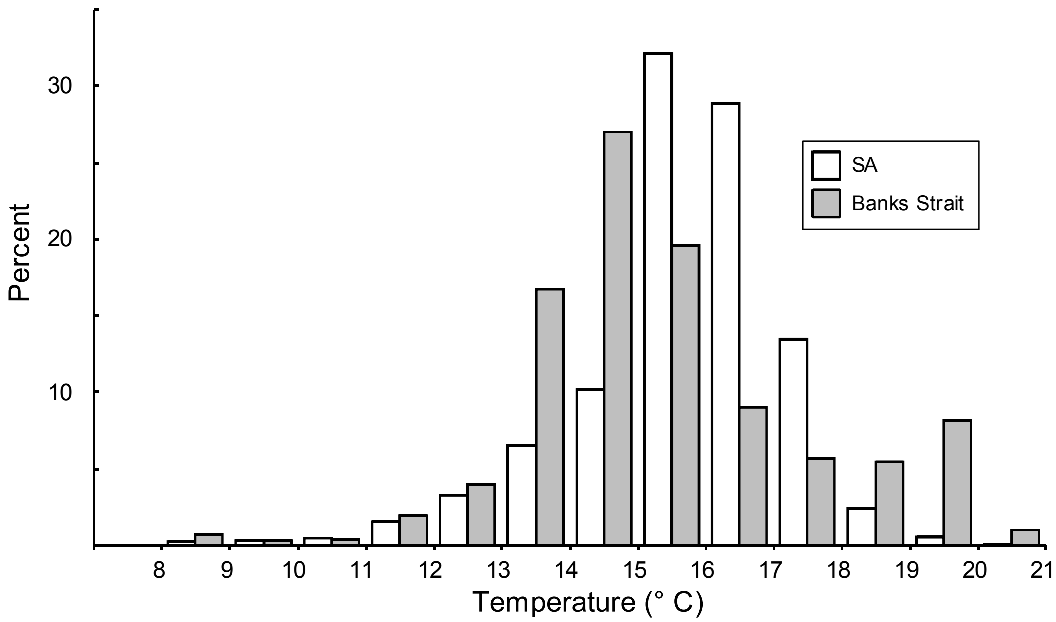
Fig. 10. Maximum ascent and descent rates for archival tagged school sharks.



6.7 Water temperature

Overall, the sharks spent 63% of their time in water between 13–16° C, and only 7% of their time at temperatures below this. Although the sharks released in SA tended to be slightly deeper than those released in Banks Strait, the temperatures they experienced tended to be slightly higher (Fig. 11). The greatest daily change in temperature was 8.0°C (18.3–10.3°C, 42–219 m) for shark 98-081 in February 1999. The depth of the sharks was the main influence on the water temperatures they experienced, which ranged from 7.5°C at 540 m in July 1998 (tag 98-079) to 21.0°C at 50 m in February 1998 (tag 1259). An example of how temperature affects depth is shown in Fig. 7c.

Fig. 11. Temperature ranges for archival-tagged school sharks.



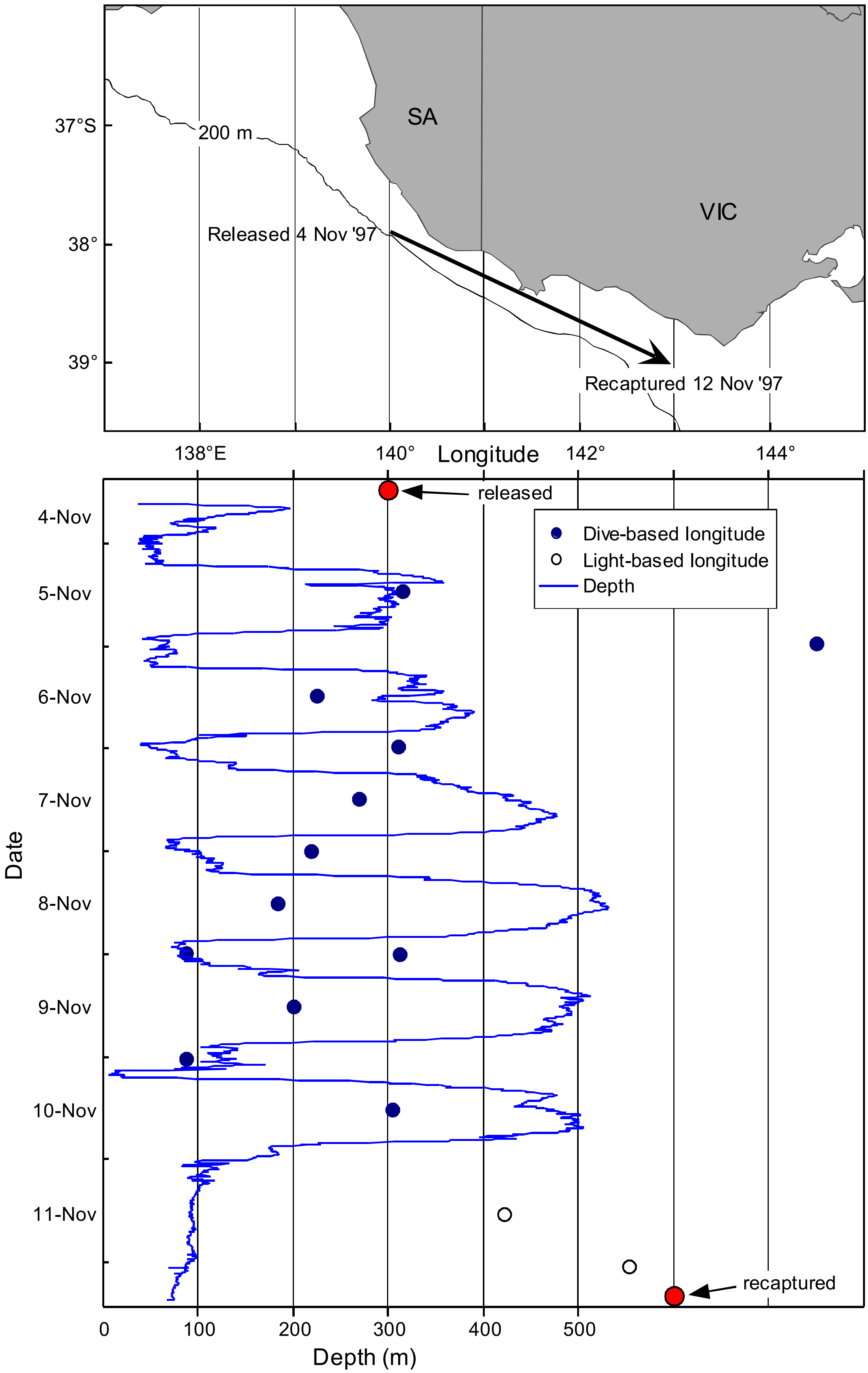
Some of the WLC tags were set up to record internal as well as external temperature. This data has not been analysed, but a preliminary inspection revealed no apparent difference between the two, except for slight lag effects when the water temperature had changed rapidly as the fish dived or ascended.

6.8 Geo-location

6.8.1 Recaptures from sharks tagged in SA with Lotek external tags

The first recapture, shark 1337, was at liberty for only 8 days. It had moved a straight-line distance of 284 km, an average daily distance of 37 km, the fastest ever recorded for a school shark in this region (about twice the maximum rate observed from conventional tagging (L. Brown, MAFRI, Queenscliff, Australia 3225, pers. comm.). Compagno (1984) gives a rate of 56 km d^{-1}, but the source of this information is not known. Shark 1337 was so deep during the day that geo-location based on light was only possible for the last day (Fig. 7). We derived an estimate of solar noon (dawn–dusk) on Nov 11, as well as the following 'solar midnight' (dusk Nov 11–dawn Nov 12) and the two corresponding longitude estimates. They were within 0.5–1.8° of the recapture longitude. We derived dive-based estimates of longitude for the remaining days (except for the first day when the fish did not reach the 250 m depth used to derive the time estimates). Because of the high movement rate for this shark, we assume it was moving east continuously, but the dive-based estimates do not reflect this (Fig. 12). The median of the dive-based longitude estimates was 139.7° (release–recapture longitudes 140.0–143.0)°, which was still encouraging as it indicated that even if the sharks spent considerable time in deep water, there were prospects of obtaining approximate longitudes for them. No attempt was made to estimate latitude based on depth, because for most of the time it appeared that the shark was in mid-water.

Fig. 12. Position estimates for school shark 1337 (female, 154 cm TL)



The second recapture, shark 1340, at liberty for 23 days, showed a daily diving pattern for the first two weeks, being deeper during the day than at night (Fig. 8), but the pattern was far less regular than for shark 1337, precluding dive-based estimates of longitude. Some light-based longitude estimates were obtained when the fish was deep, but they were very variable (121.6–151.6°E). We calculated the weekly median longitude which appeared to be robust to outliers, even in this extreme case (Fig. 13b). Both light and depth-based estimates of latitude were made, the former using particular reference depths (and their associated parameter values, Appendix Table A2) closest to the actual depth on each day. As expected, the results for the light-based estimates were more variable than the depth-based ones (Fig 13a inset).

Shark 1313, was at liberty for almost 5 months, which meant that changing reference depths to suit individual days (maximum daily depths ranged from 47 to 111 m) was impractical. The GLS was set to process the entire data set using a single set of parameter values. The longitude results (Fig. 14a) showed a steady movement east from its release position at 130.3°E in the GAB to about 137°E, over a 2.5 month period. It was caught in mid-March at 136.2°E. For this recapture we experimented with a regression approach to eliminating outliers. We fitted a 3rd order polynomial to the longitude data, and points outside an arbitrary ±1.5° either side of it were excluded from the map (Fig. 14b). There was still considerable scatter in the light-based latitude estimates, so the regression approach was extended to these estimates, with points outside ±2° excluded (Fig. 14d). However, the latitude trend shown by the regression in Fig. 14c is northward, whereas the physical realities of eastward movement in this part of the world dictate that the shark had to move southwards. The light-based latitude estimates at the beginning of the deployment were well south of the release position, but it only required a minor change in the specified value of the zenith angle to bring these north (all the parameter values for the GLS had been established in coastal waters near Tasman Island, and it would be expected that the optical properties of the water in the GAB would be different). However, all the points moved northward, and it did not change the fundamental problem with the trend in the light-based latitude estimates. As yet we have not found a solution to this problem, which meant that we had to rely entirely upon depth-based estimates of latitude for subsequent recaptures.

Shark 1391, at liberty for 4 months, moved east from Beachport to Tas. It reached longitudes of 144–145°E by the end of November, and stayed at these general longitudes until caught in mid-March. A 4th order polynomial was fitted to the longitude data (Fig. 15a) to eliminate outliers (> ±1.5° from the regression line). However, the depth-based latitude estimates (Fig. 15 b) are not reliable around Tas because the isobaths run north–south (a small variation in longitude results in a large change in latitude). At times (e.g March 1998, Fig. C2) the fish was in sufficiently shallow water that it could have been in Bass Strait, rather than the most southerly position chosen by the software.

The longitude estimates for shark 1253, at liberty for nearly 11 months, revealed problems with the regression approach to eliminating outliers – the longitude trend could not be modelled by a polynomial regression, but appeared to be well described by weekly median longitudes (Fig. 16b). The shark stayed in longitudes around 132°E from October 1997 until mid-January 1998, when it moved rapidly east (~ 6° of longitude in 4 weeks) settling at longitudes around 138°E for over 4 months. In mid-June it rapidly returned west, reaching 132° in the first week of July. It remained at this longitude for most of July before heading east again, although for most of August it was too deep (and with no regular dive pattern) to allow estimation of longitude.

Fig. 13. Position estimates for school shark 1340 (male, 131 cm TL): a – daily positions; b – daily and weekly median longitudes, plus depth.

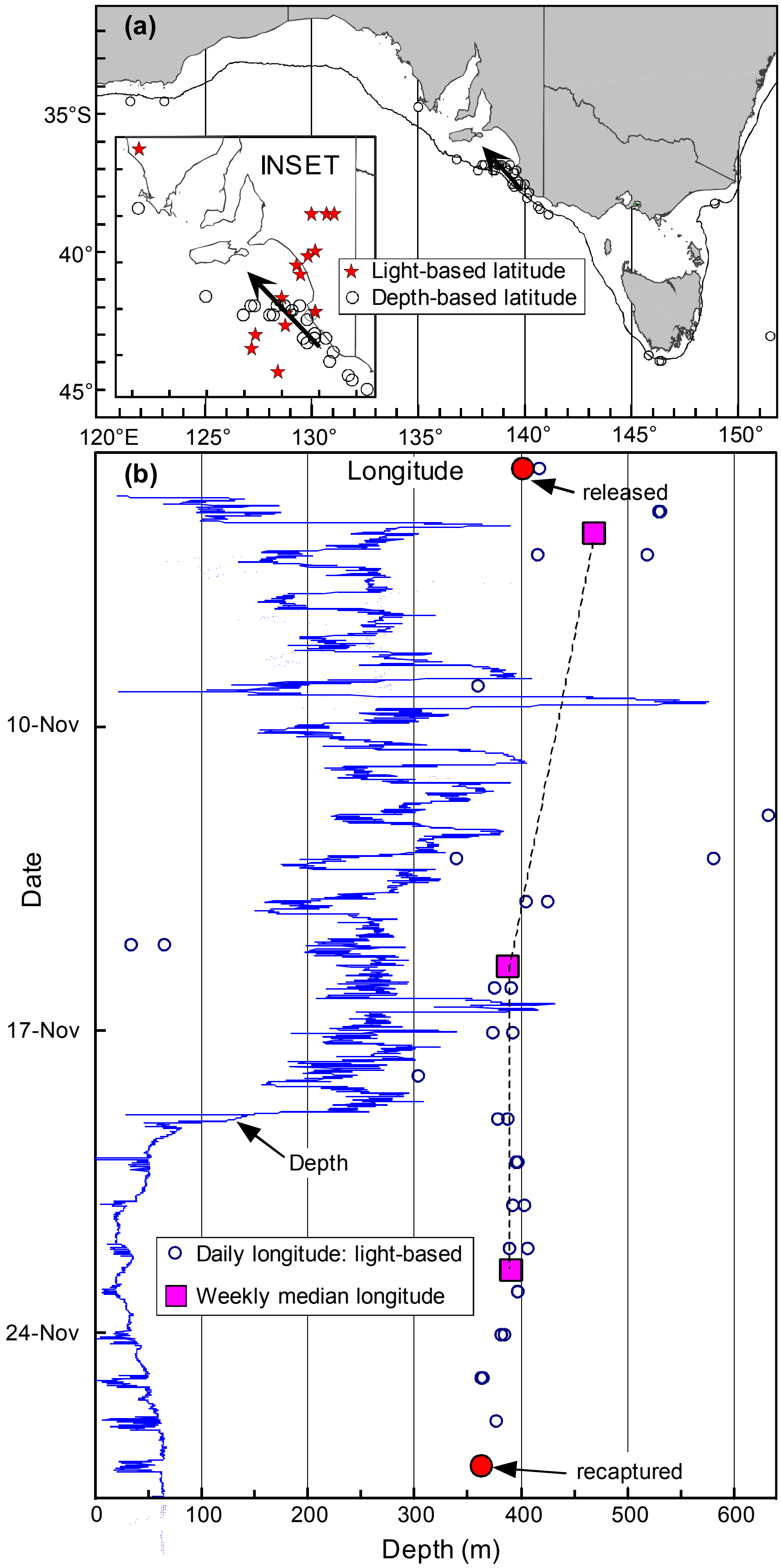
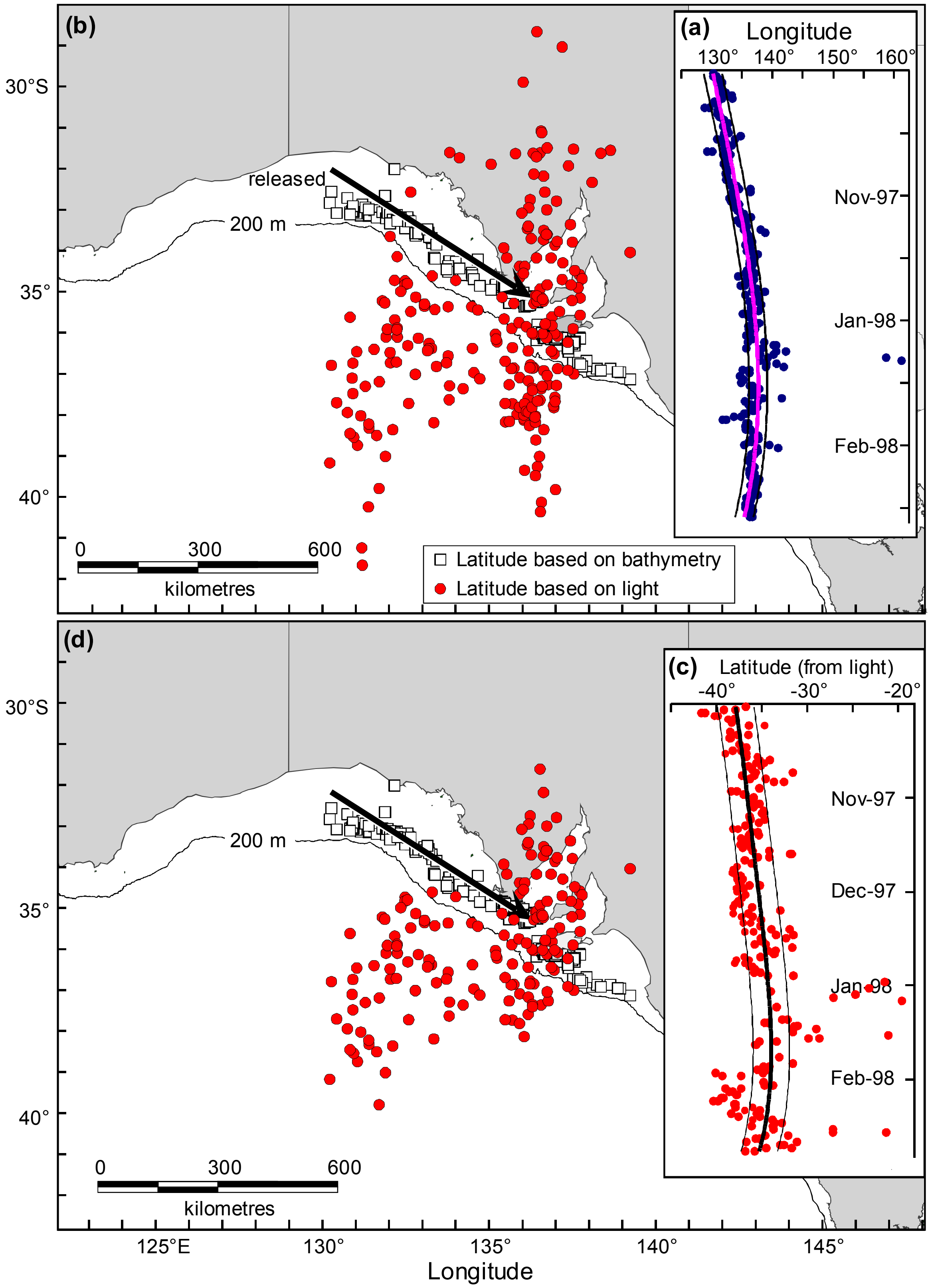


Fig. 14. Position estimates for school shark 1313 (female, 146 cm TL): a – all longitude estimates; b – longitudes outside ± 1.5° confidence bands excluded from map; c – light-based latitude outliers identified; d – light-based latitudes outside ± 2° confidence bands excluded from map.



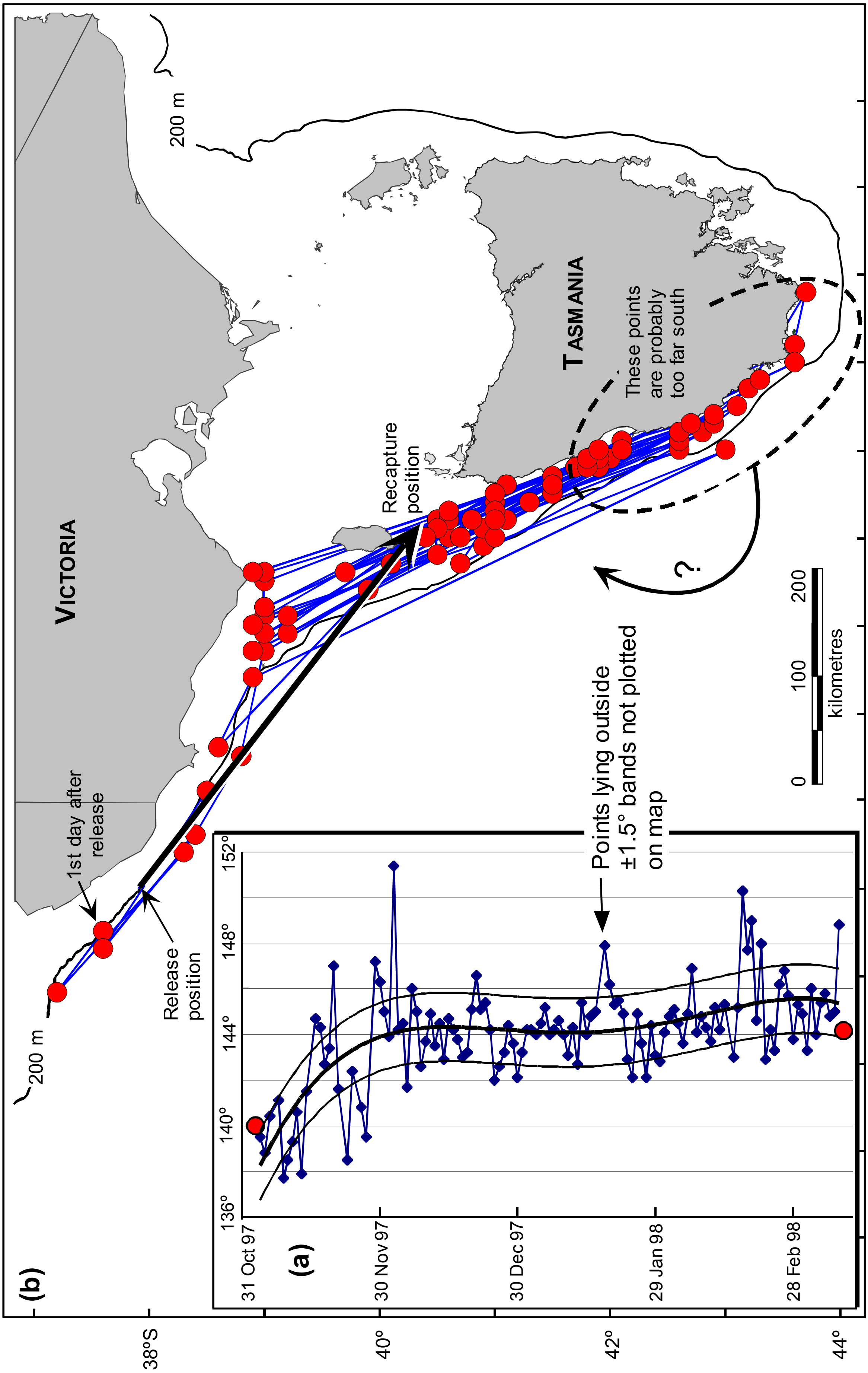
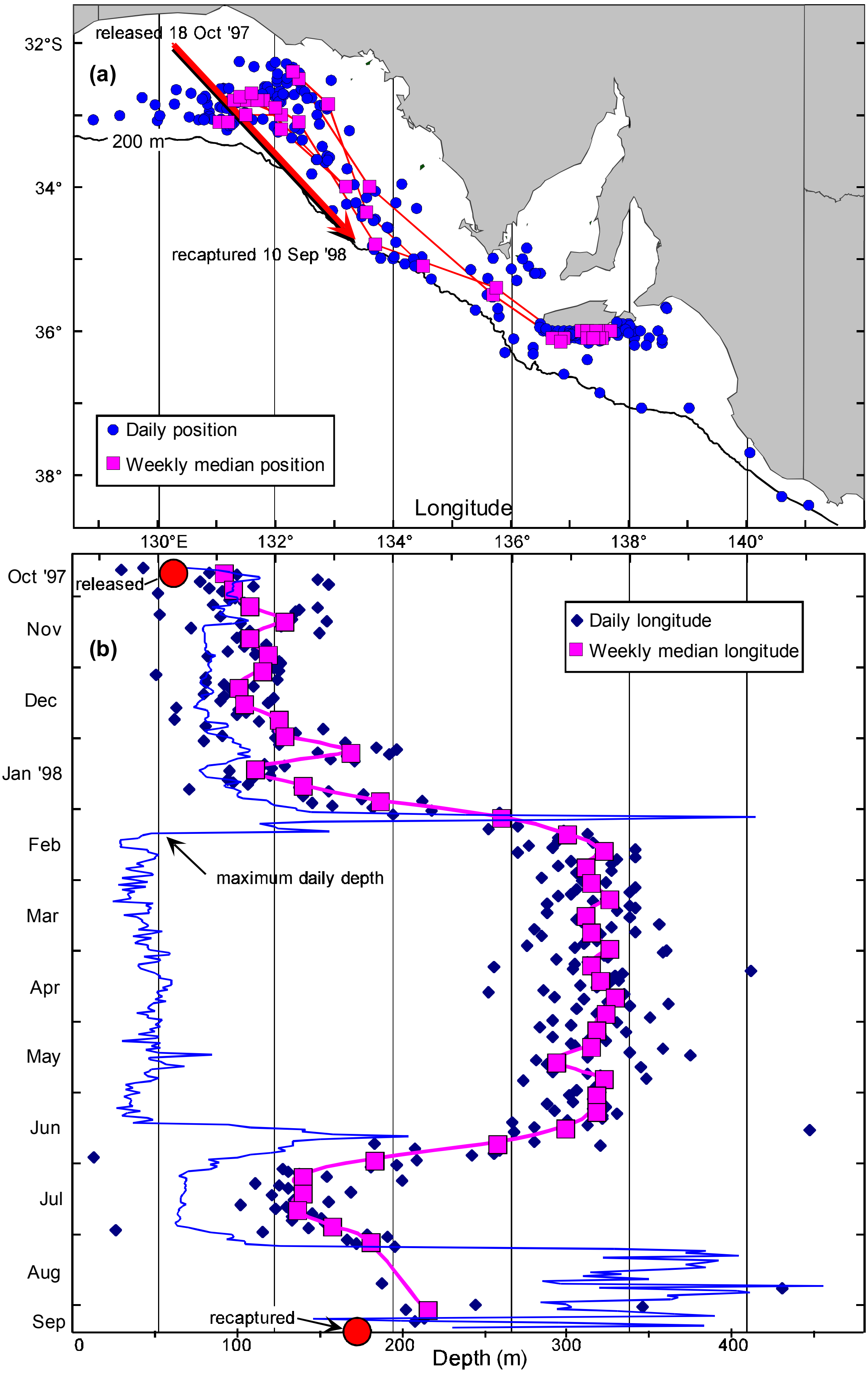


Fig. 15. Position estimates for school shark 1391 (female, 129 cm TL): a - all longitude estimates; b - longitudes outside ±1.5° excluded from map. Latitudes based on depth.

Fig. 16. Position estimates for school shark 1253 (female, 136 cm TL): a – daily and weekly-median positions; b – daily and weekly-median longitudes, and maximum daily depth.



One of the most intriguing recaptures was that of shark 1396, released in the GAB and recaptured to the east off the Eyre Peninsula (Fig. 1). When this tag was returned in September 1998, it was found that it had stopped recording on 7 July 1998. This was not unusual in the long-term Lotek recaptures – when the batteries reach a critical lower limit, sampling ceased. However, what was unusual was that the clock had stopped a month earlier, the only tag to suffer this problem.

This prevented the first and most important step in downloading the data – checking the accuracy of the clock. The geo-location analysis indicated that the shark had stayed in the GAB until March 1998, when it started moving steadily east, reaching longitudes of New Zealand in July 1998, when the tag ceased to record (Fig. 17). Considering only longitudinal movement, this required the shark to travel about 2.2° week^{-1}, something that was unusually fast, but not unreasonable (shark 1337 moved 3.0° in 8 days). However, even if the shark had returned east on the last day of recording (7 July 1998) it would have had to travel 3.5° week^{-1} in order to be recaptured back in SA on 8 September 1998. It seems an unlikely scenario for a shark to travel that far east, only to turn back immediately at an even more rapid pace. Something else that did not fit with this apparent movement was the depth pattern. There were periods from late April to early May and in mid-June when the shark was in deep water (Figs. 18 & C4b), but for a month from early May when it was east of Tas in the Tasman Sea, the depth was less than 100 m and with a pattern that suggested it was following the bottom, occasionally ascending at night. This was only possible for one small area in the Tasman Sea, the Gascoyne Seamount (Fig. 17) which rises to a depth of 90 m, but the longitudes changed more than 10° during this period (Fig. 18). Preliminary inspection of the water temperature data could not distinguish between the GAB and comparable latitudes in the Tasman Sea, but this requires more detailed investigation. There have been occasional clock failures noted in the deployment of hundreds of these tags in the North Sea (J. Metcalfe, CEFAS, Lowestoft, Suffolk UK, pers. comm.) but none in which the clocks had run several hours fast (a 1 h shift in time moves the longitude 15°). As noted in section 6.2.3 clock failures of this magnitude have occasionally been observed in other types of archival tags (M. Musyl, Uni. Hawaii at Manoa, 2570 Dole St Honolulu, HI 96822, pers. comm.). The batteries in tag 1396 were replaced and the electronics conformally coated in the Lotek factory. Upon its return we placed it on an office shelf and set it to sample at 10-day intervals for 6 months. During this period the clock only advanced by 2 days. The tag was again returned to the factory where it was found to be completely inoperable. We think that the clock was almost certainly defective during the time it was on the shark, and that the apparent movement to New Zealand was the result of it running several hours fast. The remainder of the movement plots for the SA releases are shown in Appendix D, Figs. D1–D3.

Fig. 17. Position estimates for school shark 1396 (male, 138 cm TL).

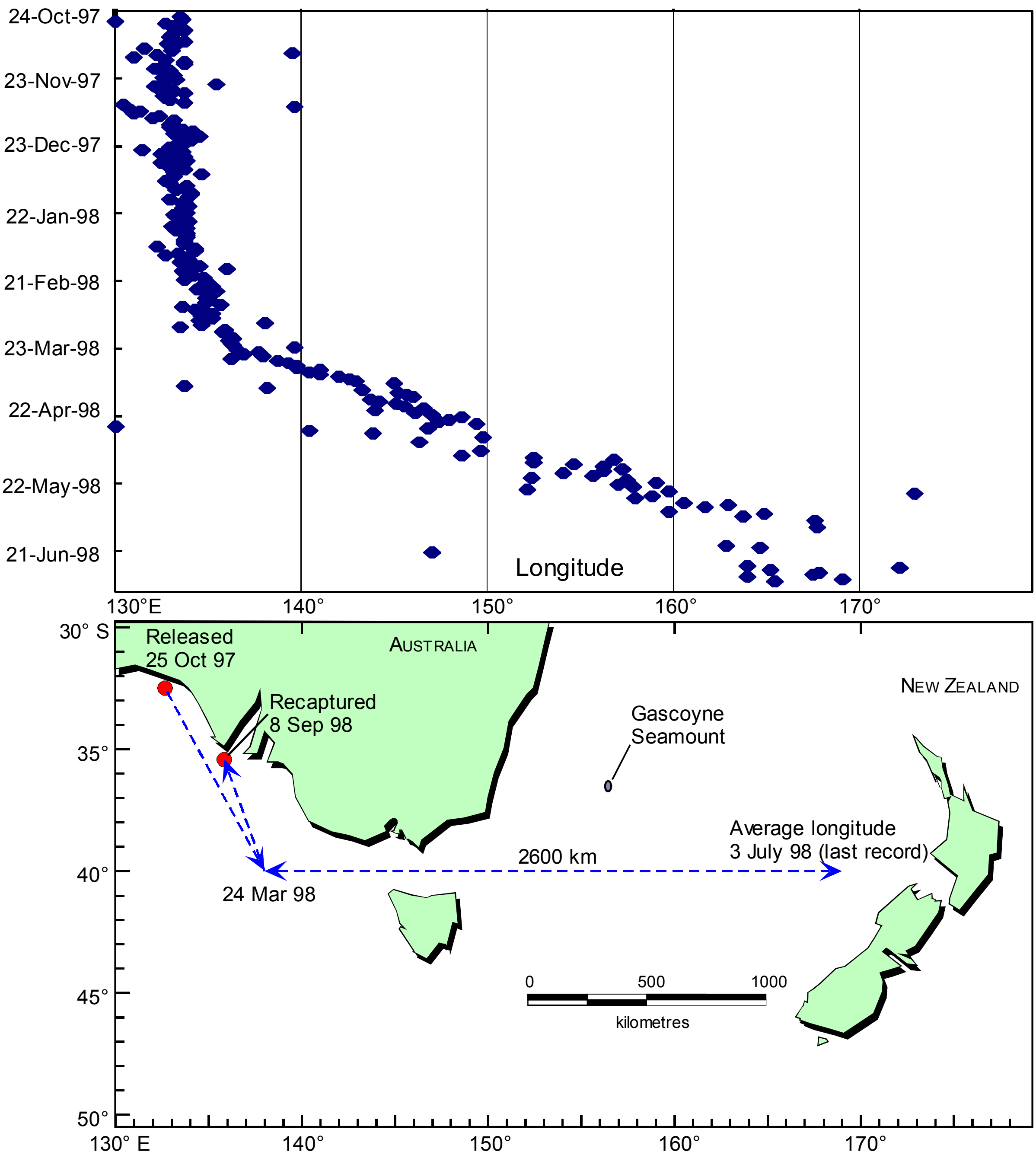
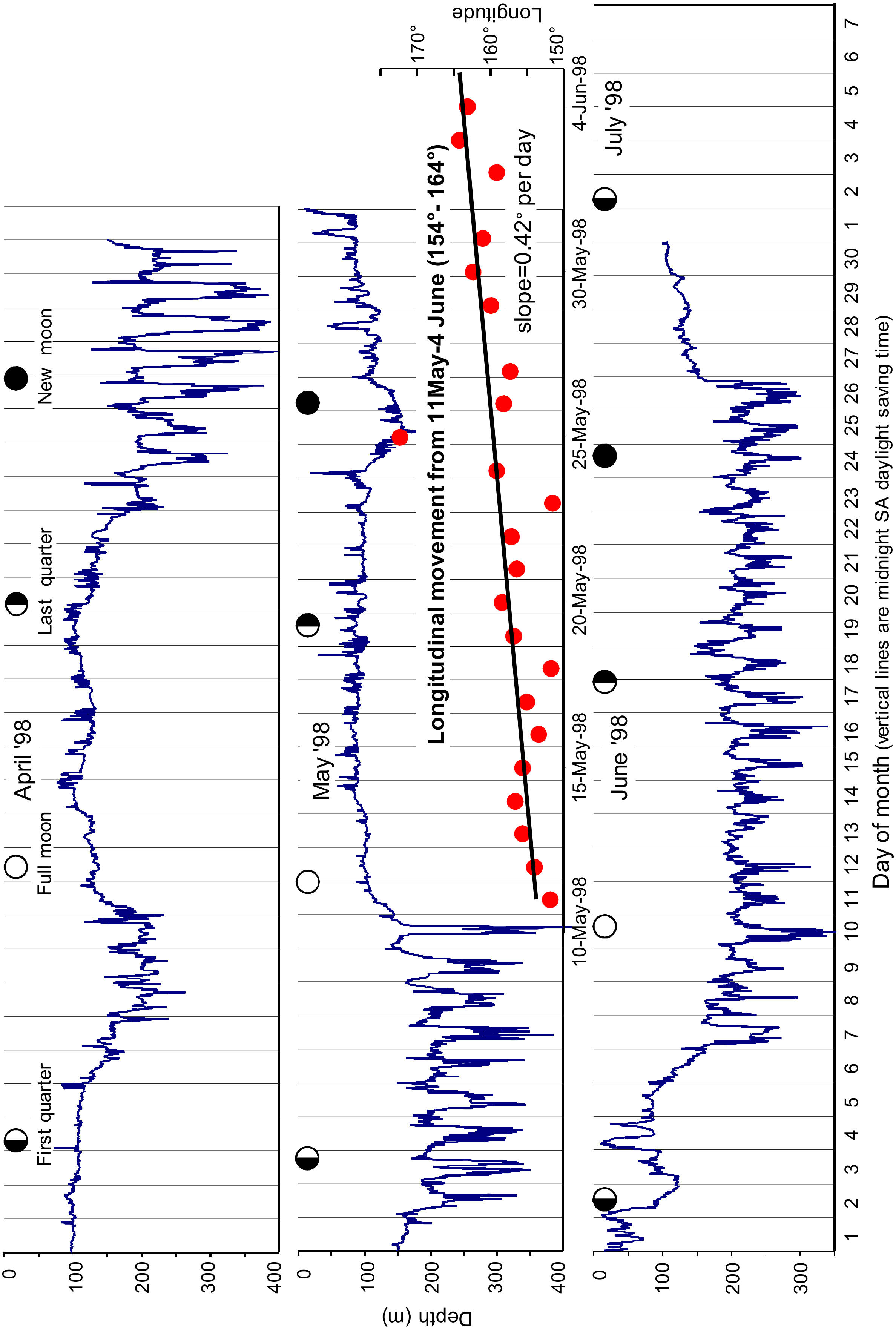


Fig. 18. Depth profiles and longitudinal movements for shark 1396.



6.8.2 Recaptures from sharks tagged in Tasmania with WLC internal tags

All of the sharks released in Banks Strait were caught to the west (Fig. 2), but it seems that they chose two different routes to get there. Latitude estimates based on depth were not attempted because of the inadequacy of the software and the north-south nature of the isobaths. However, the depth data associated with the longitude estimates is in some cases very revealing as inferences can be made as to whether the fish moved west via Bass Strait or the south coast of Tas. Figure 19 (shark 98-081) illustrates movement to the west that could only have occurred via the south coast. This shark remained at the release longitude until mid-January, when it moved slightly east into deeper water, where it remained until late March. It then moved west at depths of between ~130–350 m, which eliminated movement via Bass Strait, where the maximum depth is ~86 m. From mid-April to mid-November it was at 144–145°, in shallow water at the beginning and end of this period, so that it is possible it reached Bass Strait. When it returned east in November 1999 the depths were again greater than in Bass Strait. It remained off the east coast of Tas until early March 2000, when it returned west, again via the south coast of Tas. It must have moved fairly quickly north on the west coast to have been caught off the north-west tip of Tas at the end of March. Similar movements, but of shorter duration, are shown in Appendix D, Figs. D4 & D5 for sharks 98-073 and 98-085.

When the westward movement was associated with shallow depths the situation is less clear, but some inferences can be made. In the 10 days following its release shark 98-092 (Fig. 20) moved west to 146.6°, so therefore must have moved into Bass Strait. However, by the first week in December it was back, still in shallow water, at 148–149° where it remained until early March, when it moved west, reaching 144° by the end of March. The move was in shallow water, never more than 86 m, so it suggests it was via Bass Strait (but it could have moved west via the south coast if it had stayed inshore the whole way). It then moved eastwards and into deeper water, which implies, assuming it had crossed via Bass Strait, that it must have moved rapidly down the west coast of Tas, reaching the longitude of Maatsuyker Island (~146°) by mid-April. There followed a period in April–May in very deep water (Fig. 20, Fig.C11a) in which no light-based longitude estimates were possible, before it was relocated in mid-May at about 143.5°, at a base depth of about 100 m (with occasional dives to ~300 m), which places it at latitudes about that of King Island. It remained to the west of Tas at longitudes of ~142.5–144°, on the bottom at depths of ~120 m until early October when it started moving east (and south, because it was still following the bottom, occasionally in depths of up to 400 m). It was caught off south-west Tas on 5 November 1999. Two other recaptures, sharks 98-079 and 98-088, that almost certainly spent time in Bass Strait are shown in Figs. D6 & D7.

Fig. 19. Daily and weekly-median longitude estimates, and maximum daily depth for school shark 98-081 (male, 143 cm TL).

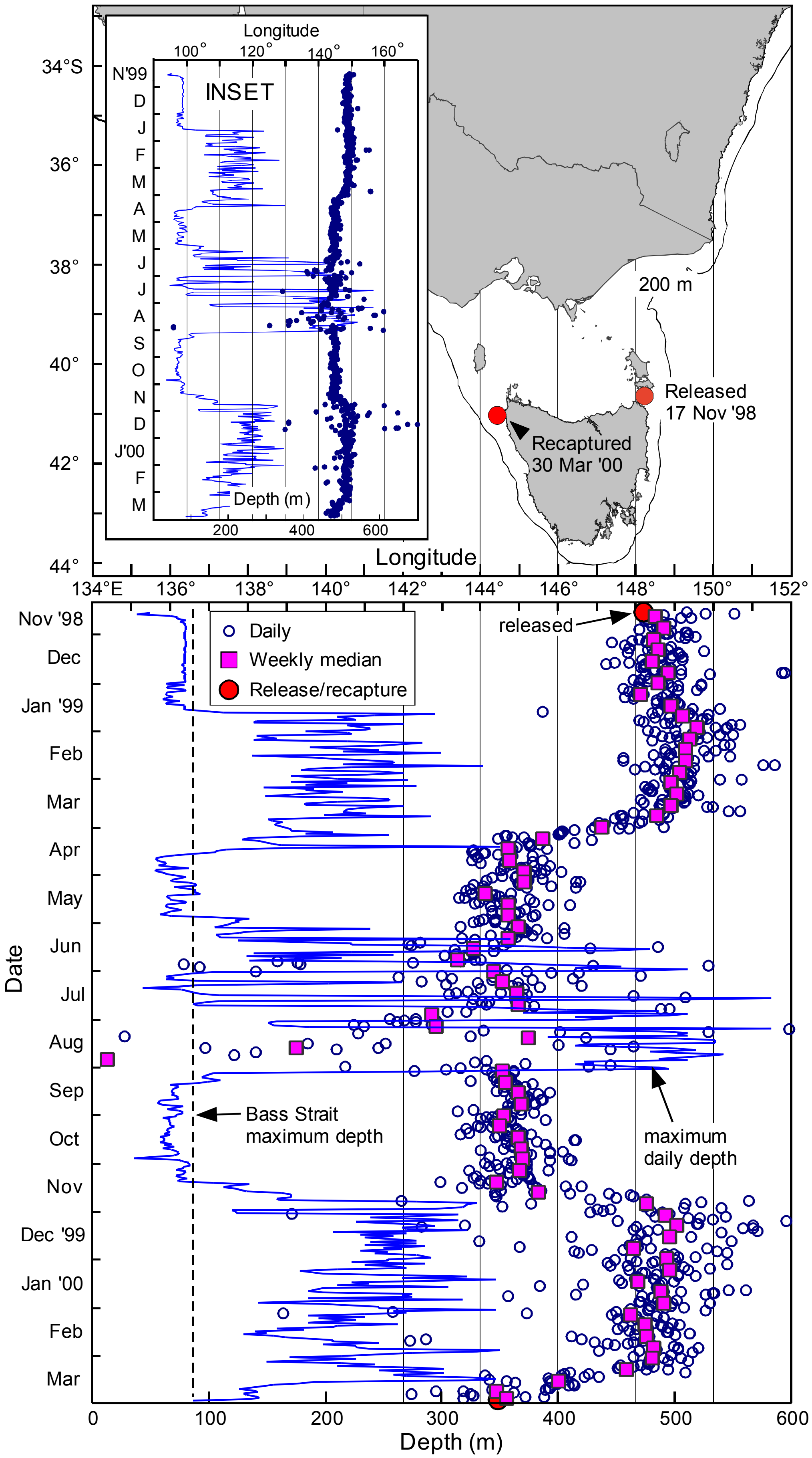
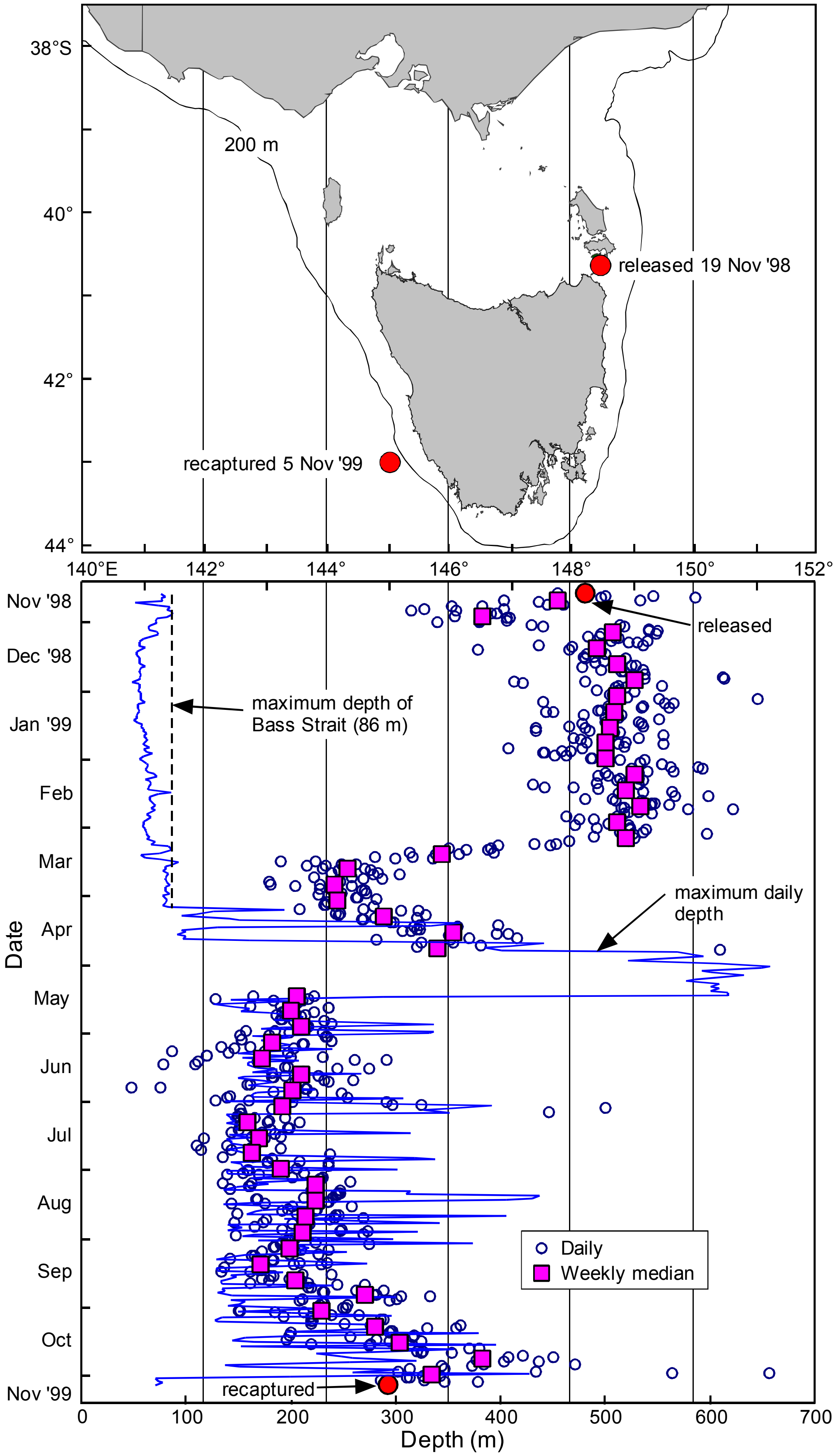


Fig. 20. Daily and weekly-median longitude estimates, and maximum daily depth for school shark 98-092 (female, 153 cm TL).



6.8.3 Summary of movement results

The weekly median longitudinal movements (minus several outliers resulting from the fish being at great depths) of all recaptures are shown in Fig. 21. The three fish released in the GAB did not move any further west, and all moved to the east although at different times. Uncertainty surrounds the results for shark 1396 because of its apparent rapid trans-Tasman crossing, but neither of the other two sharks reached further east than about 138°E (ignoring one probable outlier) in the 5 and 11 months they were at liberty.

Three of the Beachport releases moved rapidly west (sharks 1340, 1259 and 1394), two moved rapidly east (1337 & 1391) and one remained in deep water apparently at the release longitude for several months. All had been released on the same day. Of the fish that moved west, the two longer-term recaptures (4.5 and 14 months) reached the most western limits of fish in this study. The fish that moved to the east reached as far as the west coast of Tas, ~145–146°E (ignoring one probable outlier); shark 1391 reached this position within a month of being tagged.

All of the Tas releases moved west, although only one of them reached as far west as SA, about 9 months after release. Five of them remained at longitudes to the east of Tas for 4–6 months before moving west, although one of them (98-092) had initially ventured west into Bass Strait for several weeks. One shark (98-088) moved west immediately after release, and after crossing Bass Strait returned eastwards, but probably down the west coast of Tas. Movements along the west coast can be inferred for several other recaptures and in many cases the movements appeared rapid. The most easterly longitudes were reached by shark 98-081, a male. It had stayed in shallow water from November 1998 until late-January 1999, when unlike the females which continued in shallow water (Fig. 6) it ventured further east and off the shelf edge in late January 1999–mid-March. It was at similar longitudes and depths the same time the following year (Fig. 19).

In the longer-term recaptures a major shift in longitude was eventually followed by movement in the opposite direction, and particularly for the Tas releases, the pattern appeared to be annual. Major shifts in longitude often occurred in April–May and October–November. To gain an idea of the rate at which the school sharks moved throughout the year, the longitudinal movement pattern based on weekly median estimates for each fish (except shark 1396) was reduced to a series of linear movements and the daily shift in longitude calculated. This was done to reduce the variation associated with the movement rates. The data were grouped into monthly intervals (ignoring the year in which they occurred) and analysed as boxplots (Minitab Inc). For the SA releases the period June–September showed very low movement rates (Fig. 22a) although by this time there were only three fish still at liberty. Movement rates were higher from October–May and were biased towards the east except for November, which showed very high movement rates in both directions, and December in which they were biased towards the west. Exceptional movements (shown as outliers) occurred from January through August. The Tas releases (Fig. 22b) showed very low movement rates from May–September, higher rates biased to the east in October–November, very low rates in December–February and higher rates biased to the west in March–April. Exceptional movement rates occurred in most months of the year except in March and October.

Fig. 21. Weekly median longitude estimates for all recaptures by month; South Australian releases made in 1997, Tasmanian in 1998.

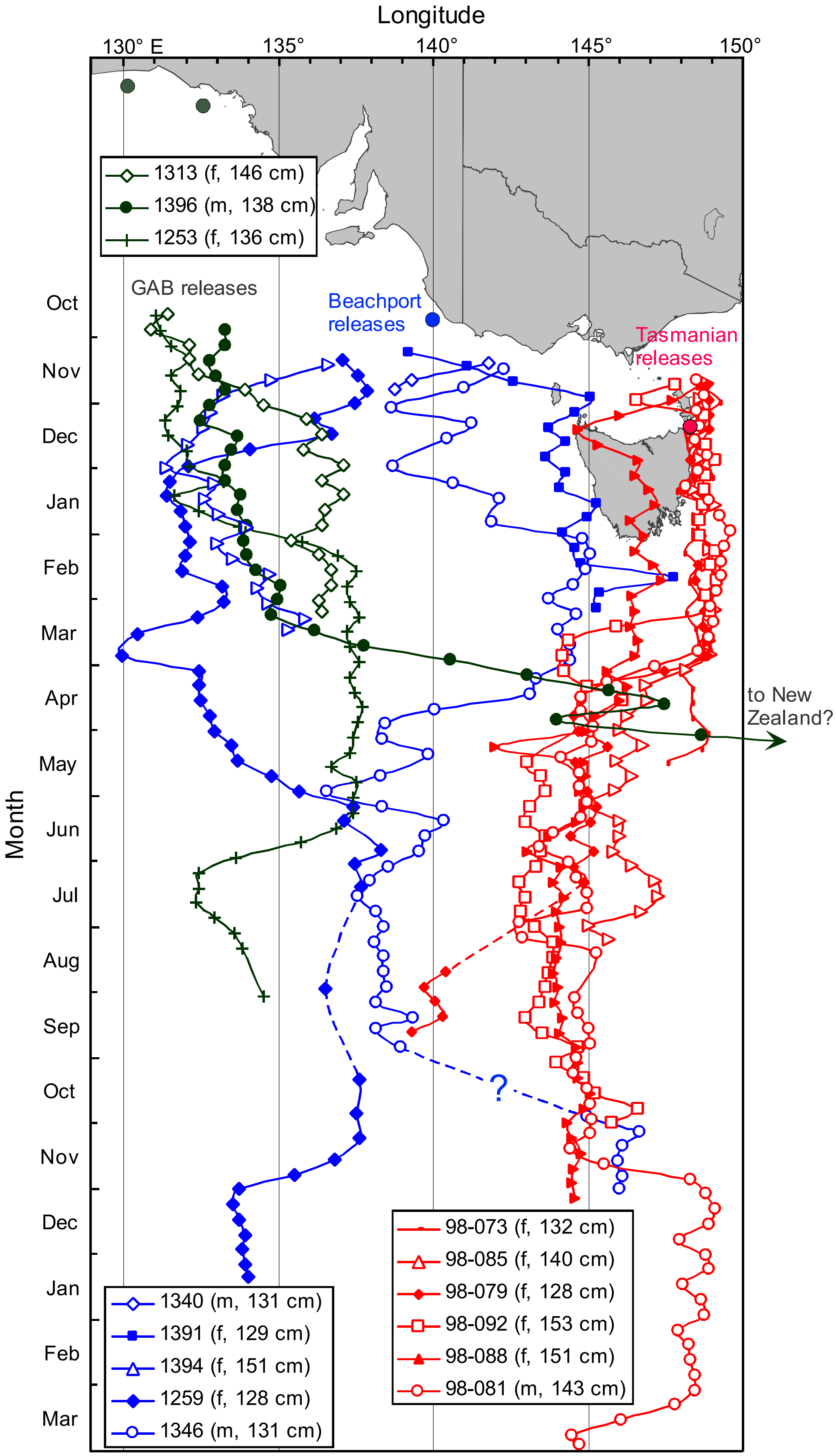
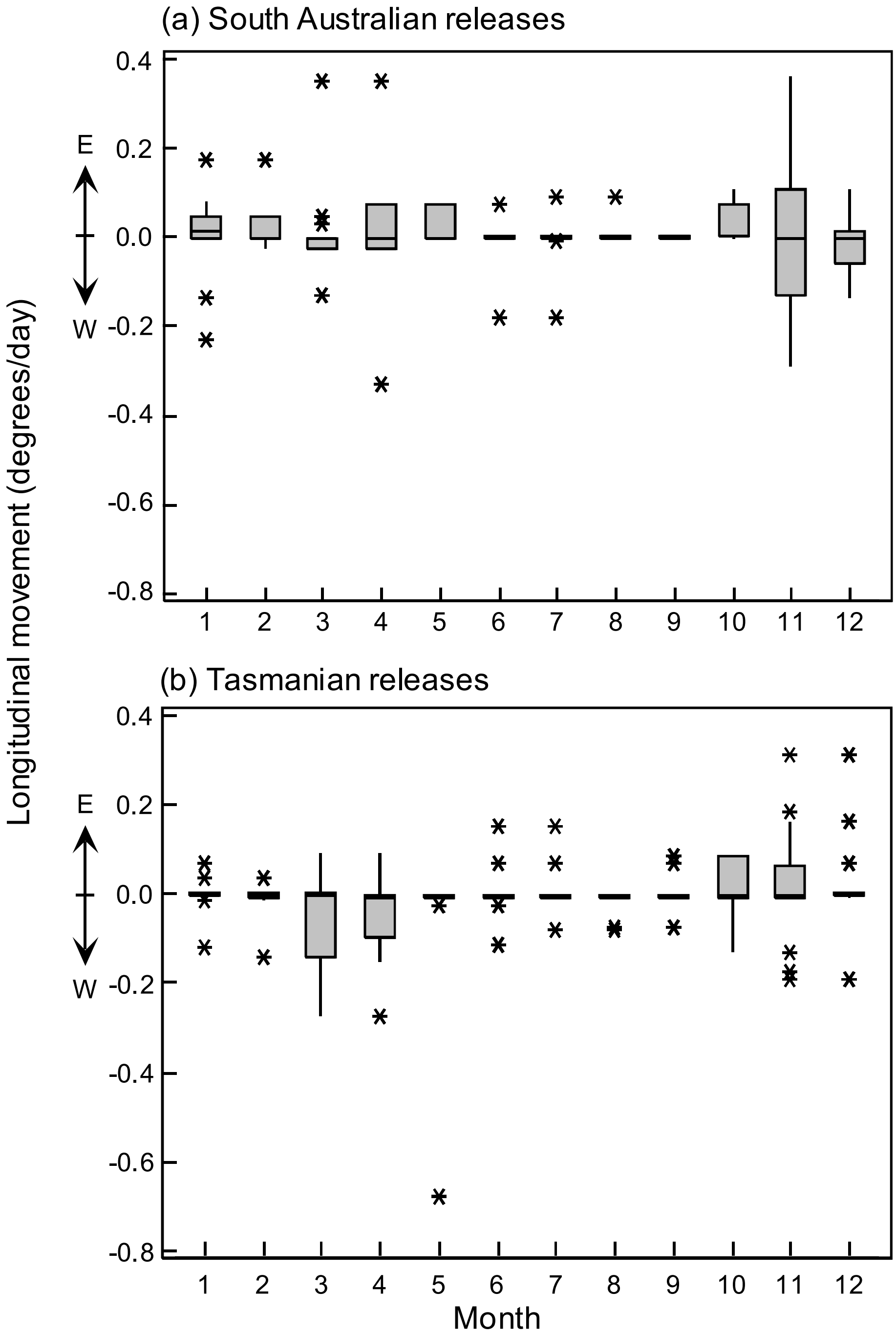
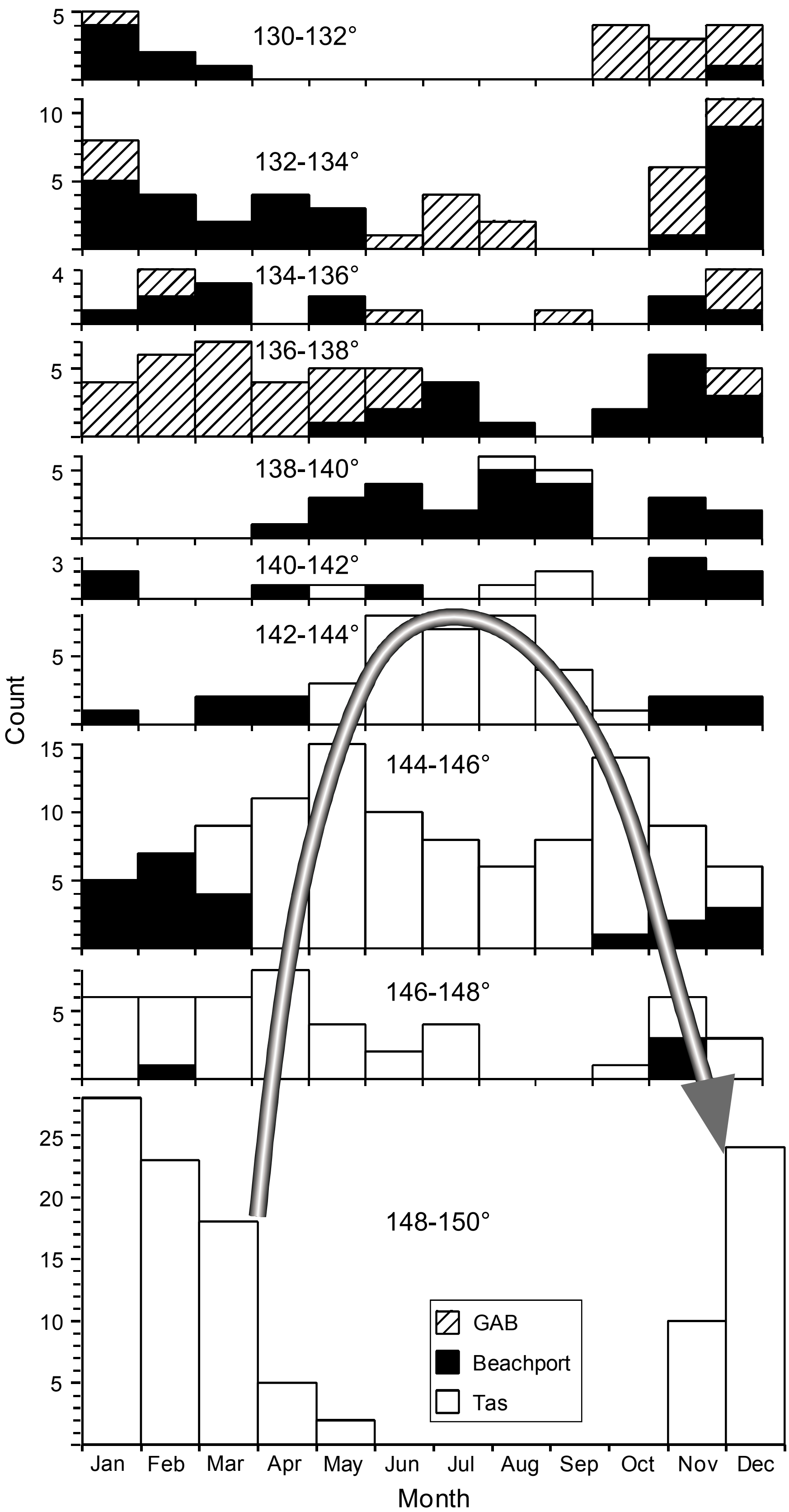


Fig. 22. Distribution of daily movement rates by month: a – South Australian releases; b – Tasmanian releases. The shaded box represent 50% of the data from the 25th to the 75th percentile; the median is the horizontal line within it. Outliers are shown as *.



The median weekly longitude estimates for all fish except shark 1396 were grouped into 2° classes, and the frequency of occurrence for each month (ignoring years, and separated into the three release areas) calculated (Fig. 23). Unlike the previous analysis, the raw data was used.

Fig. 23. Frequency of occurrence by month in 2° longitude zones of sharks released in the GAB, off Beachport and in Tasmania.

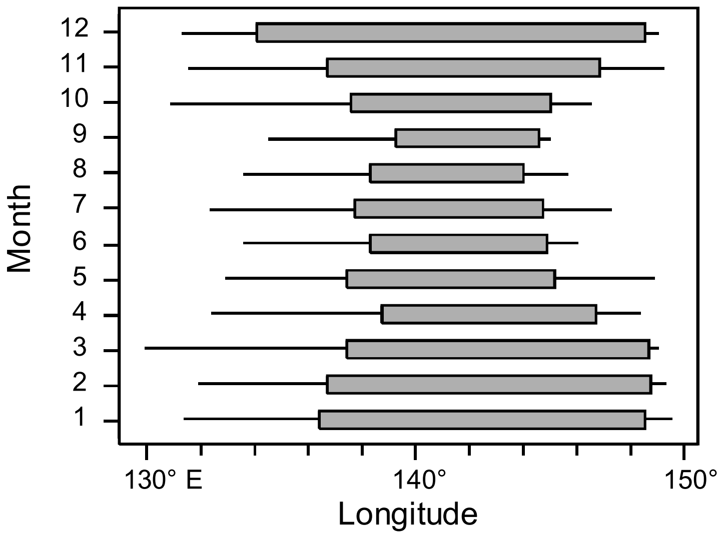


The results for zone 148–150° (east of Tas) for the Tas releases show a peak in January, followed by a decline which was greatest after March. In the zone immediately to the west (146–148°) counts increased in April, in zone 144–146° they peaked in May, and at 142–144° which marked the practical westward limit of most Tas releases, counts were highest during winter. A few occurrences occurred further to the west, but the dominant pattern was an eastwards return that saw counts progressively peak in October at 144–146°, in November at 146–148° and in December back at 148–150°E.

At the western end of the region, the fish released in the GAB were present at 130–132°E for only October–January. To the east the fish were found over a wider time period, with highest counts at 136–138° where they occurred from December-June.

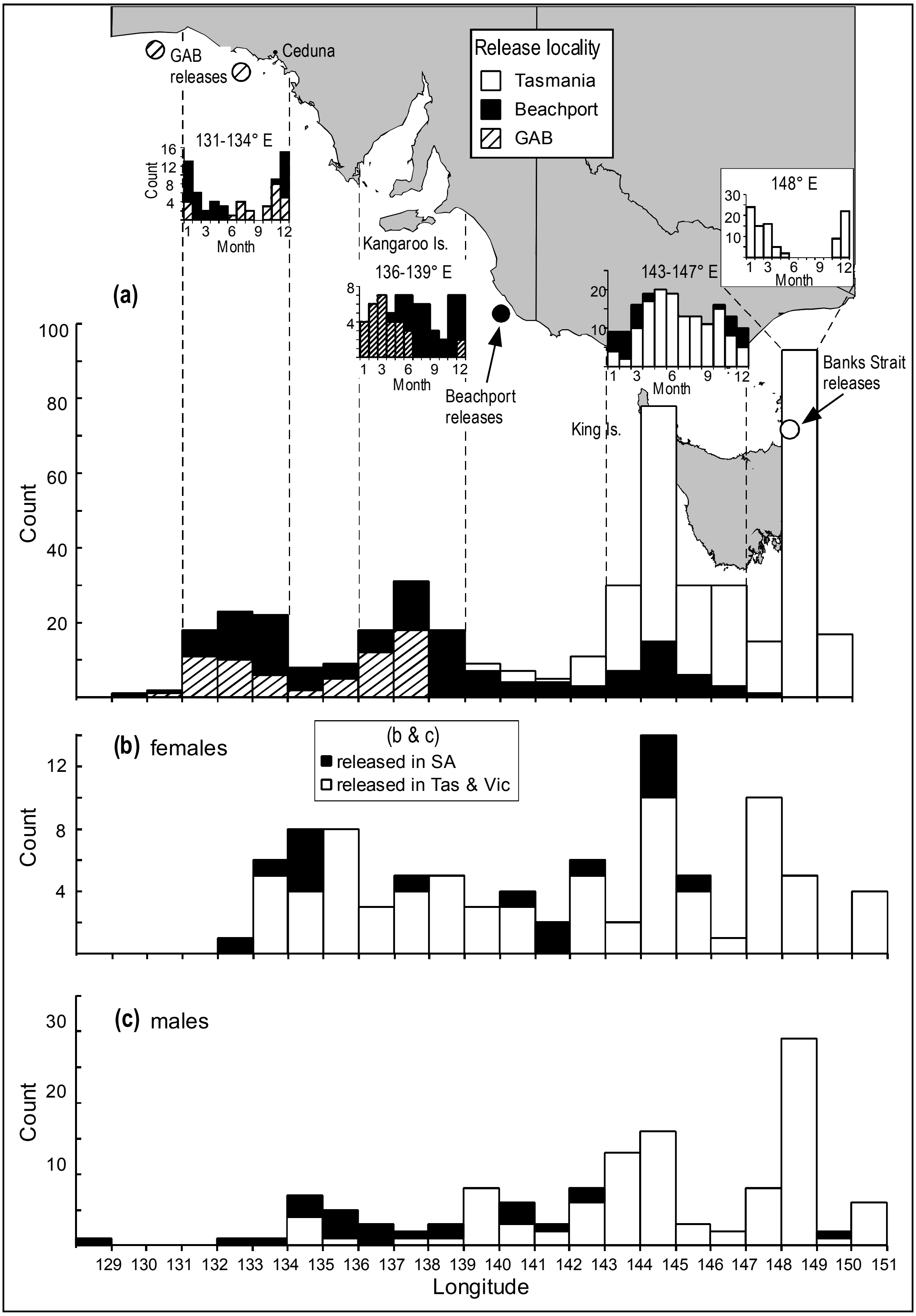
The Beachport releases at 138–140° were present from April–December (ignoring their absence in October) but counts were highest during the winter months. As they moved to the east and the west their occurrence was restricted to the warmer months at the beginning and end of the year. The consequence of this seasonal pattern in longitudinal movements is that the range of the archival-tagged school sharks was restricted during 'winter' (Fig.24)

Fig. 24. Longitudinal distribution of archival-tagged school sharks by month. Shaded boxes represent 50 % of the observations (median ± 25 %).



The zones from 134–136° and 140–142° showed lower counts than adjoining zones, suggesting that fish moved through these areas quickly. To investigate this further the frequency of occurrence based on the weekly median longitude estimates for each 1° of longitude was calculated (Fig. 25 a). The results showed four zones in which school sharks were found more frequently: 131–134° ('Ceduna'), 136–139° (Kangaroo Island), 143–147° ('Tas west coast') and 148–149 ° ('Tas east coast'). In the most westerly ‘Ceduna’ zone although archival-tagged school sharks were present all year round, the overall occurrence was highest during November–January (Fig. 25a). At the Kangaroo Island zone the overall occurrence showed no obvious seasonal pattern, except perhaps for a decline in September–October. In this zone the occurrence of the fish tagged in the GAB differed from those that had been tagged off Beachport. The GAB fish that had moved east were found only from December–June, with a peak in February–March, whereas the Beachport fish were found from April–December with peaks in July–August and November–December. However, the GAB returns may be biased because one of the recaptures was at liberty only until March 1998, and shark 1396 was excluded from the analysis.

Fig. 25. a: Frequency distribution of school shark weekly median position estimates (excluding tag 1396) by longitude, and monthly distribution for four selected zones: b and c – recapture-longitude frequency distribution of females (b) and males (c) (≥ 95 cm TL) tagged in SA and Tas -Vic in the 1947-56 tagging program.

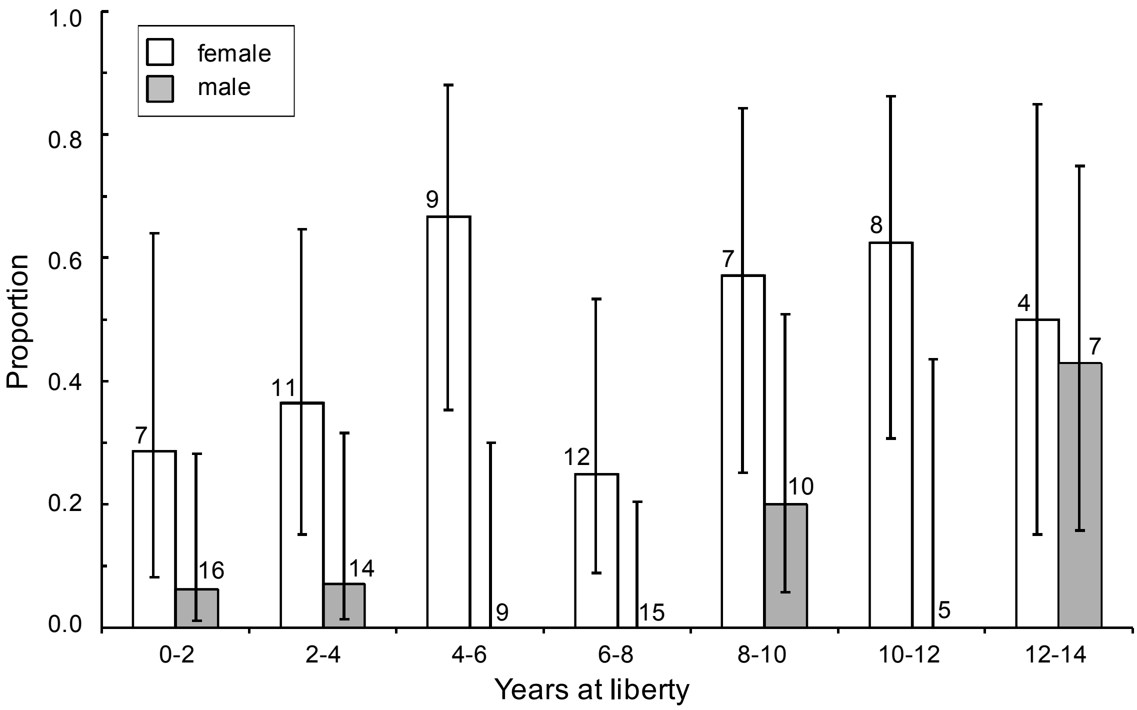


In the Tas west coast zone (note that in these longitudes the fish could have been in Bass Strait, rather than off the actual west coast, similarly in the east coast zone) the sharks were present year round, but occurrences peaked from April–June and were lowest from December–February. On the Tas east coast the sharks were absent from June–October, with peak occurrence in December–January.

We analysed the recaptures from the 1947–56 tagging program (Olsen 1954)[2] to compare the pattern of recapture longitudes with that from the archival tagging program, although the (unknown) distribution of fishing effort for the earlier study complicates this comparison. We restricted the data to sharks of ≥ 95cm TL to avoid recaptures of small fish in nursery areas. The results for females (Fig. 25 b) showed peaks to the east and west of Tas, although the most easterly peak was 1° inshore of that shown by archival tagging. In SA the peaks did not coincide with the archival tagging results, except perhaps near Kangaroo Island. The males showed a similar pattern to the females, except that the most easterly peak was shifted 1° offshore and the peak off western Tas was less concentrated, extending ~ 1° to the west (Fig. 25 c).

School shark can move across the entire longitudinal range of the fishery in relatively short times (Olsen 1954). We analysed the 1947–56 data set to examine the proportion of school shark tagged in Tas-Vic waters recaptured in SA, by time at liberty. Only fish of ≥95cm TL at release were considered, recaptures were grouped into 2 year time-at-liberty intervals and the series was curtailed after 14 y to maintain reasonable sample sizes. The proportion of females recaptured in SA peaked at about 0.7 at 4–6 y at liberty, and again at about 0.6 at 10–12 y (Fig. 26). The proportion of males recaptured in SA remained very low in the early years, but increased to about 0.4 by 12–14 y.

Fig. 26. Proportion, and 95% confidence limits, of school shark tagged in Tas-Vic waters recaptured in SA for the 1947–56 tagging study. Length at tagging ≥ 95 cm TL. Numbers are total number of recaptures for each sex and time group.



[2] Olsen (1954) reported on 237 recaptures of tagged school shark. Recaptures continued until 1993, yielding a total of 594 returns (Walker et al. (1997).

7 DISCUSSION

7.1 Dummy tagging

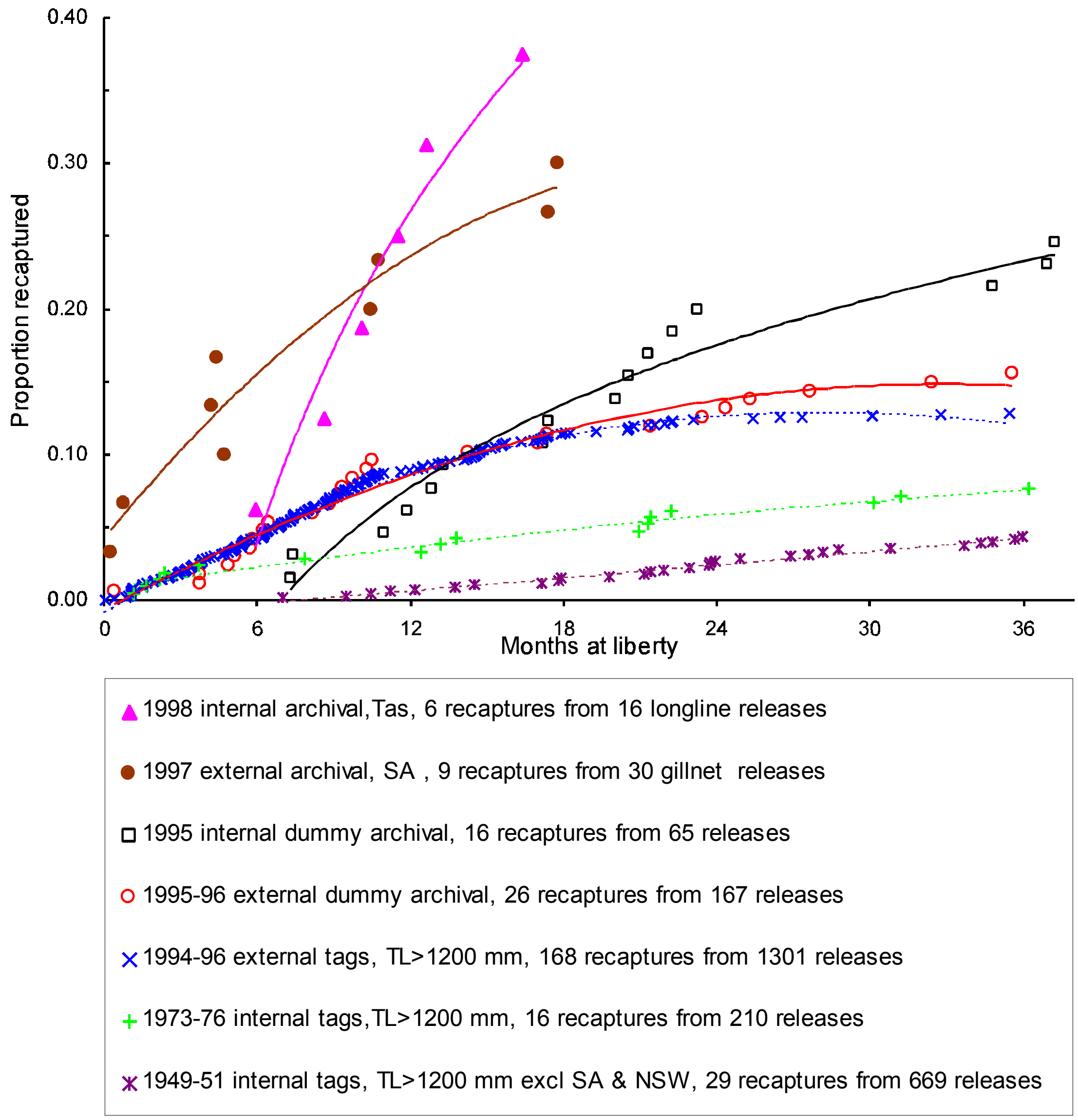
When the archival tagging project was proposed, we had no information on the effects of applying archival tags to school shark. External tags cause drag, and are subject to shedding. Internal plastic-label tags have been used successfully on school shark without suturing of the wound (Olsen 1953), but in our case the light stalk was to protrude through the body wall, possibly affecting healing of the wound. The relatively large size of the internal archival tags compared with conventional internal tags also raised the possibility of damage to internal organs caused by abrasion against the tag, and tissue reaction to the presence of the tag. The superiority of the internal tags was evident from the recapture rate of 27.5%, almost twice that of the block-shaped external tags (14.8%) and considerably higher than the external streamlined tags (17.4%). The external tags may be lost through shedding or from being torn from the fin when the net is hauled.

7.2 Recaptures of archival-tagged sharks

Although the results from the dummy tagging experiment clearly favoured internal tags, we used the Lotek external tags for the first batch of releases in 1997 (West & Stevens 2001) because of problems with the WLC internal tags at that time. The return rate of the Lotek tags from the longline-caught sharks was twice that from the gillnet-caught ones (6 vs 3 tags from 15 releases by each method). The longline releases were much more lively than those from gillnets but the gillnet releases were also released in an area remote from much of the fishing effort. The recapture rate for the external tags of 33.3% (9 tags returned plus 1 with only the base-plate, out of 30 releases) was close to that of the internal tags (37.5% – 6 tags returned from 16 releases), although the external tags had been deployed a year earlier than the internal ones. Return rates of conventionally tagged school shark in size categories of 950–1399 mm TL, similar to the present releases, were 24.8, 23.8 and 19.9% % for fish tagged in 1947–56, 1973–76 and 1990–96 (Walker et al. 1997, L. Brown, MAFRI, Queenscliff, Australia 3225, pers. comm.). However, it is difficult to directly compare these results because of the different periods over which recaptures have been made (up to 42 years for the 1947-56 releases, 12 years for the 1973–76 releases and with returns still coming in for the 1990-96 releases). As an alternative, we considered recaptures from fish at liberty for up to 3 years for these three studies, restricting the release periods to 1949–51, 1973–76 and 1994–96. We also included the dummy-tagging and archival-tagging experiments. Each return was sorted by time at liberty and assigned a cumulative proportion-recaptured value (1/n, 2/n etc where n was the total number of releases) (Fig. 27).

Although the comparisons are affected by many factors including tagging mortality, tag shedding and tag reporting rates, the inescapable conclusion is that the rate of exploitation (the number of recaptures from the total number released) has increased considerably over the years. In the first study (1949-51) the majority of fish tagged were juveniles caught in nursery areas, so to enable a more realistic comparison with later studies, only fish larger than 1200 mm TL were used in the comparison of return rates presented in Fig. 27. In addition only fish tagged with internal tags were considered to avoid the high tag shedding rates associated with the Petersen discs used in this early study (Xiao et al. 1999). 'Non-sighting' of the internal tags by fishers undoubtedly occurred, as a small number of double-tagged fish were reported to have had only the external tag present (Xiao et al. 1999). The fish tagged in 1973-76 were all internally tagged, although the tags had a streamer projecting through the body wall (Walker et al. 1997) to aid detection. The analysis for the 1994-96 study includes fish tagged with dart tags, roto tags or both. Shedding rates for the dart tags were considerably higher (and varied according to the position of insertion– into the muscle or base of the first dorsal fin) than for the roto tags pinned through the first dorsal fin (Xiao et al. 1999), and this could be expected to depress the number of returns. Indeed, the proportion of recaptures for the external dummy tags applied during the same study is higher after two years at liberty (Fig. 27). Reporting rates for the 1994-96 conventional tag study were estimated to be relatively high (84-92%, Walker et al. 2000), although the novelty of the dummy tags might be expected to result in even higher reporting rates. The internal dummy tag experiment resulted in higher return rates again, although still lower than the two archival tagging experiments. It could be argued that the high return rates for archival-tagged fish were because they were in better condition than fish released in conventional tag experiments, where the cost of the tag is of no consequence. In fact, many of the archival tag gillnet releases were not very lively, a consequence of the scarcity of live fish in the catch. The longline releases were in much better condition. Thirty one of our 46 releases (67%) were made from longlines, a higher percentage than in the 1994-96 study (42%) and it is possible that this could have resulted in better survival after tagging and higher recapture rates. A comparison of the recapture rates for the longline and gillnet releases in the 1994-96 study would be required to take this any further. We consider that the reporting rate for the archival tags was 100%, given the intense interest by fishers, and the high numbers of recaptures provided an unexpected scientific bonus. While the high recapture rates for the archival tags are based on only small numbers of releases and as such might not be representative of the general population, the high exploitation rate is a concern. The current and future rate of returns of conventional tags applied during the 1990's may present a clearer picture.

Fig. 27. Proportion of tagged sharks recaptured by time at liberty for conventional tagging, dummy archival and archival tag releases.



One of the drawbacks of releasing only small numbers of archival tags is that the chances of getting long-term recaptures that would provide the best movement information, are very small. However, the particular tags we used did not appear to be able to perform reliably for extended periods. The Lotek tags used in our study failed after 8–14 months (they have since been modified), and the WLC tags developed problems with the light signal that might prevent geo-location after extended periods. These problems were not predictable – they were not evident in the stringent tests the tags were put through in the factory, and it will only be from extended deployments in the field that the long term reliability of the tag designs will be proven. Despite the inherent problems of working with leading edge technology, in our study only one of the 16 tags had problems (clock error) that resulted in unreliable position estimates. This reflects highly on the design and production skills of the manufacturers.

7.3 Depth behaviour

7.3.1 Diving behaviour immediately after tagging

The diving pattern of archival-tagged school shark was sometimes quite atypical for periods of several hours to several days after release – they often came near the surface during daylight, something that was never subsequently observed. Sciarrotta and Nelson (1997) noted ‘abnormal’ plunge behaviour in about half of the blue sharks (*Prionace glauca*) they tagged, with the sharks diving to about 95 m within 30 min of being darted with acoustic transmitters. This initial effect disappeared within 90 min of being tagged. Similarly, Carey & Scharold (1990) observed that tagged blue sharks, when first released, commonly went below the thermocline for many minutes to several hours. Their diving pattern was commonly less well developed, and their course heading different for the first half-day or so. Presumably, this different behaviour is related to the stress of capture and tagging. Holts and Bedford (1993) noted that the trauma of capture and release probably lasted only 30–90 min in shortfin mako sharks (*Isurus oxyrinchus*)that they tracked. ‘Atypical’ behaviour lasting several hours after tagging has been noted in tracked marlin (*Makaira spp*) (Holland et al. 1990, Block et al. 1992). The prolonged disruption to the normal diving behaviour we saw suggests that capture by commercial gillnet and longline subjects our animals to considerable stress.

7.3.2 Depth distribution and dive behaviour

The maximum depth of 657 m recorded during this study exceeds the 600 m depth recorded by Cowper & Downie (1957) line-fishing off the south-eastern Australian slope. In New Zealand waters school shark have been caught in bottom trawls at depths of 890–1060 m (P. McMillan, NIWA, Wellington, New Zealand, pers. comm.), but it is possible that the sharks were caught in mid-water. Catches of school shark in surface drift nets off California (Ripley 1946), on tuna longlines with hooks set at depths of 90–150 m deep (Walker et al. 1998), 50–140 m (W. Whitelaw SPC Noumea, pers. comm.) in the Tasman Sea, and the occurrence of pelagic prey in their stomachs (Ripley 1946, Olsen 1954) indicates that at times they may also be near the surface. The archival-tagged school shark spent most (91%) of their time on the continental shelf (<200 m), although males spent more time at 150–300 m than females. Ripley (1946) noted that in the Santa Barbara region females predominated in depths of <55 m and males at depths >70 m.

The most dramatic diving behaviour shown by the archival-tagged school shark was when they made regular descents during daytime from near the surface to depths of up to 650 m. However, this type of diving behaviour was uncommon. Four fish released at Beachport showed this pattern for a short period in early November, in an area extending from ~138–142.5°. One fish released in Tas showed this diving pattern for about three weeks in April–May 1999 while moving from 146–144°E (SW Tas). Another fish tagged in Tas showed this diving pattern for about three weeks from mid-July 1999 at ~145° (SW Tas) and for about a week during a two week period in mid–late August when it moved from 145° to 140°E (SW Tas to eastern SA). A more common behaviour in deep water also involved diving during the day, but very irregularly with fish not generally descending or ascending as far as the regular deep-diving pattern. This type of depth behaviour, in which animals descend beyond the photic zone, is consistent with a predator that uses olfactory as well as visual cues in search of prey (Carey & Scharold 1990). Information from fishers operating from Beachport during our tagging suggest that squid (*Nototodarus gouldi*) are a common component of the diet of school shark at this time of year. *Nototodarus gouldi* apparently feeds mainly at night, probably moving up from the bottom into the water column (O'Sullivan & Cullen 1983, Nowara & Walker 1998). Certainly, some species of squid undergo similar daily vertical movements to those we observed in school sharks. Nakamura (1993) found that *Ommastrephes bartramii* was near the surface at night, but descended to depths of over 700 m during the day. Tricas (1979) found that pelagic cephalopods were a major prey item of blue sharks in California, and suggested they were captured at night when the cephalopods migrate from deeper water to near the surface.

By far the greatest proportion of time (91%) was spent at depths of <200 m, where a wide variety of dive patterns was observed. One of the most common was a pattern of nightly ascents, often to near the surface, although the extent and timing varied considerably. At the time of the full moon, these ascents were usually, but not always, suppressed. Fishers report better catches with their bottom-set gear at times around the full moon, but in any case generally ensure that their gear is in the water at dusk and dawn, which would increase their chances of encountering fish on the bottom. We have yet to estimate the amount of time the fish spent off the bottom when they were less vulnerable to the fishing gear, one of the major objectives of this study, because of the complexity of other dive patterns shown by the species, and the uncertainty this introduces as to whether the fish were actually on the bottom. Another common pattern in the deeper waters of the shelf was a pattern of descents from a steady depth, mainly at dusk or night, and often to considerable depths. This implies that the fish were either near the shelf edge, or close to deep canyons. Yet another pattern in shallow water was for the fish to spend the daytime on a plateau, often showing very little vertical movement, and to be deeper at night. Fishers often concentrate their fishing on shoal areas, and Olsen (1954) observed that many of the school sharks' prey species were restricted to reef habitats. Klimley et al. (1988) found that scalloped hammerhead sharks spent the daytime in a relatively inactive state in a restricted area on a seamount in the Gulf of California. In the evening the animals dispersed to feed. Most shark species observed show some diel periodicity in activity patterns and movements (Bres 1993).

7.4 School shark movements

7.4.1 Technical evaluation of archival tag geo-location

We were fortunate that we were able to build upon the software developed by the CSIRO tuna researchers. At present there is only one source of commercial geo-location software (GLS) available in the world, and that is from researchers in Germany who developed it for research on air-breathing animals (Wilson et al. 1992). As a result this software does not incorporate any corrections for the attenuation of light with depth. Wildlife Computers hope to have software available in the near future, and Lotek have purchased the rights to the GLS used in the Northwest Marine Technology archival tags. However, in a rapidly developing field producing robust software is not an easy task.

Our mooring experiments with Lotek tags showed that the accuracy of both latitude and longitude daily estimates degraded rapidly with depth, although it was possible to produce reasonable 'average' positions over periods of a week or longer. Much of the uncertainty in the estimates can be attributed to inherent variation in weather conditions, but correcting for the attenuation of light with depth is an additional problem. While the light attenuation can be estimated from experiments, it does not necessarily apply to tags on fish that are moving through different water masses. We think this is probably the main reason for the failure of our light-based latitude estimates on fish, and why we had to rely upon depth-based estimates for latitude.

Welch & Eveson (1999) noted that an objective basis for eliminating position outliers was called for. We tried two methods to deal with the variance in our light-based longitude estimates: curve fitting and weekly medians. The regression approach involved fitting polynomial regressions to the longitude data, and eliminating points lying outside arbitrarily defined confidence bands. This method appeared reasonable for longitude trends with few areas of changing curvature, although it was compromised by the desire to have the curve fit through the release and recapture positions at the ends of the regression, where polynomials tend to flare. Weekly median longitude estimates were more suitable than curve fitting for fish that showed many changes in direction, and appeared to successfully describe the central trend in longitude, although occasionally they were deflected by outlying estimates. Choosing a longer period would have helped in this situation, but at the risk of missing some of the dynamics of the movements. It would be possible to develop objective criteria to eliminate outliers, either based on some property of the light curve, or if the maximum daily depth exceeded some set limit. However, it seems clear that the path of a tagged fish is better defined by some central measure rather than by individual days.

7.4.2 Previous studies on school shark movement

The tagging study that Olsen commenced in 1947 eventually (the last recapture was at liberty for 42.4 y!) yielded movement information on 587 school sharks. Both adults and juveniles were shown to make extensive migrations. The most rapid westward movement was from a 147 cm female, which moved 10.1° of longitude in 10.4 months (the greatest westward movement was 13.1° in 20.9 y) and the most rapid eastward movement was also a female, which moved 7.7° of longitude in 3.9 months (the greatest eastward movement was 15.6° in 15.8 y). Olsen (1954) hypothesized that: "In the late summer and winter months the adult school sharks, which during the summer were distributed within the limits of the continental shelf, either move toward the edge of this shelf (70-100 fm) or else migrate into the warmer waters of South Australia and New South Wales. The return movement from these northern waters commences about October or November. The sharks which move out to the edge of the continental shelf, where copulation takes place in May and June, disperse in these deep waters by July or August. About 2 months later they begin their leisurely return movement and by November have reached the shallower inshore waters. Superimposed on this main movement is the purposeful migration to nursery areas of the gravid females to release their young". Olsen (1984) described the movement from inshore waters to deeper or more northern waters as occurring 'as winter approached' (in autumn in an unpublished paper on migration) and water temperatures fell. Reversal of this movement occurred in spring as temperatures rose. Walker et al. (1997) described a computer visualization package developed by B. Taylor (MAFRI, Queenscliff, Australia 3225) in which default dates for eastward migration were 16 August–1 November, and for westward migration 1 March–30 May. Stevens (1990) reported movements of tagged school shark of up to ~18–20° of latitude north and ~15–17° of latitude south of the release sites in the UK, and could not detect any obvious seasonal pattern to the movements. Hurst et al. (1999) reported movements of school shark from New Zealand to Australia of some ~22–43° of longitude. School sharks were caught mainly in spring and summer when large sharks, particularly pregnant females, moved into shallow coastal waters (Francis 1998). In Argentinian waters large school shark are caught as they migrate south in September–December and again in March–April when they return north (Walker 1999). In Brazilian waters to the north, school shark are most abundant from June–September (Peres & Vooren 1991). In South African waters mature females appeared to be absent from the area in winter, while males were present both summer and winter. Off the Californian coast there were marked latitudinal and seasonal shifts in sex ratios. In the southern part of the fishery catches were highest in April–July (spring–summer), nearly all were female and restricted to depths of <60 m. In northern California where catches were restricted to October–December (autumn–winter), nearly all the fish were males (Walker 1999). These seasonal and spatial differences in sex ratios indicate that although there is clear evidence of movement in autumn to warmer waters (and a reversal in late spring) there may be differences between the sexes.

7.4.3 School shark movements based on archival tagging

One of the major objectives of the archival tagging was to study the movements of pregnant school sharks, to ascertain whether recruitment was completely dependent upon south-eastern pupping areas. By tagging in SA just prior to the pupping season the movements of the females could be followed, knowing that they would give birth within several months. However, the scarcity of pregnant females prevented this. Archival tagging might contribute to this question from knowledge of the movements of mature females, but long-term recaptures would be needed to encompass the reproductive cycle. This in itself would require large numbers of releases, something that with the present price of archival tags would be difficult to justify. There is also the problem of interpreting the movement data given that the year of parturition would be unknown.

The primary objective of the archival tagging was however, to determine the frequency and extent of movements of individual school sharks. We found that in Tas waters March–April were times of major movements to the west coast, and October–November were times of major movements to the east coast. In SA the movements occurred over a wider time period, with elevated movement rates from October to May. Movement rates peaked in November with fish moving both east and west. In Tas waters the period from May–September (June–September in SA) was a period of low movement rates. However, there were still longitudinal shifts, though not necessarily rapid, during this 'winter' period, especially in SA. This is in general agreement with Olsen's conclusions: movements in late summer–winter and October–November. In Tas the tagged sharks were absent from the east coast from June–October, having moved to the west coast where their occurrence peaked in April–June (Fig. 25). There was a similar, but less obvious trend in SA where the highest occurrence of archival-tagged fish in the most western region was in the warmer months; they were largely absent from March–October. The consequence of this is a range contraction during 'winter' (Fig. 24).

The archival-tagged fish favoured 4 regions (Fig. 25a), two of which, the Tas east and west coast, also had higher numbers of recaptures from school shark tagged in Olsen's (1954) study (Fig. 25 b & c). Further west the recapture pattern for the conventional tags was different from that shown by the archival-tagged sharks, but as with all recapture positions, they depend upon the distribution of fishing effort. There was a strong seasonal effect with the distribution of the archival-tagged fish, with the two outer regions (GAB and Tas east coast) being occupied mainly in summer. The converse applied to the Tas west coast, while there was not a clear seasonal pattern at the Kangaroo Island zone. While archival-tagged fish occupied longitudes ranging from 129–150° E, none of them (excluding shark 1396) moved more than about half-way across this region in the period they were at liberty (up to 18 months). In particular, the fish released in Tas showed a marked tendency to stay in this region – only one female ventured west as far as SA. This suggests a staged movement across the fishery over a number of years, rather than an annual migration across the entire region. While Olsen's (1954) study revealed that a few individuals make rapid movements across the fishery, re- analysis of the tag data from the 1947-56 releases showed that for females of ≥95cm TL tagged in Vic and Tas waters, only about 30% were recaptured in SA after 0–2 y at liberty. The recaptures of females in SA peaked at 4–6 and 10–12 y, possibly indicating some periodicity in their movements (Fig. 26). The movement of similar size males to SA was much slower, suggesting different movement patterns for the sexes. We saw evidence of this in the behaviour of the one male recapture (98-081) tagged in Tas, which unlike the females moved further east into deeper water off the shelf edge in eastern Tas during late summer.

These restricted movements have some interesting implications for the movements of pregnant school shark, and it is unfortunate that we were able to tag only one. If the longitudinal movements of pregnant females are similarly restricted, and all pupping occurs in the south-east of Australia, then we would not expect females in advanced stages of pregnancy to be found in the far west of the fishery. Yet the one fish we considered pregnant, a 165 cm TL female with a girth of 93 cm, was tagged at 130°E on 15 October 1997. The pupping season is thought to be from November to January (Walker 1999). This fish would either have had to make an eastward movement of 15–18° of longitude over a period of several months, or, as fishers contend, pup in SA. A compilation of all available Australian data on the date and locality of capture of pregnant school sharks might assist with this question.

While the archival tags deployed on school shark revealed the movement patterns of a small number of individuals, the question remains whether it is appropriate to extend these conclusions to the entire stock. Olsen's study yielded 587 fish with known release and recapture positions. We had 15 fish with this information, but in addition had 475 (excluding tag 1396) estimates of weekly median longitude. While the releases were made in three wide-spread areas, the Beachport and Tas releases were each made in the same area and on the same day, very likely from fish in the same school, which could give us a biased result. It was surprising therefore to see the disparate movement patterns of the Beachport releases. The Tas releases showed more coherency: five of them remained to the east of Tas for 4–6 months before moving west, although one of them (98-092) had initially ventured west into Bass Strait for several weeks. However, in the first 2–3 months there were few periods in which fish were at the same longitudes, and the depth patterns generally differed between individuals (Fig. 6), so it seems unlikely that they schooling together even shortly after release.

The movement hypotheses generated from archival tagging can be evaluated by comparison with the results of conventional tagging. The timing of movements in our archival tagging study showed good agreement with Olsen's (1954) conclusions, and the limited movements between regions of the fishery revealed by the archival-tagged sharks also appears consistent with the results of the 1947–56 study. The results for the conventional tagging depend however, upon the (unknown) fishing effort in these two areas in the years following the releases. Details of school shark movements in the recent tagging study by Walker et al. (1997) have not yet been published, but will also provide a basis for comparison, especially as the distribution of fishing effort in recent years is much better documented. Ideas generated by the archival tagging such as the ‘summer’-‘winter’ shifts in school shark from the east to the west coasts of Tas could be tested by examining the recaptures from recent conventional tagging.

The archival tagging movement hypotheses could also contribute to the movement assumptions used in stock assessment. School shark stock assessments have until recently treated the stock as a single freely mixing unit, based upon the proven long-distance dispersal of the species. However, within Australia the school shark stock is spatially structured by size, age and reproductive condition and there are regional differences in catch-rates (Prince 1992, Walker 1998). This has lead to considerable debate about the single-stock assumption of earlier assessments. Punt et al. (2000) developed a population dynamics model that accounted for spatial structure by allowing for multiple stocks and by modelling the movement patterns of school shark explicitly. Parameter values were derived by fitting the model to catch-rate and conventional tagging data. They used a two-stock model because it fitted the data better than a single stock, and because the data could not support estimation of parameters for models based on more than two stocks. The two 'stocks' (actually 'movement types') differed quite markedly in their movement behaviour. One was estimated to be local to Bass Strait, and the other was more dispersed, spending very little of its life in the Bass Strait area. The results from the archival tagging sit comfortably with these conclusions, and make the generalisations based on such a small number of recaptures more credible.

The archival tagging did not contribute to the debate over the extent of trans-Tasman migrations revealed by conventional tagging. Hurst et al. (1999) considered that there was a relatively high emigration of New Zealand school shark to Australia (20 recaptures of New Zealand tags in Australia, only 5 showing the reverse movement). However, quantitative analysis of the tagging data is hampered by a lack of fishing effort data for the New Zealand fishery. In addition the very low recapture rate for trawl-caught releases (4.7%) compared with line-caught releases (22.1%) indicates that differential tagging mortality would need to be considered. None of our archival-tagged sharks (ignoring tag 1396 that was shown to be defective) moved further east than 149–

150°, but they were at liberty for only a maximum of 1.5 y. The school shark that moved to Australia were at liberty from 0.7 – 9 y (mean 3.9 y). The chances of getting long-term archival-tag recaptures from small numbers of releases are poor, a consequence of the rapid decay in the number of recaptures with time. It seems more likely that the contribution that archival tagging in Australia could make to this debate is to place upper limits on the likely probability of movement to New Zealand (given an hypothesised movement probability, what is the probability of none of the recaptures moving). Archival tagging in New Zealand might be more promising if in fact the movement rates are reasonably high. Pop-up archival (as opposed to single point) tags could also be considered. When these tags release they transmit summaries that allow description of the depth and temperature regimes and calculation of position. They store all collected data, but this can only be retrieved in the unlikely event that the tag is found. However, pop-up tags were designed for species with very low recapture rates. With our relatively high recapture rates and the higher cost of the pup-up tags they are marginally cost-effective (for the same outlay 2.3 times as many archival tags could be bought and a recapture rate of 1/2.3 = 0.44 would yield the same number of 'recaptures'). In addition the onboard geo-location is relatively untested and the tags require external attachment. To increase the chances of detecting a trans-Tasman movement they would need to stay attached for at least several years, and no attachment methods have yet been tested for pop-up tags on school sharks. Being external, they are subject to the normal problems of increased drag and possible shedding. One area where pop-up tags could make a valuable contribution is in estimating mortality after tagging as current tags are designed to release if the animal has died.

8. BENEFITS

The beneficiaries of this project were identified in the original proposal as 90% to AFMA for the sustainable management of the fishery and 10% to the general study of fish movements.

The outcomes of the research are as expected: the principal benefit from this project is its contribution to the sustainable management of the southern shark fishery. The movement patterns discerned in this study support the current approach in stock assessment and may prove useful if a reduction in the targeting of school shark is required in the future. The research has made a substantial contribution to the study of fish movement and in addition the information may be of commercial value to fishers and contribute to their greater efficiency.

9. FURTHER DEVELOPMENT

Geo-location

We used a reference light level approach based on average light levels at certain sun angles because this was the method developed for the southern bluefin tuna GLS. This approach was originally developed for air-breathing animals, without the need to account for the attenuation of light underwater. However, there are other measures, such as a percentage of the light level at noon or the time at which light changes most rapidly, that might be superior. It would also be desirable to develop a way of assessing water clarity, such as the average light intensity and depth at noon, that might assist with the problem of fish moving into waters of different optical properties.

Further improvements to the software would also speed up the geo-location process. At present the software has two modes: a batch approach with a single set of parameter values applied to the whole data set, or estimation day by day, changing parameter values to suit conditions. The former approach is rapid, but fails on many days. The latter approach could be improved to allow simultaneous display and estimation of both solar noon and solar midnight.

Estimation of longitude.

The use of weekly median longitudes appeared to account for much of the variance in the daily estimates, but the method needs closer statistical scrutiny, to look for possible biases and to examine the optimum time period over which to calculate median (or average) longitudes. At times the weekly median longitude was badly affected by outliers, and further work is needed to develop an objective method for removing them. There is also a need to develop the software to allow routine dive-based longitude estimates for those times when the sharks are making regular dives to depths below the level of light detection. At present this analysis is done by hand.

Estimation of latitude

Our initial attempts at using light-based estimates of latitude showed them to be seriously biased. While for much of the south coast of Australia we can estimate latitude from the depth data, this breaks down around Tasmania While there will always be high variability in light-based latitude estimates, if they are unbiased, then average or median estimates might be effective. It would also be an advantage to further refine the depth-based latitude estimates, to show if more than one position is possible for a given longitude, rather than just choosing the most southern one. This would help in areas where there might be basins on the continental shelf, as well as indicating if a position is possible both in Bass Strait and southern Tas.

Temperature

It would be useful to describe the seasonal changes in water temperature that the sharks experience and their relationship to movement, as Olsen (1984) associated movements in Tas with changes in water temperature. It is also possible that the water temperature data could contribute to some of the questions surrounding latitudes (e.g. Bass Strait vs southern Tas). At times the school shark are near the surface at night, and if the temperature data from the tags indicate that the water column is well mixed, we could estimate sea-surface temperatures, and compare them with satellite observations. At times when the sharks make deep dives, it will reveal the temperature structure of the water column, and provide clues to the oceanographic conditions (e.g. possible upwelling) in those areas. On some of the sharks fitted with internal tags we have information on both body temperature and external temperature. Analysis of this data would provide an insight into the physiology of these sharks that has never previously been available.

Lunar periodicity and seasonal effects on depth

We have not attempted to examine whether sharks tend to be deeper at certain moon phases or whether they tend to be deeper in winter, as suggested by Olsen. However, this could require combining the data from each tag into a file with approximately 1.4 million lines, and would present a serious challenge to our software and hardware.

Application of archival tag movement hypotheses to conventional tag data and catch data

One of the challenges facing the use of archival tags is how to integrate the results obtained from a small number of animals into the existing knowledge base derived from extensive conventional tagging. The school shark archival tagging resulted in three generalisations about movement:

1. There was a strong seasonal signal (March–April and October–November) in the timing of longitudinal movements, with movements early in the year tending to be reversed towards the end of the year. No fish moved across the full expanse of the fishery in the relatively short time (< 1.5 y) they were at liberty.
2. There was a contraction of their range in winter, the school sharks retreating from the far western and eastern regions and concentrating within regions in South Australia and off the west coast of Tasmania.

3. The school sharks were not uniformly distributed across southern Australia, but were found in 4 preferred longitudinal zones.

The credibility of the archival tag movements needs to be assessed by comparison with conventional tag results. The converse also applies: the modelling of conventional tag movements, an essential part of the stock assessment process, may benefit from the insights provided by archival tagging into the seasonal nature of the longitudinal movements.

Ecological aspects of school shark movement patterns

The factors that influence the timing and direction of school shark movements are also likely to affect the movements of other species. Fishers note that school shark arrive in Bass Strait at the same time as the short-tailed shearwater (around September), and depart when the birds leave in April–May. School shark archival-tagged in Tasmania spent summer to the east of Tasmania, where a summer fishery exists for jack mackerel. In winter the school shark moved to the west of Tasmania, where a winter fishery exists for blue grenadier. Both of these species appear in the diet of school shark. Arrow squid are also an important component of the diet of school shark and show similar daily vertical movements in the water column. Juvenile southern bluefin tuna migrate across southern Australia and adults make seasonal returns to the GAB. There has been a long history of conventional, and more recently archival tagging of this species. Marine mammals also make seasonal movements into southern Australian waters. It would be highly desirable to synthesize the biological and oceanographic information to investigate the seasonal cues that might influence the timing of animal movements in this region.

Future releases

The 15 returned tags will be refurbished and re-deployed in the future, which should result in an additional 4–5 returns.

Industry collaboration

It is envisaged that this report will be publicised by both FRDC and AFMA, so that all shark fishers will have access to it. Industry involvement in the interpretation of the results is essential, and would be best done in conjunction with meetings of southern shark fishers for other scientific or management purposes.

10. CONCLUSION

Objective 1. To determine the frequency and extent of movements of individual school sharks within the fishery leading to an improved understanding of spatial structure required for regional assessments of school shark stocks.

Outcome: The archival tag results showed that the school shark did not migrate across the entire range of the fishery in the time they were at liberty (<1.5 y), and that there was limited mixing between the eastern and western regions of the fishery in this time frame. They were also not evenly dispersed across southern Australia, but were concentrated into four regions. The outer regions (GAB and Tas east coast) were frequented during summer, and in winter the fish moved to more central regions (Kangaroo Island and the Tas west coast respectively), resulting in a contraction of their longitudinal range. The restricted movement shown by the archival-tagged sharks provides additional support for the move to spatially-structured stock assessments (Punt et al. 2000).

In Tas waters March–April were times of major movements to the west coast, and October–November were times of major movements to the east coast. The timing is in general agreement with Olsen's (1984) conclusions: movements before winter and in spring. In SA the movements occurred over a wider time period, with increased movement rates from October to May. Movement rates peaked in November with fish moving both east and west.

Objective 2. To determine whether the total population of mature female school sharks migrate to Tasmanian and Victorian waters to pup and consequently whether recruitment is dependent on south-eastern pupping areas.

Outcome: The strategy was to tag pregnant females in SA just prior to the pupping season and follow their movements from returned archival tags, knowing that they would give birth within several months. However, this objective was not met, because of the scarcity of pregnant fish in the catch. Only one tagged shark was considered to be pregnant (based on a girth measurement) and it was not recaptured. The scarcity of pregnant females in the catch makes it doubtful that archival tagging can address this question.

Objective 3. To provide information on the swimming depth of school sharks and to estimate the amount of time they spend off the bottom and unavailable to commercial fishing gear. This information is required in assessing the relative impact of current fishing effort directed at school and gummy shark.

Outcome: The school sharks were shown to be in depths from the surface down to 660 m. One of the most striking dive patterns was seen in deep water when the sharks would make regular descents during day light hours to depths of up to 660 m and return to near the surface at dusk. At other times in deep water, although the fish were deeper during the day, the depth pattern was very irregular. However, the amount of time spent in deep water was minor – overall, school sharks spent 91% of their time on the continental shelf at depths <200 m, where a wide variety of dive patterns were observed. One of the most common was a pattern of nightly ascents, often to near the surface. At the time of the full moon, these ascents were usually, but not always, suppressed. We have yet to estimate the amount of time the fish spend off the bottom because of the complexity of other dive patterns shown by the species, and the uncertainty this introduces as to whether the fish were actually on the bottom.

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13 Appendix A1: Intellectual Property

Until the movement hypotheses resulting from the analysis of such a small number of archival tagging have been thoroughly tested by comparison with conventional tagging results it is difficult to assess how much commercial value they will be to the fishing industry. If the results are valid, particularly the range contraction in winter, it should already be apparent in the catch records and fleet dynamics. There is no doubt however, that the movement and depth information will be intensely studied by many operators, as it represents a quantum leap in our understanding of school shark behaviour. However, CSIRO cannot guarantee that the data and analyses are free from errors or omissions, and CSIRO Marine Research or FRDC will not be liable in any way for the use of this information by fishers.

Appendix A2: Staff

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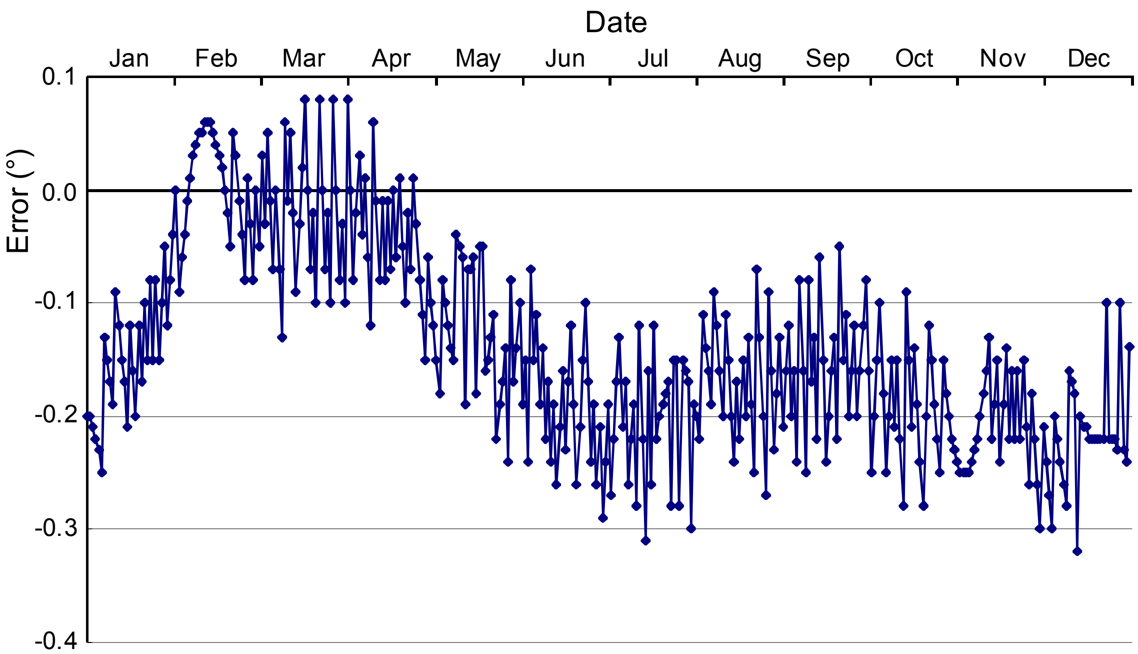
14. APPENDIX B: Detailed geo-location methodology

14.1. Validation of geo-position software.

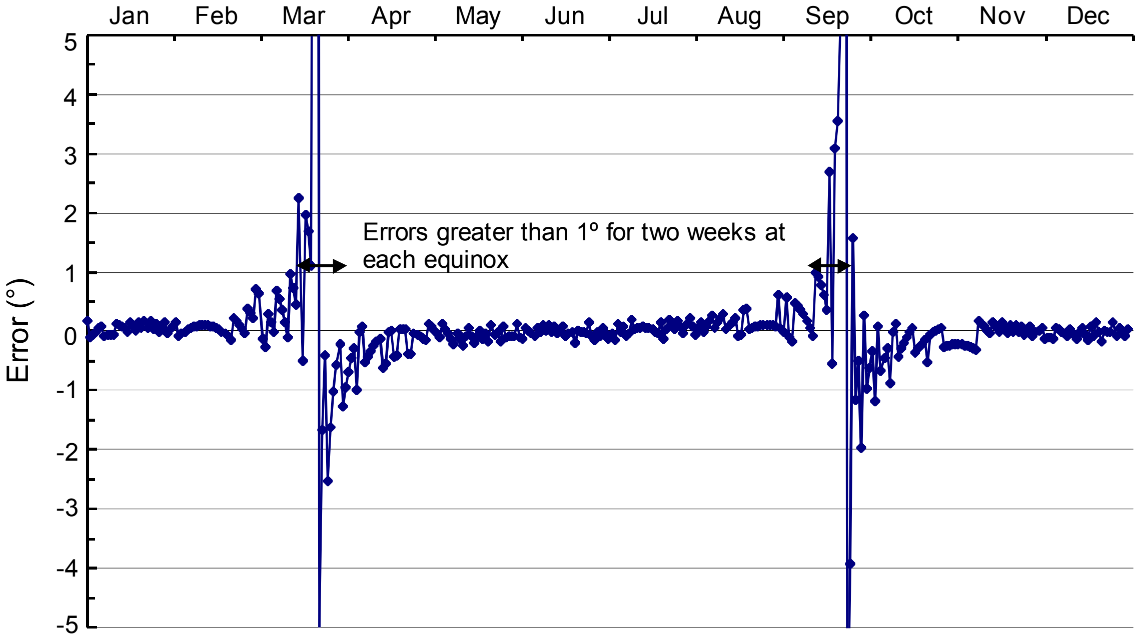
The iterative approach to solving the astronomical formulae requires relatively complex programming, and in addition the program has to locate the appropriate parts of the light curves to operate on. A first step to check for the correct operation of the software is to use times of sunrise and sunset (to the nearest minute) for a known location on the earth's surface, and check that the software correctly estimates the locality. There are a number of sources of sunrise and sunset times for particular localities, the most convenient being on the World Wide Web (e.g. http://aa.usno.navy.mil/AA/data/, http://www.auslig.gov.au/geodesy/astro/sunrise.htm). This approach was useful in eliminating several programming problems, and the results are shown in Fig. B1 for longitude, and in Fig. B2 for latitude.

Fig. B1. Longitude errors based on times from US navy website (nearest minute) for 5°E, 35°S.



It is thought that the cyclical pattern to the longitude errors may be caused by approximations in the astronomical formulae. On average, there is a slight bias towards estimating longitudes too far west, but the size of the bias is irrelevant to the problems of estimating positions for tags on fish. The estimation of latitude from day length appears satisfactory, with the expected problems around the times of the equinoxes.

Fig. B2. Latitude errors based on times generated by the US navy website for 5°E, 35°S.



14.2. Parameter requirements of the CSIRO geo-location software

The CSIRO geo-location software requires values for the following parameters:
1. Reference light level
2. Zenith angle of sun at which the reference light level was derived
3. Light attenuation characteristic of the tag
4. Reference depth for standardisation of light

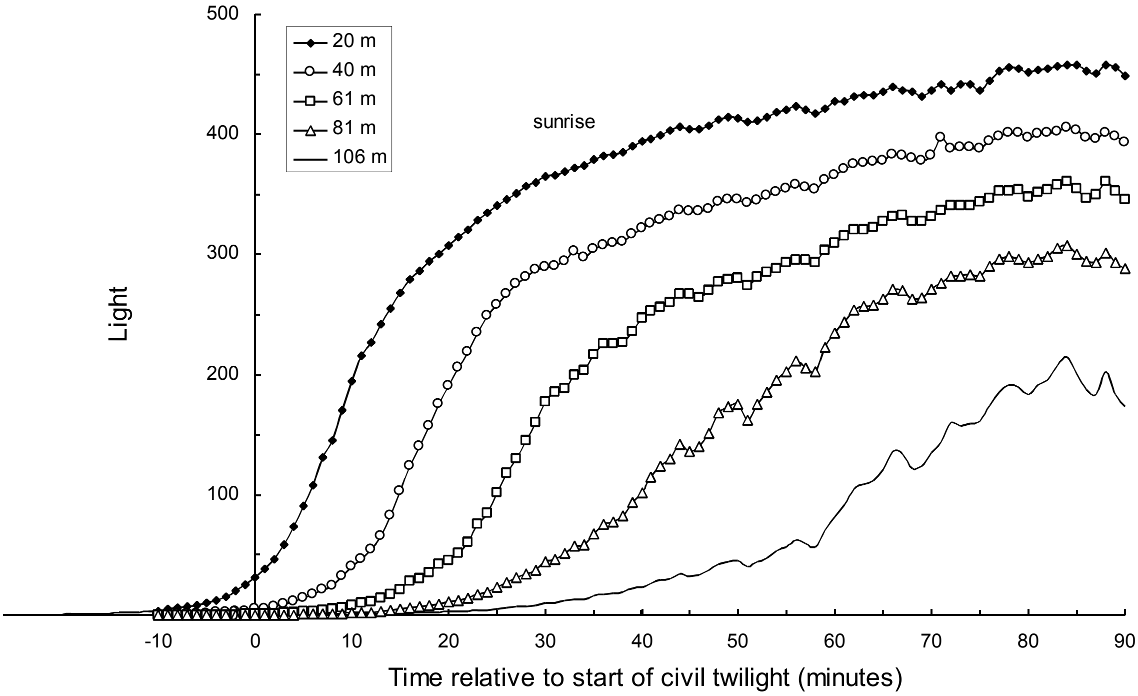
To date all geo-location has been based on sun angles around the time of civil twilight (the time at which light intensity changes most rapidly at the surface) and light has been corrected to surface levels. This is because either the work has been carried out on air-breathing animals or on pelagic fish such as tunas that spend time near the surface. However, with demersal fish, there is no necessary reason to correct light levels to surface values. If a sub-surface reference depth is used, it is necessary to describe how this might affect the time at which light changes most rapidly. Logically, this time must be delayed as depth increases, as eventually there will be a depth when light does not penetrate even when the sun is at its highest point during the day. Since the tags from the different manufactures differ in their sensitivity to light, these values are likely to be tag-specific.

14.3. Lotek tags

14.3.1 Time at dawn and dusk at which light changes most rapidly

We carried out a dawn experiment to investigate the effect of depth on the time at which light changed most rapidly. An array of tags at five depth intervals from 23–112 m [Footnote 1] was suspended from a boat during dawn on 11 Nov 1998. The distance from shore was approximately 10 km and depth about 130 m. The tags were set to record light and depth every second. All deck lights were extinguished. The results are shown in Fig. B3. Cloud conditions were totally overcast, and ambient light appeared to increase fairly smoothly through the dawn.

Fig. B3. Light sensor response (1 minute interval subsets) of Lotek tags during dawn, 11 Nov. 1998, at depths of 20–106 m.



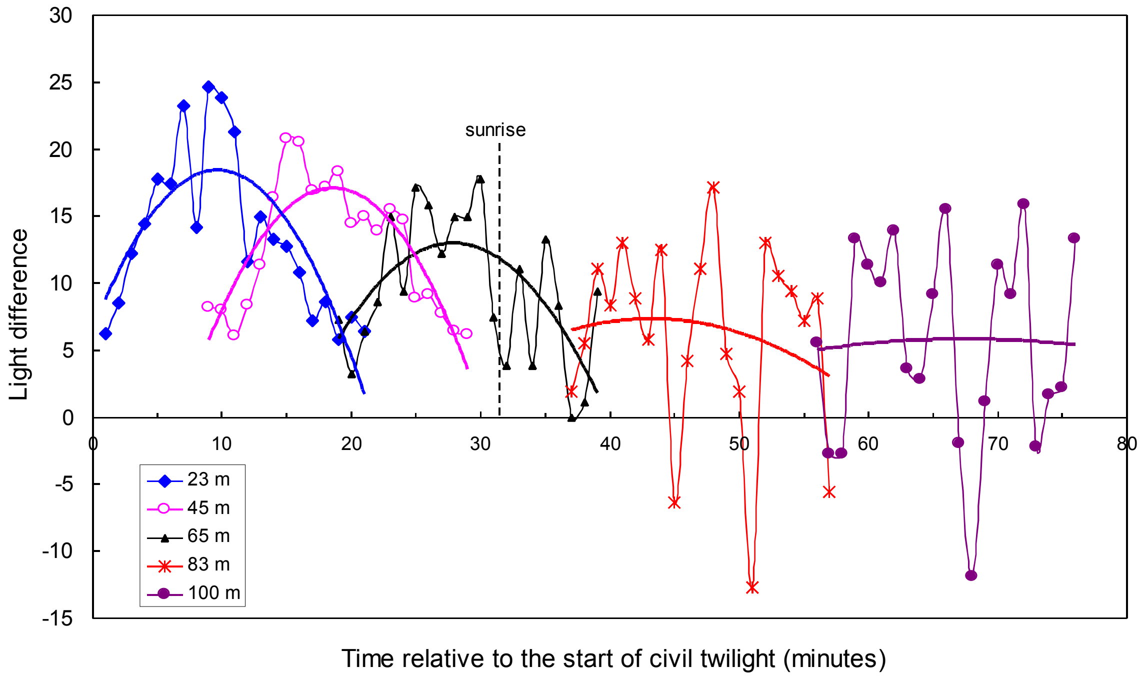
The time when light is increasing most rapidly is the steepest part of each curve. Wildlife Computers 1994[2] defined dawn and dusk as occurring within the time segment in which light was changing most rapidly. They located the maxima (or minima) by fitting a quadratic curve to the log-transformed rates of change of slope (the log transformation was used to smooth the data). Welch & Eveson (1999) used a similar method in which they first smoothed the light data using either digital signal processing or curve fitting techniques, calculated the difference between successive light readings, and then fitted polynomial curves to the difference data. Maximum (or minimum) values were obtained by differentiating the polynomial equations with respect to time, and finding when the derivative equalled zero. For the Lotek tags 2nd to 4th order polynomial curves were fitted to the differences between successive light readings, and the

[1] The drift of the boat caused a progressive decrease in the depth of the array. The depths quoted are the average from the start of civil twilight to 90 minutes later, during which time depths decreased by 7-16 m from the most shallow to deepest tag respectively.

[2] Geolocation v.2.0 software documentation, revised 01/94. Wildlife Computers, 16150 NE 85th Street #226, Redmond, WA 98052, USA.

maxima (t_{max}) was located by visual inspection[3]. The results are shown in Fig. B4 in which 2nd order polynomial curves were fitted to points 10 minutes either side of the time at maximum change (itself derived from 2nd order polynomial fits)

Fig. B4. Difference between successive 1-minute light readings for tags at depths from 24 to 113 m, at dawn on 11 Nov. 1998. Second order polynomial regressions fitted to data 10 minutes either side of t_{max}.

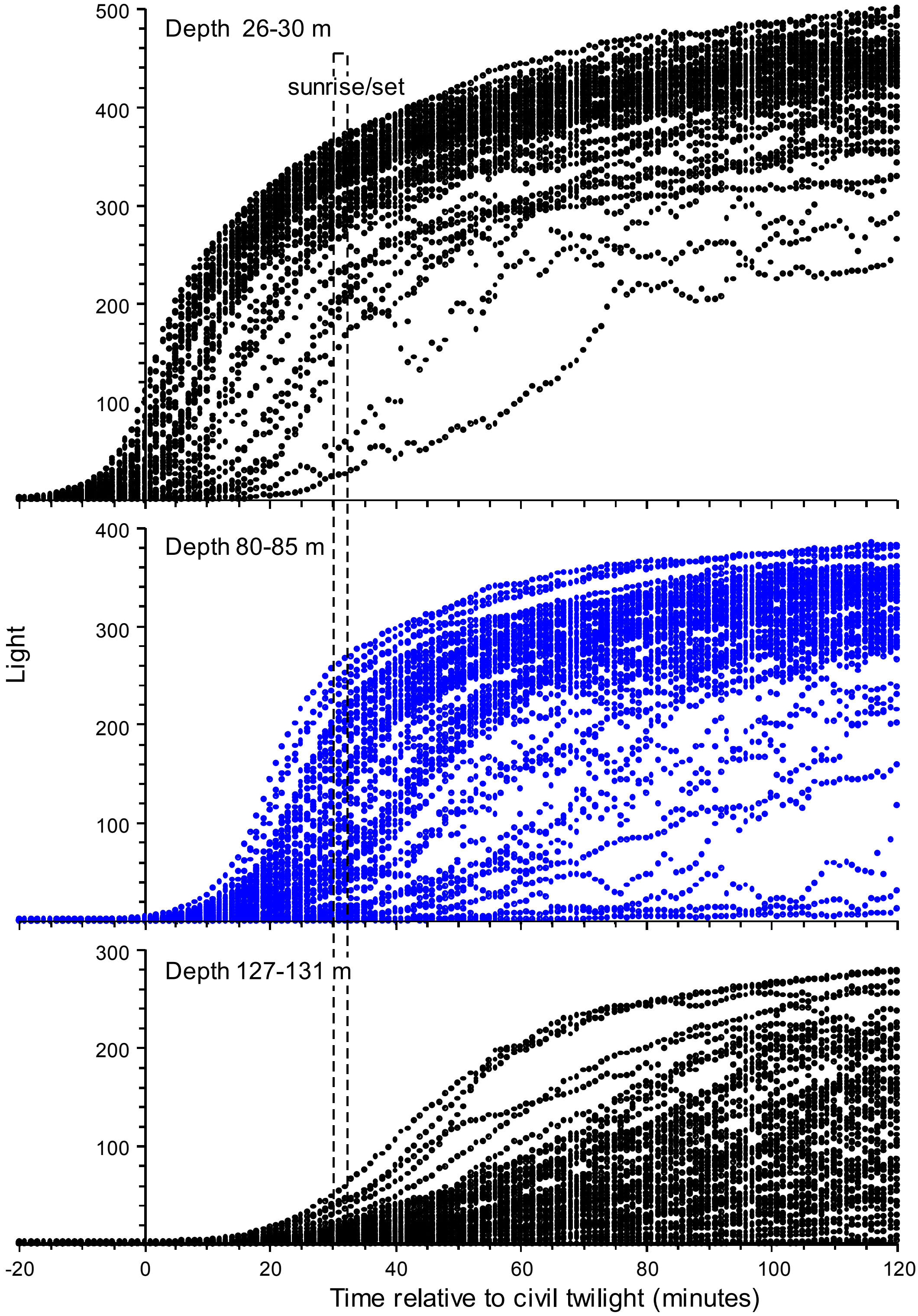


The time at which light changes most rapidly is delayed with depth, and at 100m is poorly defined, which is consistent with the relatively linear increase in light for this depth (Fig. B3, bottom curve). This will result in less precise estimates of the time of dawn and dusk at greater depths, but make the choice of zenith angle less critical. While these results present a coherent account of light at dawn for one (cloudy) day, they cannot be taken as generally representative.

We conducted a mooring experiment with a tag at a depth of approximately 40 m during January–February 1998, and again in May–June 1998 when we had three tags at depths of approximately 30, 80 and 130 m. The tags were set to record every minute (note that on tags deployed on fish, the interval was 4 minutes, to prolong the duration of recording). The location was approximately 7 km from shore (3.5 km from Tasman Island) at a bottom depth of 132 m. The light data during twilight for the three tag experiment are shown in Fig. B5. Because the depth of the two uppermost tags changed with the current, their depths were restricted to 5 m intervals.

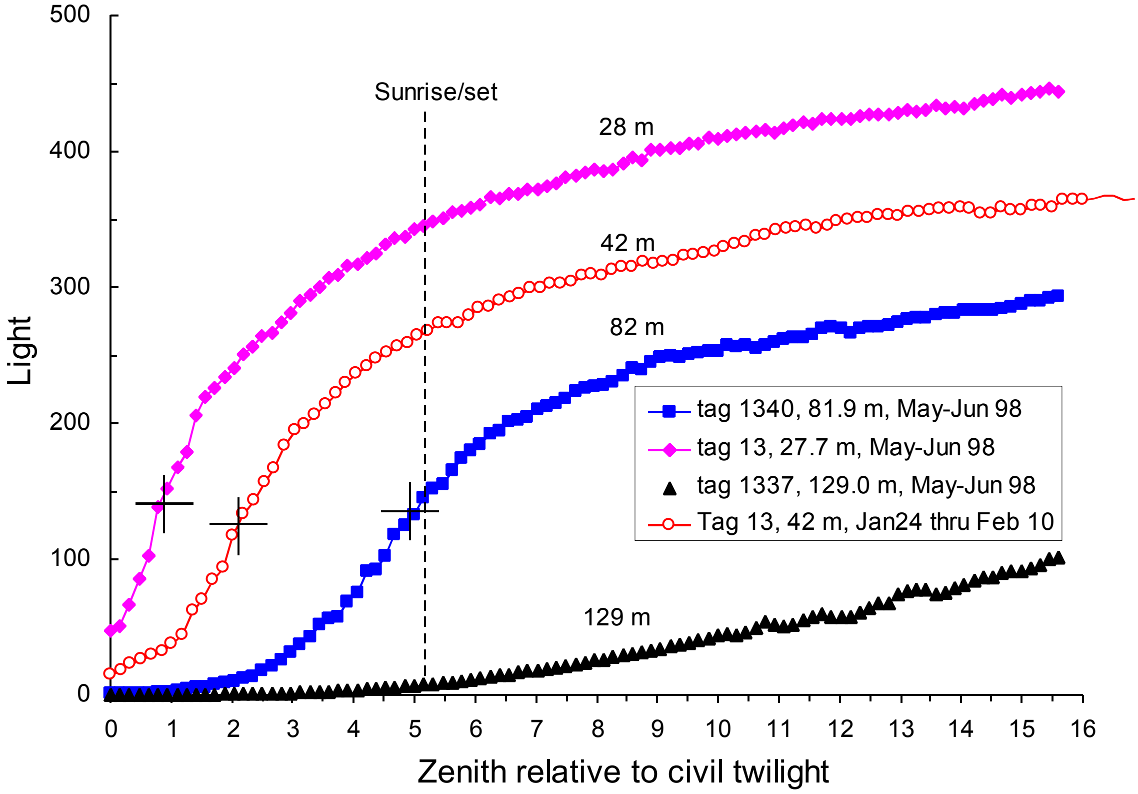
[3] While differentiation is the preferred method to use, in our case with light recorded at 1 minute intervals and time scales on the x-axis at 0.5 minute , it was possible to identify local maxima and minima to the nearest minute. Given that atmospheric variation causes the apparent time of sunrise and sunset to vary by up to several minutes (Nielsen 1963, Hill 1994) we considered that visual inspection was satisfactory in this developmental context.

Fig. B5. Light regimes during twilight at three depths, Tasman Island, May–June 1998



The results show the pronounced influence of variations in weather and possibly water clarity, particularly for the deepest tag, which on some occasions failed to register light even approximately 90minutes after sunrise (conversely at dusk). To gain an idea of the central response we calculated median light levels (average light levels would be more influenced by outliers) at 1 minute intervals from the start of civil twilight at dawn (conversely at dusk) until 100 minutes later, to generate composite light curves for the January and May–June experiments (Fig. B6).

Fig. B6. Median light at four depths for sun elevations of -6º to 10º above the horizon.



Time is presented as the angular elevation of the sun with respect to the start of civil twilight (centre of sun 6º below the horizon), rather than minutes after the start of civil twilight. This allows comparison with results achieved at different times of the year, as the time interval between civil twilight and sunrise, for instance, varies throughout the year and with latitude. A value of 12º on the x-axis for example means that the sun is 6º above the horizon.

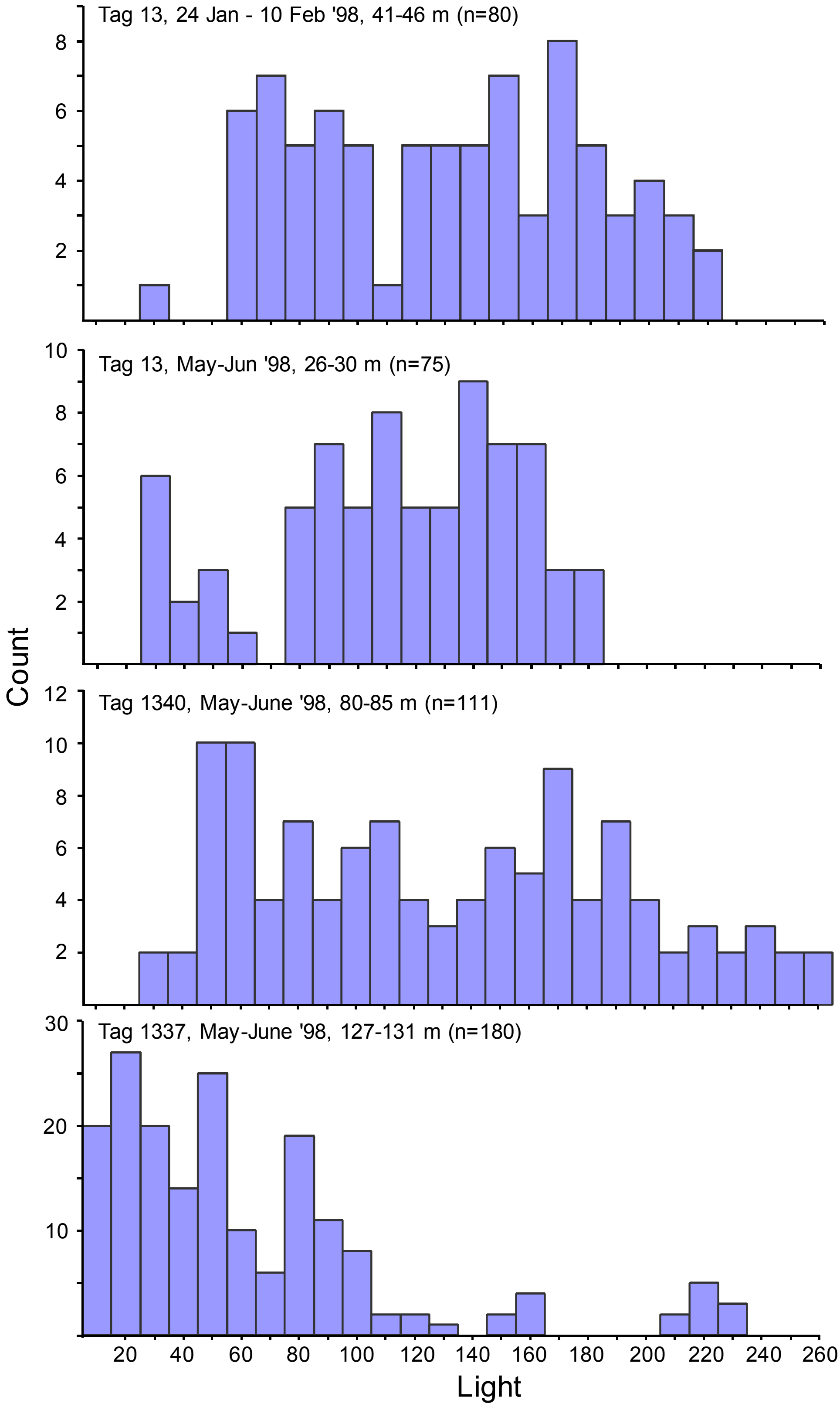
The time at which light changed most rapidly, based on the average of results from 2nd – 4th order polynomials was calculated for the three upper curves. A t_{max} could not be estimated for the deepest tag as the rate of light increase was approximately linear, so we used two arbitrary zenith angles: 86°and 81° (centre of sun approximately 5° and 10° above the horizon). Three different tags were used in these experiments, and since each tag differs in its sensitivity to light the raw values were standardised to a value based on tag 1340 (Table B1).

Table B1. Values for reference light levels (median) and zenith angles at four depths.

Tag no.	Date	Average depth (m)	t_{max} (º relative to civil twilight	Zenith angle º	Median light level	Median light level standardised to tag 1340
13	May–Jun '98	27.7	0.87	95.1	130.5	145.3
13	Jan–Feb '98	41.8	1.93	94.1	116.1	129.2
1340	May–Jun '98	81.9	4.92	91.1	121.6	121.6
1337	May–Jun '98	129.0	10.0	86.0	43.0	44.2
"	"	"	15.0	81.0	92.9	95.4

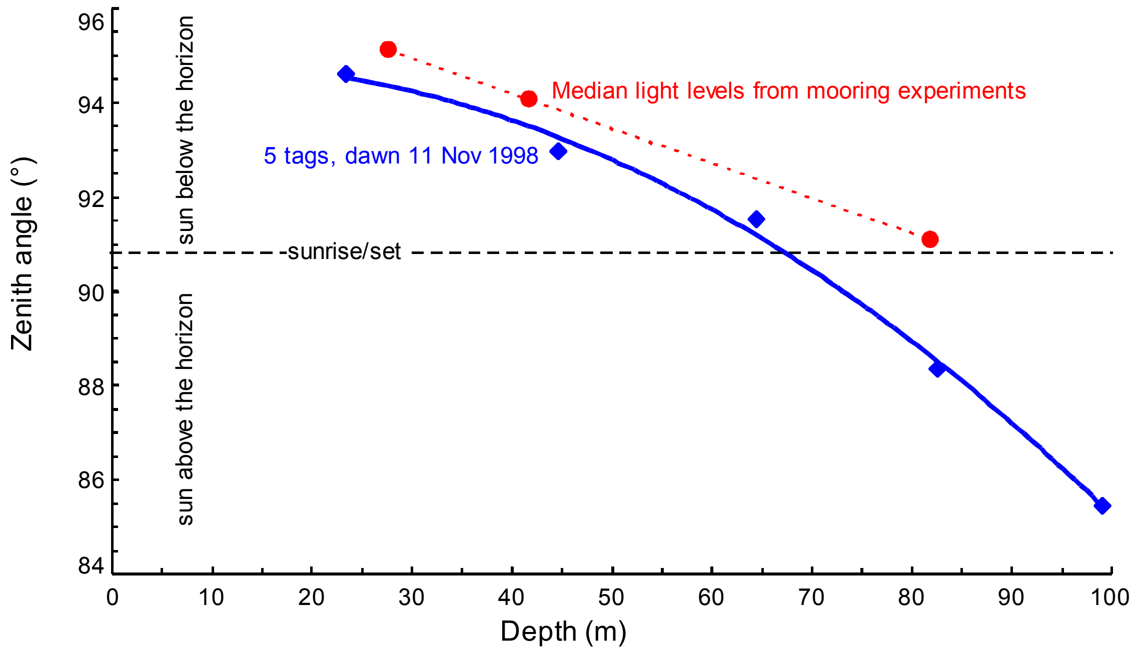
The distribution of light values at the times of most rapid change in light for this experiment is shown in Fig. B7. The bi-modality evident in most of these distributions will be reflected in very different times of dawn and dusk assigned to twilight events by the reference light level method.

Fig. B7. Distribution of light values at the time when light is changing most rapidly for tags on a mooring at depths of 28, 42 and 82 m, and at zenith angle of 86° for tag at 130 m.



The relationship between depth and t_{max} obtained from these mooring experiments is shown in Fig. B8, together with the results obtained from the single dawn experiment on 11 Nov '98. The results from the mooring experiments show that under 'average' conditions t_{max} is not as delayed as for the 11 Nov experiment, which was carried out under heavily overcast conditions. With only three points for the mooring experiments there is no evidence that the apparent linear relationship would continue at greater depths, but in any case, by 130 m there is no period of most rapid change in light.

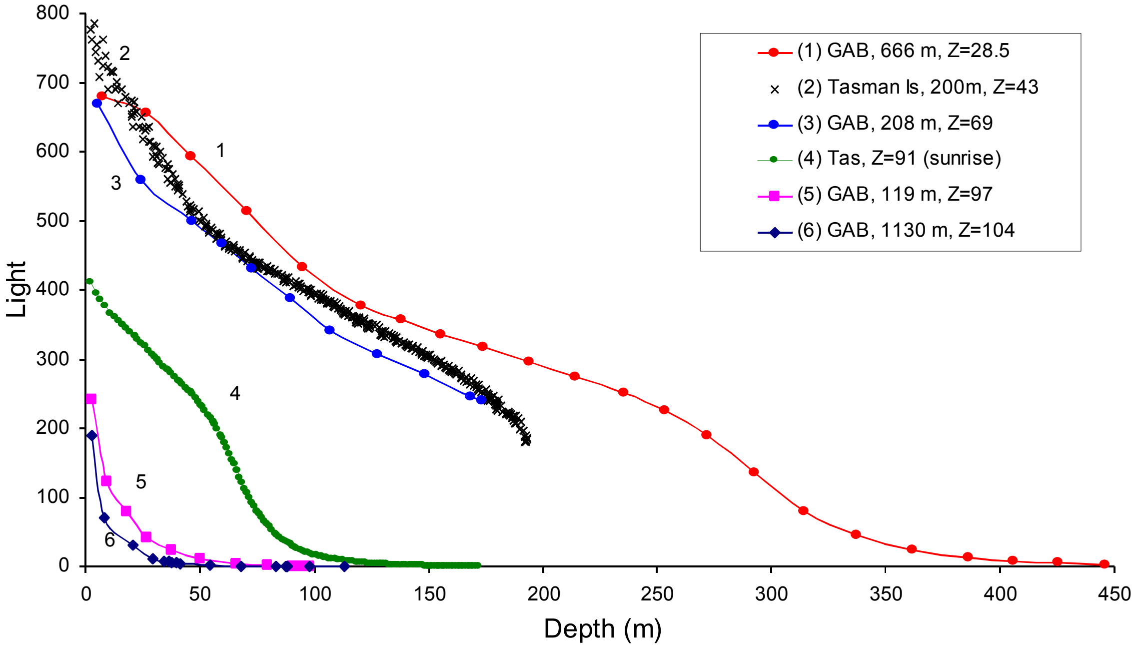
Fig. B8. Effect of depth on the time at which light increases most rapidly



14.3.2 Light attenuation with depth for Lotek tags

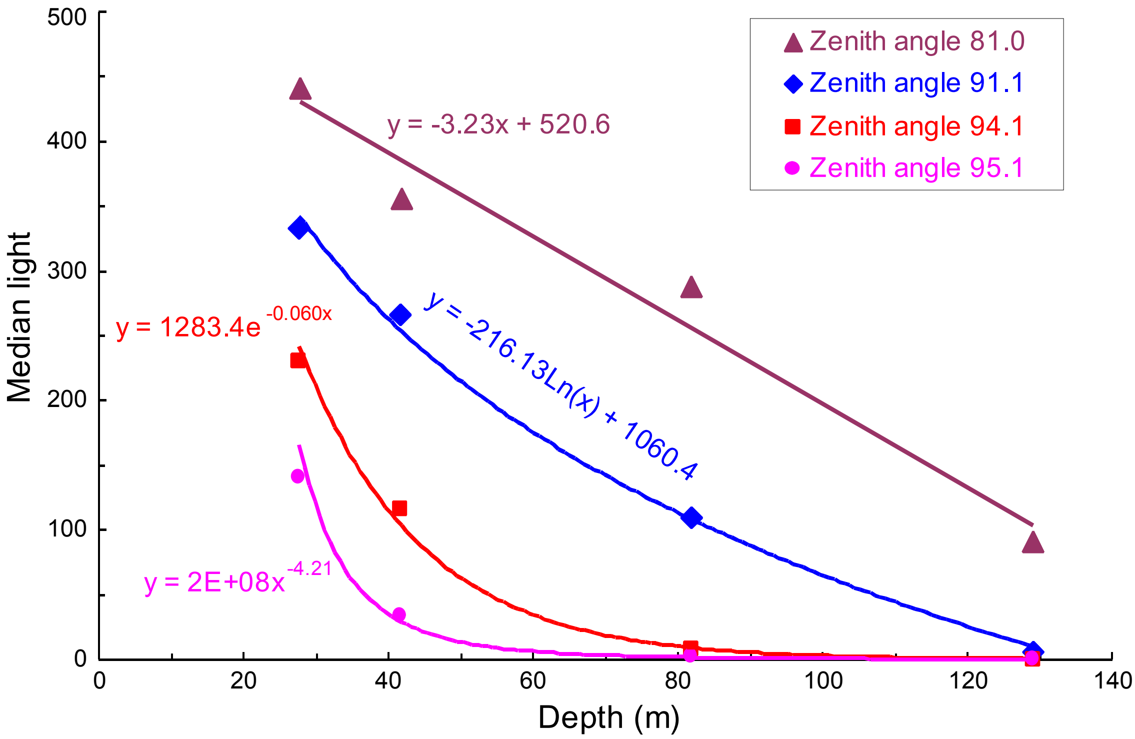
The mooring experiments provide for three depths at least, the median light level to use as a reference level at the appropriate time (i.e. zenith angle) of greatest change in light intensity. Regardless of which depth was used as the reference depth, there remains the problem of adjusting the light data from returned tags to the standard depth chosen. The usual way of doing this is to carry out casts with the tags down to the maximum depths at which they respond to light. Typically, the casts would be carried out towards midday, to maximise the depth penetration. Most of our casts were carried out with the tags attached to the CTD probe on our research vessel, and results were obtained for different times throughout the day (Fig. B9)

Fig. B9. Lotek tag light-attenuation characteristics at different times of the day.



The light attenuation relationship shown by these tags changed during the day in quite a dramatic fashion, which was not expected. We had expected that there would be a rapid fall in light in surface waters, as the Lotek tags we used had not been fitted with filters over the light sensors, which have a peak spectral sensitivity at 750 nm (longer wavelength radiation is rapidly attenuated with depth). At sun angles below the horizon (curves 5 and 6 in Fig. B9) the decay in light appeared exponential, but at sunrise and later the relationship was more complex, and not readily described by a single regression. For restricted depth ranges linear fits appeared possible (e.g. between 25–100 m and 120–250 m for curve 1 in the mid-afternoon). What appeared common to all curves was that at light levels below about 200 units, the decline in light with depth was curvilinear. It was encouraging that there did not seem to be large differences in light attenuation between the inshore site used to test tags in Tasmania (approx 8 km from shore) and the offshore stations in the GAB (curves 2 & 3, Fig. B9), an area where we intended to tag sharks. Given that the three optimum zenith angles were all at sun angles below the horizon, we needed more information on the behaviour of the light sensor in the tags during twilight. To do this with depth casts is difficult because the casts must be rapid as light is changing quickly at these times, all deck lights on the vessel need to be switched off and it would need to be repeated under a variety of weather conditions. The approach we used was to use the data from the mooring experiments to examine light levels at different times during twilight at the four depths used. The median light levels at the depths and zenith angles corresponding to t_{max} in Table B1 were obtained by linear interpolation of median light levels at 1 minute intervals during dawn and dusk. In addition, data were derived for zenith angle 81° to obtain a light attenuation relationship for that arbitrarily chosen zenith angle (Fig. B10).

Fig. B10. Light attenuation with depth for Lotek tags at zenith angles of 95.1, 94.1 and 91.1 and 81.0° from mooring experiments.



At the lowest sun angle, Z = 95.1°, a power curve was the best fit (exponent -4.21). At Z = 94.1° an exponential regression was fitted, with exponent -0.060. At Z = 91.1°, close to sunrise/set, the best fit was a semi-log curve, with a co-efficient of -216.3 for the log transformed depth. The curve at Z = 81° showed some of the awkward characteristics expected from casts during the day; a linear regression was fitted, but it failed to capture the underlying relationship. Because the mooring experiments were only carried out to depths of 130 m, for deeper depths the mid-afternoon light attenuation shown in Fig. B9 (no. 1) was used to derive corrections for two separate parts of the depth regime. A summary of the parameter values and light attenuation corrections is shown in Table B2.

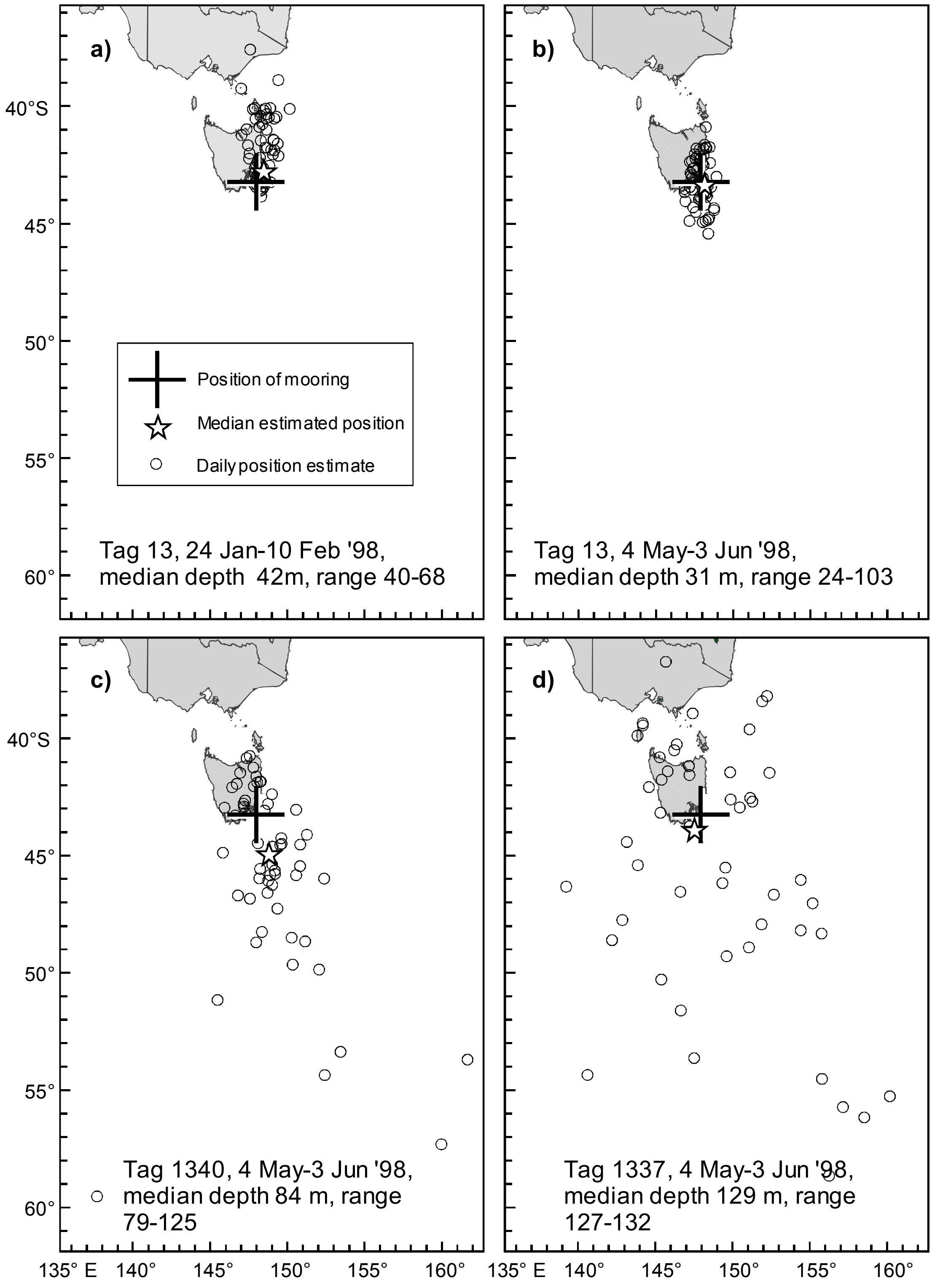
Table B2. Summary of parameter values required for geo-location with Lotek tags using the CSIRO reference level software.

Reference depth (m)	Zenith angle °	Reference light level	Depth correction for light attenuation	Type of attenuation relationship	Applicable depth range for light correction (m)
27.7	95.13	145.3	exp[ln (light+0.001) - 4.21(ln 27.7-ln depth)]	power	28–129
41.8	94.07	129.2	light $[e^{-0.060(41.8\text{-depth})}]$	exponential	"
81.9	91.08	121.6	light - 216.1(ln 81.9-ln depth)	semi-log	"
129.0	86.0	44.2	light - 3.39(129.0-depth)	linear	"
"	81.0	95.4	light - 3.23(129.0-depth)	"	"
138–272	mid-afternoon cast		light - 1.19(reference depth-actual depth)	linear	138–272
272–406			light $[e^{-0.025(\text{reference depth-actual depth})}]$	exponential	272–406

14.3.3. Accuracy of position estimates for Lotek tags based on mooring experiments

Having derived estimates of reference light levels, zenith angles and attenuation coefficients from tags at different depths on two moorings off Tasman Island, we used them to estimate the known position of the moorings. In the experiment in Jan–Feb 1998, the tag had a heavy growth of a hydroid *Obelia sp*. so estimates were derived for only the first half of the experiment (Fig. B11).

Fig. B11. Position estimates for two mooring experiments at Tasman Island, Jan–Feb and May–June 1998.



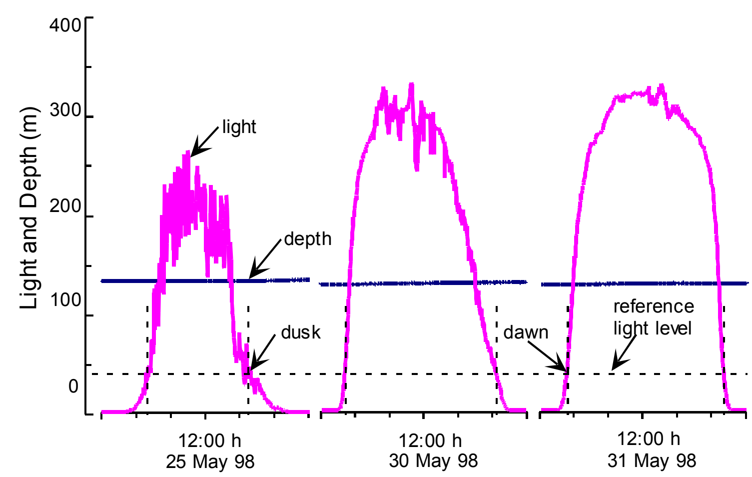
These estimates were derived using a single set of parameter values for each tag from Table B2. Estimates were not possible for all days because on occasions the light regime was incompatible with these settings, although this was more of a problem with the two deeper tags. The most conspicuous result was the dramatic increase in the variability of both longitude and latitude estimates for the two tags at ~80 and ~130 m. A statistical summary of the position errors is given in Table B3

Table B3. Position estimation errors for Lotek tags on two moorings off Tasman Island.

	Longitude errors (°)				Latitude errors (°)			
	Tag 13	Tag 13	Tag 1340	Tag 1337	Tag 13	Tag 13	Tag 1340	Tag 1337
	24 Jan–10 Feb '98	4 May–3 Jun '98			24 Jan–10 Feb '98	4 May–3 Jun '98		
Mean	0.29	-0.02	1.00	0.92	0.81	0.00	-2.39	-1.86
Median	0.25	0.04	0.64	-0.39	0.63	-0.01	-1.49	-0.61
Standard Deviation	0.57	0.49	3.23	4.74	1.03	1.04	4.05	5.45
Range	2.39	2.07	23.98	20.95	3.77	4.55	18.77	23.68
Minimum	-0.90	-1.07	-10.29	-8.68	-0.59	-2.27	-16.26	-15.36
Maximum	1.49	1.01	13.69	12.27	3.18	2.29	2.52	8.33
Inter-quartile range	0.53	0.74	2.71	6.54	1.54	1.62	4.02	7.15
Count	33	58	56	51	33	58	56	51
Depth range	40–68	24–103	79–125	127–132	40–68	24–103	79–125	127–132

Outlying positions are not the result of failure of the software, but of the vagaries of the daily light curves. An example is shown in Fig. B12, in which longitude estimates shift by 8° because of asymmetric increases and decreases in light at twilight. Future developments of the software may allow comparison of the dawn and dusk slopes, and generation of a measure of similarity that could be used to classify the data, and allow objective removal of outliers. This would not necessarily help to identify latitude outliers, as the curve may be symmetrical but still have a much shortened apparent day length

Fig. B12. Examples of daily light curves and the effects of asymmetry on the longitude estimates for tag 1337 at 129 m off Tasman Island. Figures in brackets are the longitude errors - positive indicates bias to east.



Longitude error (°)	8.3	4.3	0.9
Latitude error (°)	-15.4	5.1	8.3

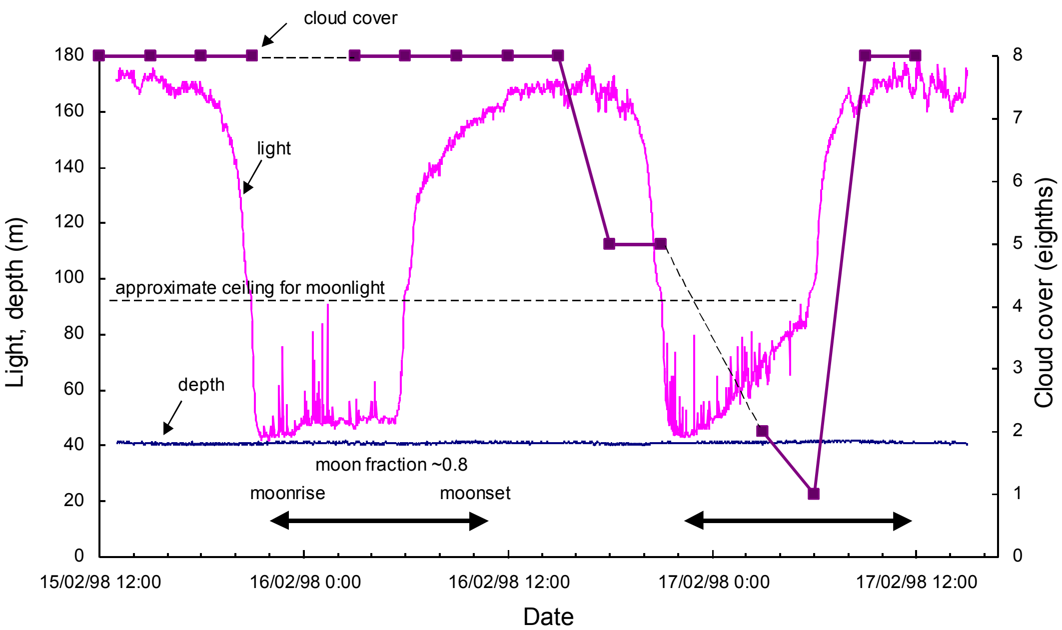
It was expected that there would be some bias in the longitude estimates because at the position of the mooring, while the sun rose over the sea it set over land. In the January–February mooring experiment (Fig. B11a), the sun set behind the mountains of southern Tasmania (elevation approximately 1150 m above sea level) some 100 km away. Ignoring the curvature of the earth, the mountains would subtend an angle of about 0.7°, which at this time of the year would advance sunset by about 4 minutes, advance midday by 2 minutes, and produce longitude estimates about 0.5° towards the east of the real position. In reality the effect would be less than this. The median longitude for the January–February experiment was biased 0.25° to the east (Table B3). At this time of year our GLS has an inherent bias of about 0.04° of longitude to the west (Fig. B1). In May–June the landmass effect would be expected to be greater, since the sun set behind hills of elevation 470 m only 15 km away, making an angle of about 1.8°, sufficient to make the sun set about 6.5 minute early. At this time of year the GLS has a bias of about 0.13° of longitude to the west. The median longitudes for the three tags showed no consistent bias to the east (Table B3), although if average longitudes had been used, it may have been apparent.

14.4. Wildlife Computer tags

14.4.1 Response to light

A Wildlife Computer (WLC) tag (1997 year of manufacture) was also deployed on the mooring from 24 January to 25 February 1998. These tags proved much more sensitive to light than the Lotek tags, even detecting moonlight at depths of 40 m. An example of this is shown in Fig. B13 for the period 15–17 February, about 4 days after full moon. The fraction of the moon visible at this time was 0.86–0.78, and it rose about 2 hours after sunset. For the first night (15–16 Feb) the cloud cover recorded at a nearby weather station (estimated on a scale of 0–8) indicated that it was completely overcast, although there were a few spikes in the raw light data (up to a maximum value of about 90 units) during the night. The following night the cloud cover decreased, and the effect of the moon was more pronounced. The WLC software does not normally allow the user to see the raw light data, instead showing data that has been smoothed using a weighted moving average of 5, and corrected for temperature in a way that generally results in a slight elevation of the readings.

Fig. B13. Moonlight effects on raw light record from Wildlife Computers tag 97-747

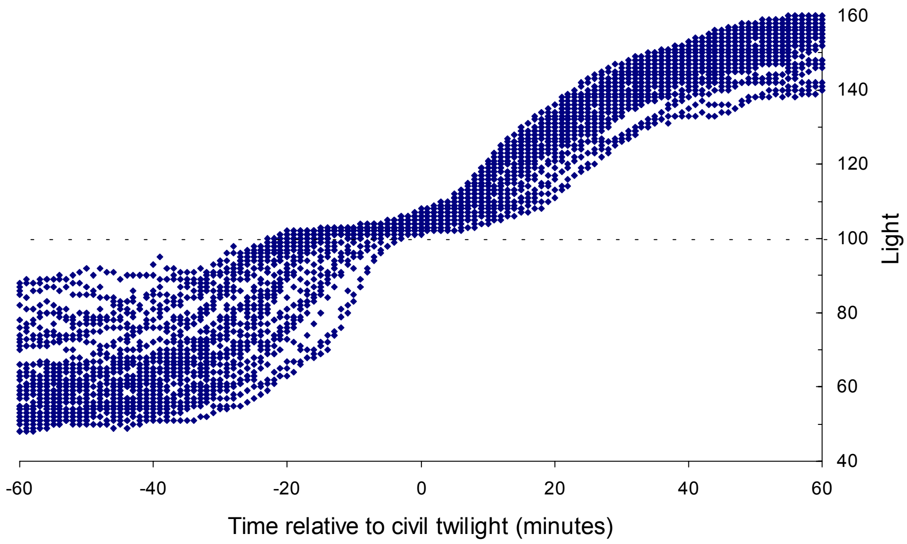


At times around full moon this signal would need to be avoided, requiring setting of the reference light level above the highest moonlight level.

14.4.2 Time at dawn and dusk at which light changes most rapidly.

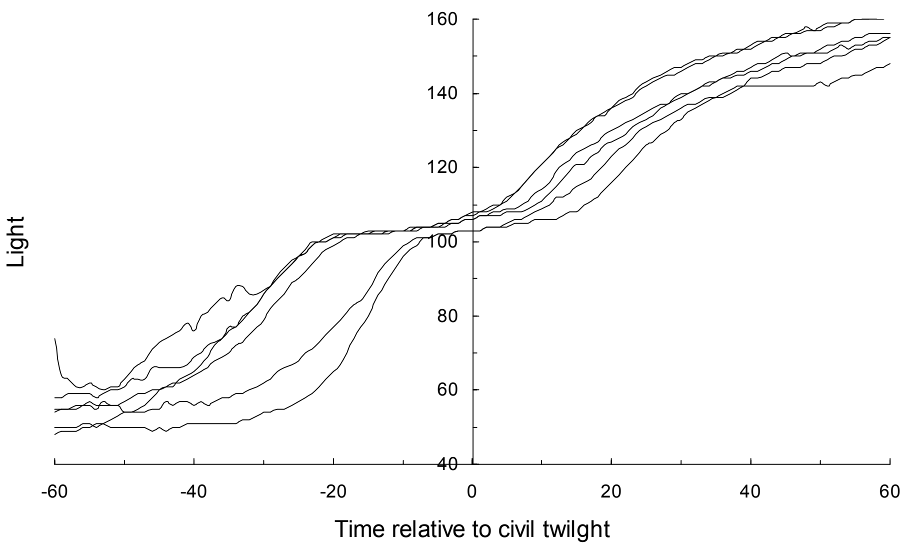
To identify the time at which light changed most rapidly the light data at dawn and dusk were examined for the entire mooring experiment. Because the depth varied with the current, a restricted depth range of 40–45 m was chosen (median depth 42.0 m). The light data is shown in Fig. B14.

Fig. B14. Light at dawn and dusk for depths of 40–45 m



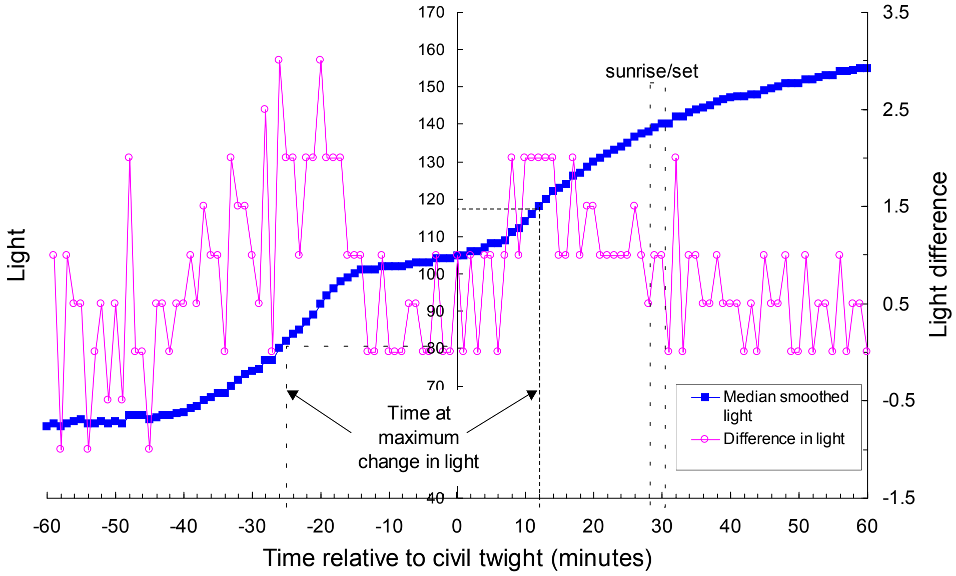
At this depth, it appears that light levels above 100 units would exclude any effects due to moonlight. However the response of the light sensor through twilight appears to be irregular. This is shown more clearly in Fig. B15 for six twilights that cover a range of light conditions.

Fig. B15. Selected twilight light curves for the Jan–Feb 1998 mooring experiment



Median light levels were derived for one minute intervals throughout twilight, and the differences between each light interval calculated, for all depths between 40–45 m. (Fig. B16)

Fig. B16. Median light levels through twilight for depths of 40–45 m.

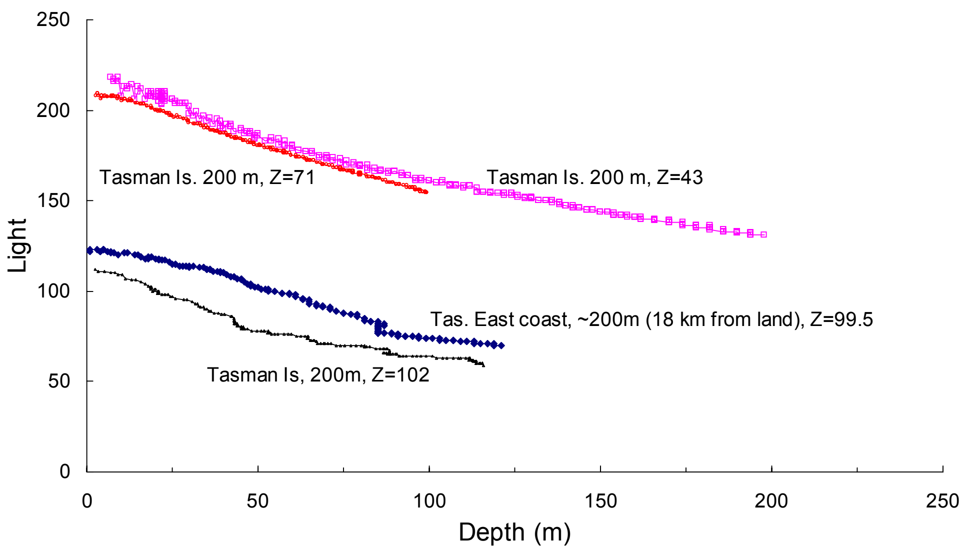


The light difference pattern was bimodal, as expected. The first maxima was at 25 minutes before civil twilight, corresponding to a zenith angle of 100.2° and a median light level of 83 units. The second maxima was at 12 minutes after civil twilight, corresponding to a zenith angle of 94.0° and a median light level of 118 units. The first maxima would not be useable during times of full moon, but might provide a slightly better estimate of the time of dawn and dusk at other times, because the increase in light levels at this time was more rapid than the second peak.

14.4.3 Light attenuation with depth for WLC tags

The remaining parameter value required by the reference light level method is a light extinction coefficient for these tags. The results of a series of casts with a WLC tag are shown in Fig. B17.

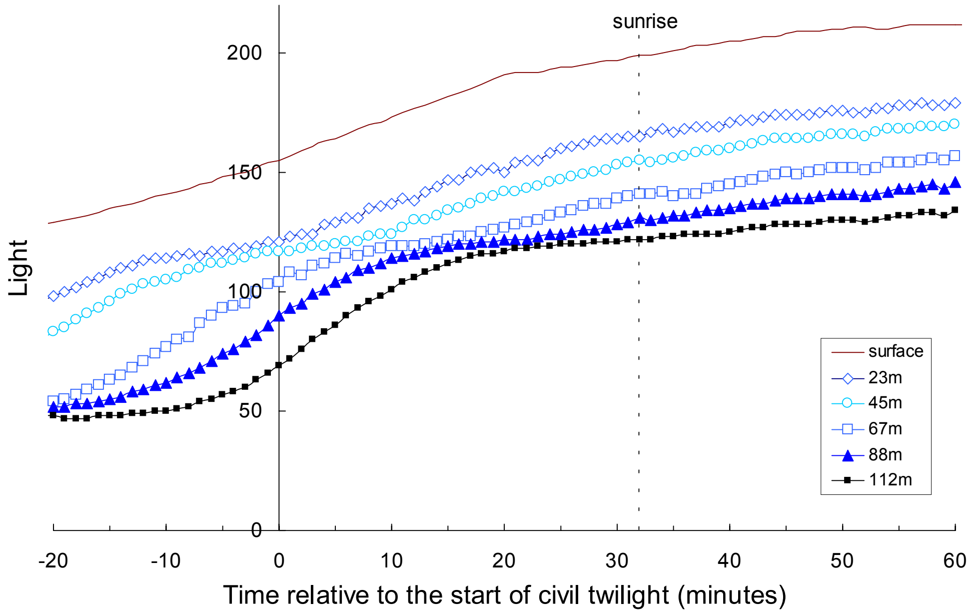
Fig. B17. Depth casts with WLC tags, Tasmania.



A feature of these tags is that the decrease in light with depth is generally linear. An alternative way of examining light attenuation at any time during twilight is with a multi-tag experiment.

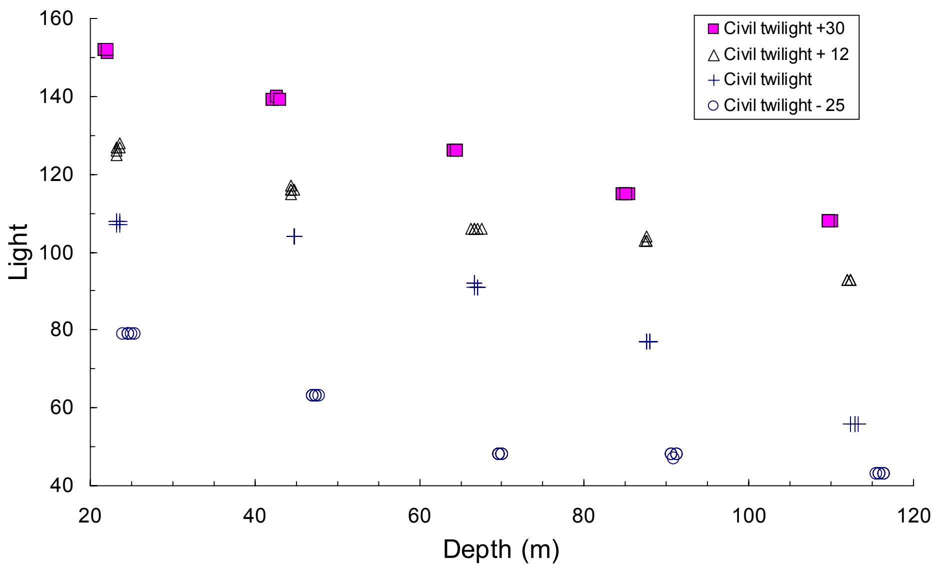
Data from a 5 tag experiment at dawn on 11 Nov 1998, with tags at approximately 20 m intervals, was examined (Fig. B18).

Fig. B18. Response of WLC tags at dawn, 11 Nov 1998, Tasman Island.



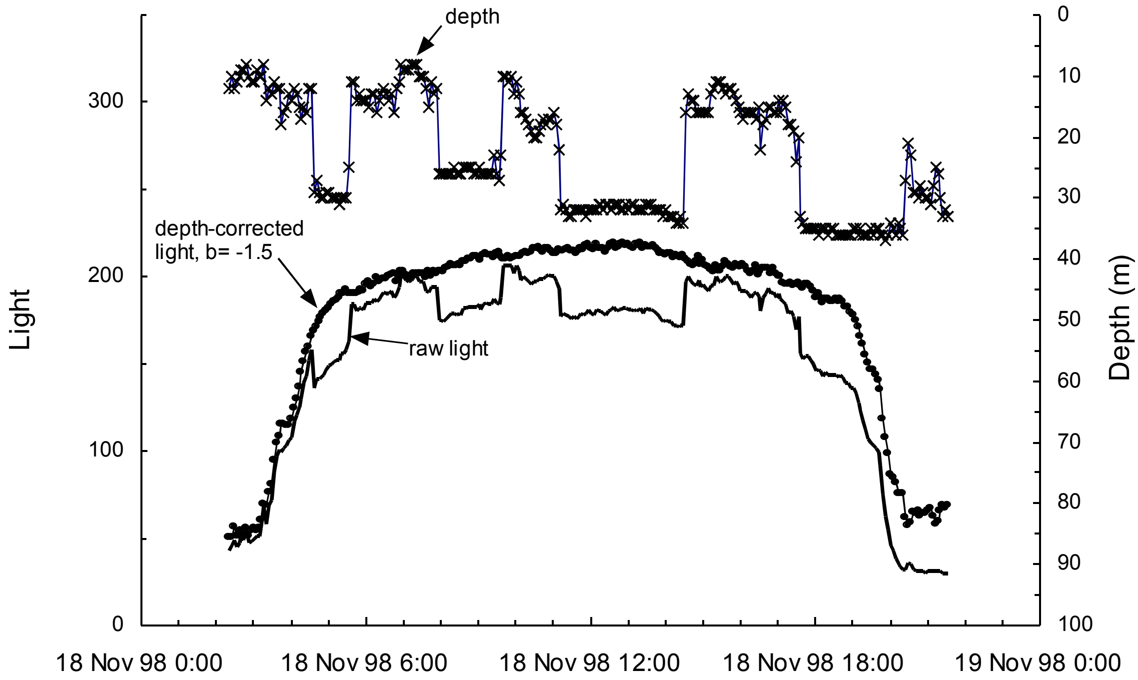
These tags were made in 1998, a year later than the tag used in the mooring experiment, but they still showed a 'flat spot' at light levels just above 100 units (raw light values), most noticeably in the three most shallow submerged tags. Data were selected for a number of times relative to civil twilight (5 light values for each depth for each time) and are plotted in Fig. B19. When linear regressions were a poor fit, they were carried out only over restricted depth ranges.

Fig. B19. Light attenuation response of WLC tags at selected times throughout dawn, 11 Nov 1998.



A third approach to deriving extinction co-efficients is to use light data from recaptures and adjust the attenuation co-efficient until the adjusted light curve no longer reflects the depth signal. An example is shown for school shark tag 98-081, released in Banks Strait (Fig. B20). In this location an attenuation coefficient of -1.5 was required, whereas in deeper water a value of -0.25 was more appropriate

Fig. B20. Example of depth correction from recapture data: tag 98-081, 18 Nov 1998.



A summary of the attenuation results is given in Table B4.

Table B4. Regression slopes for Wildlife Computer tags

Type of experiment	Time	Regression slope	Applicable depth range (m)
Depth cast Tas. E. coast 18 km offshore, 7 Jun 99	CT-21 min	-0.54	0–120
Depth cast Tasman Is. 11 Nov 98	2 h after sunrise	-0.58	0–100
Depth cast Tasman Is. 19Mar 99'	solar noon+0.5 h	-0.47	7-198
Multiple tag expt. 11 Nov '98 dawn	CT - 25 min	-0.69	24–70
"	CT	-0.71	44–112
"	CT + 12 min	-0.36	22–112
"	CT + 30 min	-0.51	22–112
Tag 98-081 recapture data	Twilight and	-1.5	10–35[a]
	during the day	-0.7	< 80 m
		-0.5	>80 and <200 m
		-0.25	>200 m

a: this only applied for several days after the shark was released

For the WLC tags it appears best to use attenuation values derived from the recapture data. However, there are often extended periods in which the depth behaviour of the shark offers no scope for estimating the attenuation. While this is not such a problem with estimating longitude, it could have a serious effect on the estimation of latitude.

A summary of the starting point geo-location parameter values for the WLC tags is presented in Table B5.

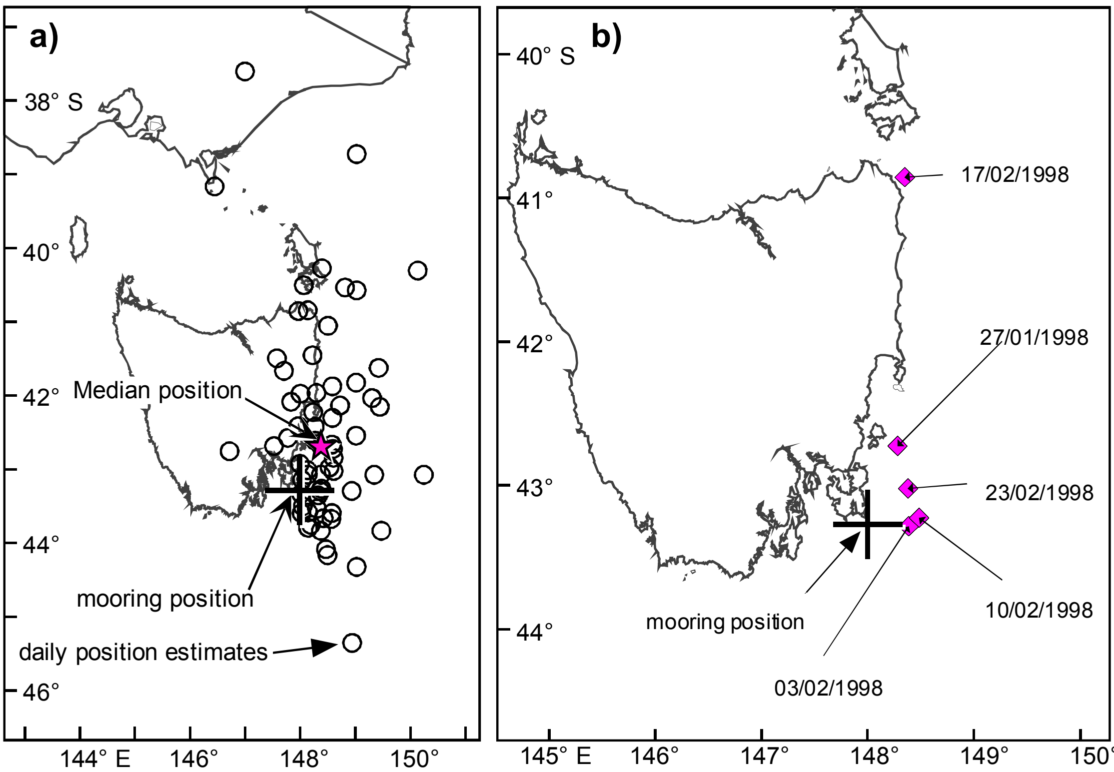
Table B5. Geo-location parameter values for WLC tags

Reference depth (m)	Zenith angle (°)	Median light level	Attenuation slope
42	100.2	83	-0.25 to -1.5
	94.0	118	"

14.4.4 Accuracy of position estimates from a WLC tag on a mooring.

Position estimates using the parameter values in Table B6 (attenuation -0.7) for the month long mooring experiment in Jan–Feb '98 off Tasman Island were obtained in order to evaluate the method. To avoid the effects of moon rise, and allow automatic estimation of position for the whole period, the higher reference light level was used. The daily position estimates are shown in Fig. B21a, together with a median position for the month. Weekly median positions are shown in Fig. B21b.

Fig. B21. Position estimates from a WLC tag on a mooring at 42 m off Tasman Island, from 24 Jan–25 Feb 1998: a – daily and overall median positions; b – weekly median positions.



The median longitude was biased to the east by 0.43°, and the median latitude 0.57° to the north. The weekly median positions (Fig. 21b) showed that while longitude was well estimated, latitude was in error by as much as 2.4°. The bias in the longitude estimates may be due to landmass effects advancing sunset by about four minutes, which would also tend to shorten day length and affect latitude estimates. However, the latitude errors became greater towards the end of the mooring experiment, and the likely cause is the heavy growth of a hydroid (*Obelia sp.*) observed upon recovery of the tag. The northern bias in the latitude estimates is reduced to 0.28° for position estimates for only the first two weeks of the experiment. A summary of the position errors is given in Table B6.

Table B6. Position error statistics for mooring experiment with WLC tag 97-747, 24 Jan–25 Feb 1998.

	24 Jan– 25 Feb		24 Jan–9 Feb	
	Long. error	Lat. error	Long. error	Lat. error
Mean	0.47	0.83	0.47	0.39
Median	0.43	0.57	0.43	0.28
Standard Deviation	0.67	1.40	0.65	0.84
Range	3.80	7.75	3.53	3.27
Minimum	-1.50	-2.10	-1.23	-1.07
Maximum	2.30	5.65	2.30	2.20
Inter-quartile range	0.68	1.53	0.57	0.82
Count	63	63	33	33

15. APPENDIX C. Monthly depth plots

Fig. C1. Female school shark 1313 depth profile.

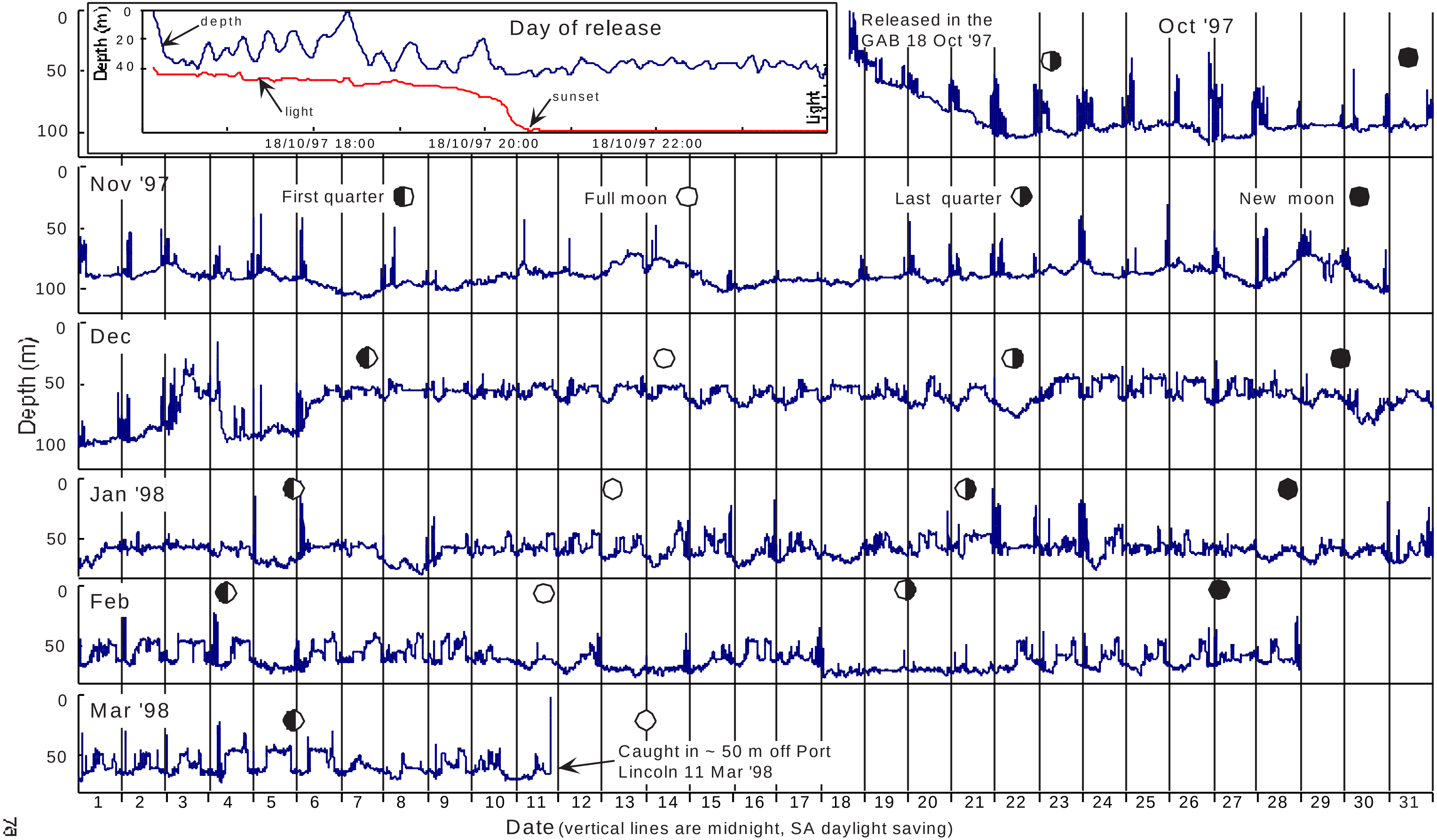


Fig. C2. Female school shark 1391 depth profile.

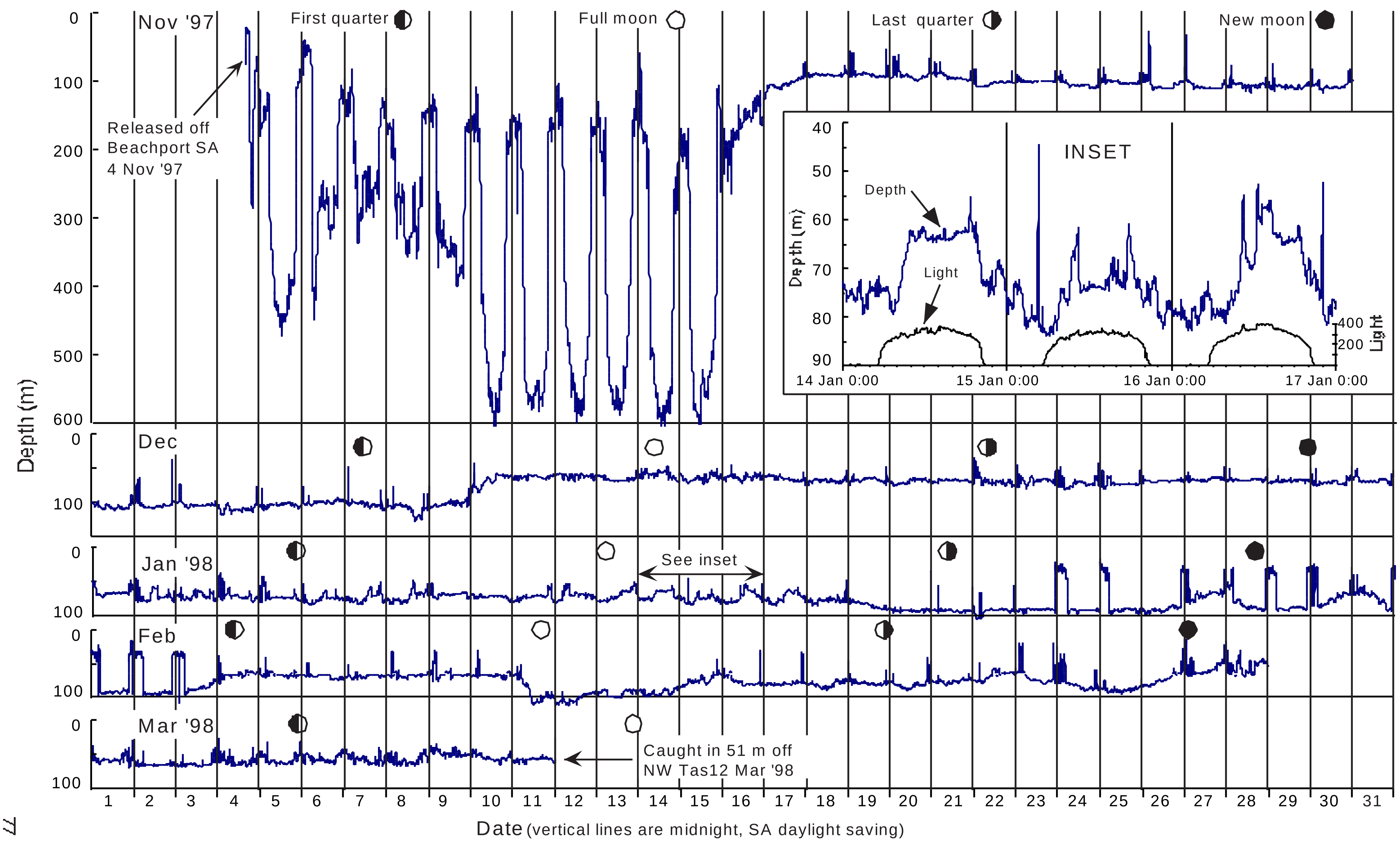


Fig. C3. Female school shark 1394 depth profile.

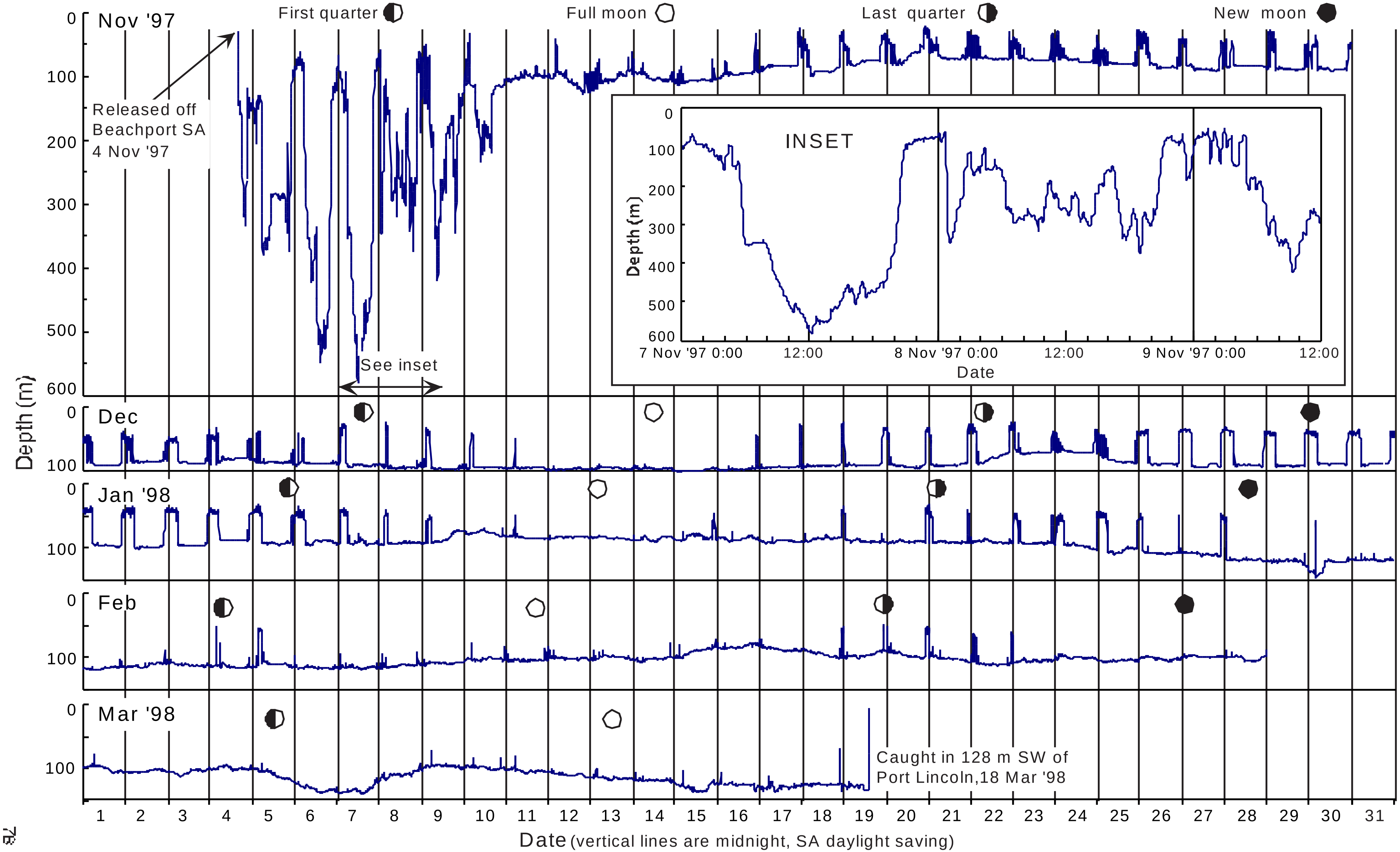


Fig. C4a. Male school shark 1396 depth profile.

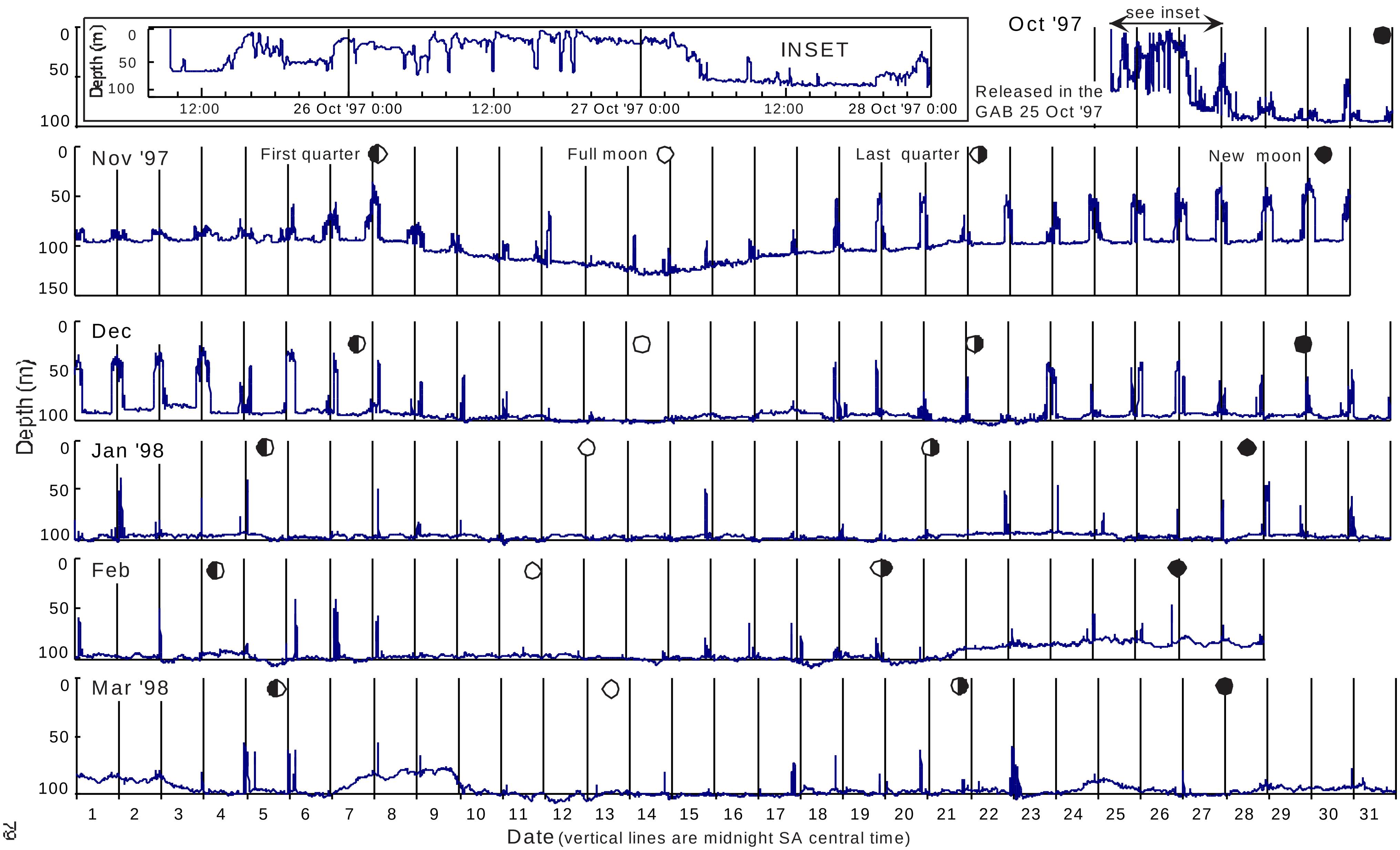


Fig. C4b. Male school shark 1396 depth profile.

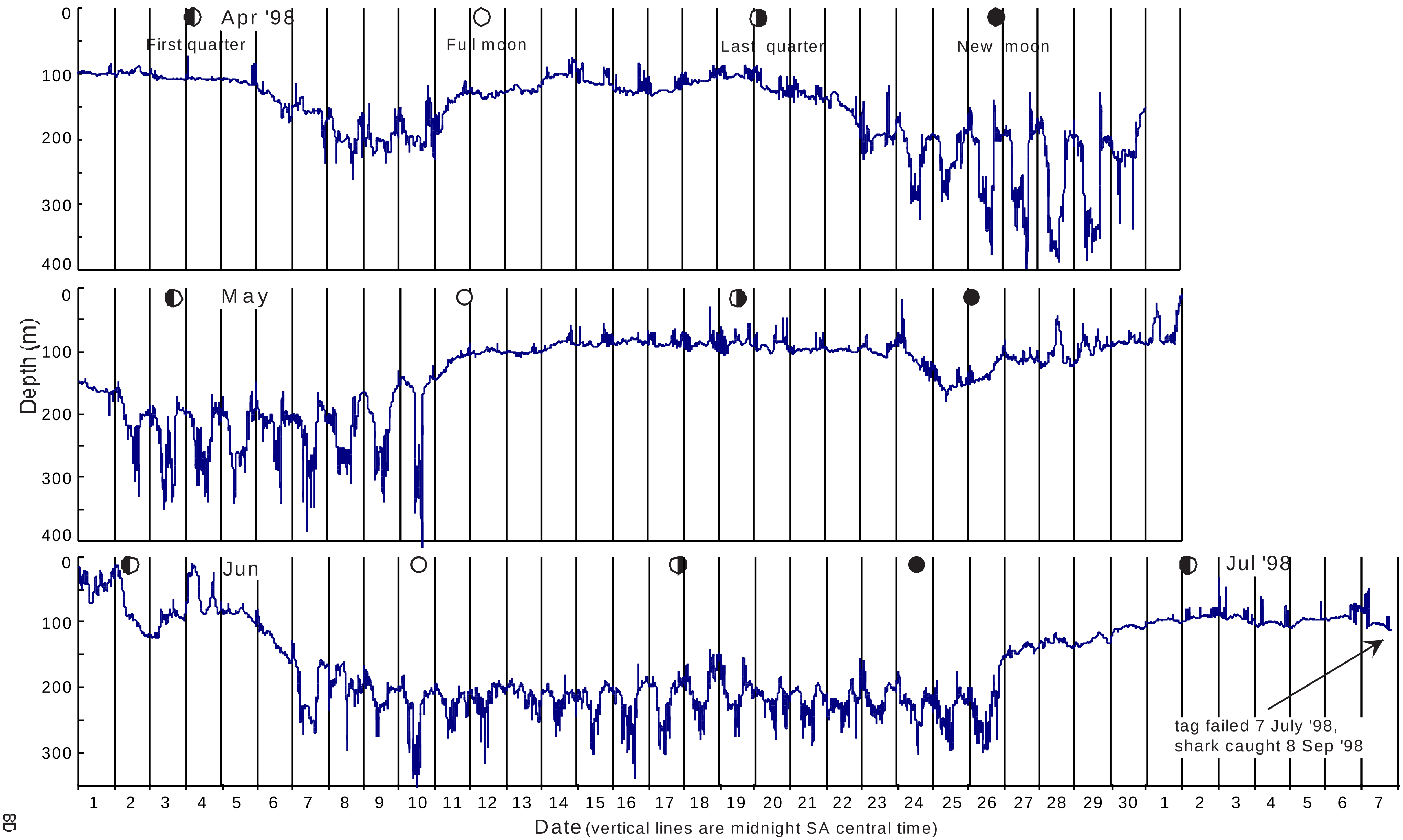


Fig. C5a. Female school shark 1253 depth profile.

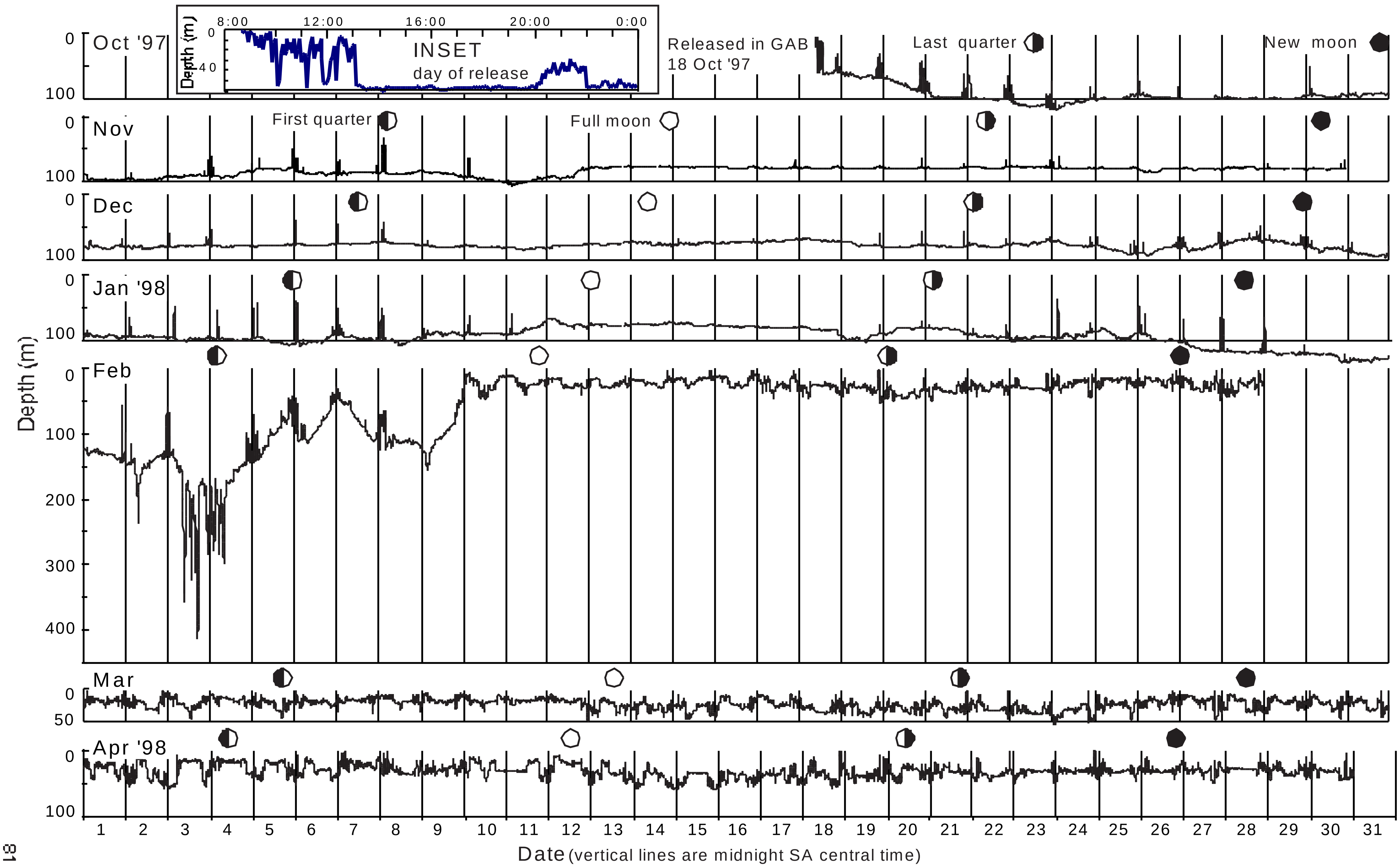


Fig. C5b. Female school shark 1253 depth profile.

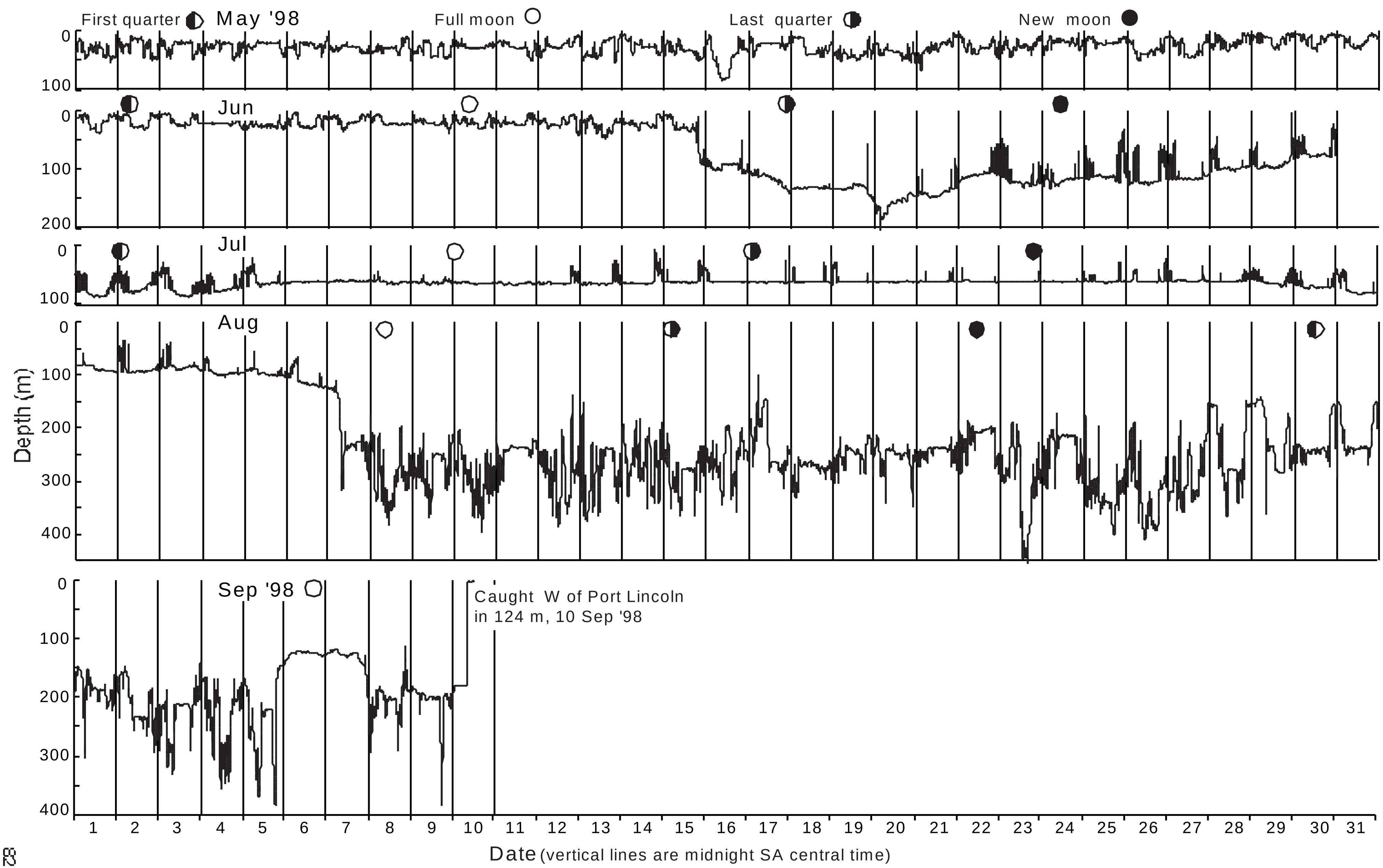


Fig. C6a. Male school shark 1346 depth profile.

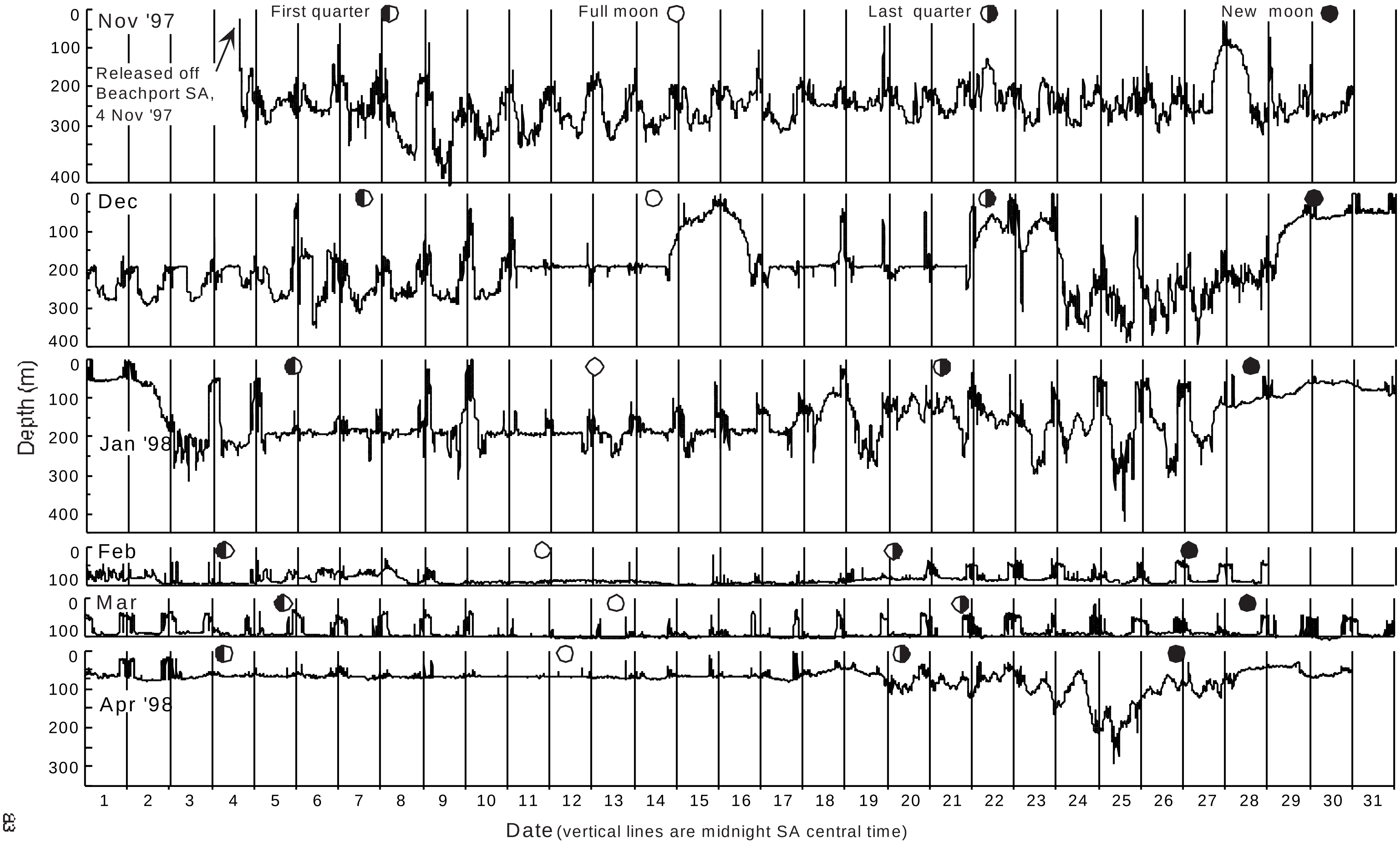


Fig. C6b. Male school shark 1346 depth profile.

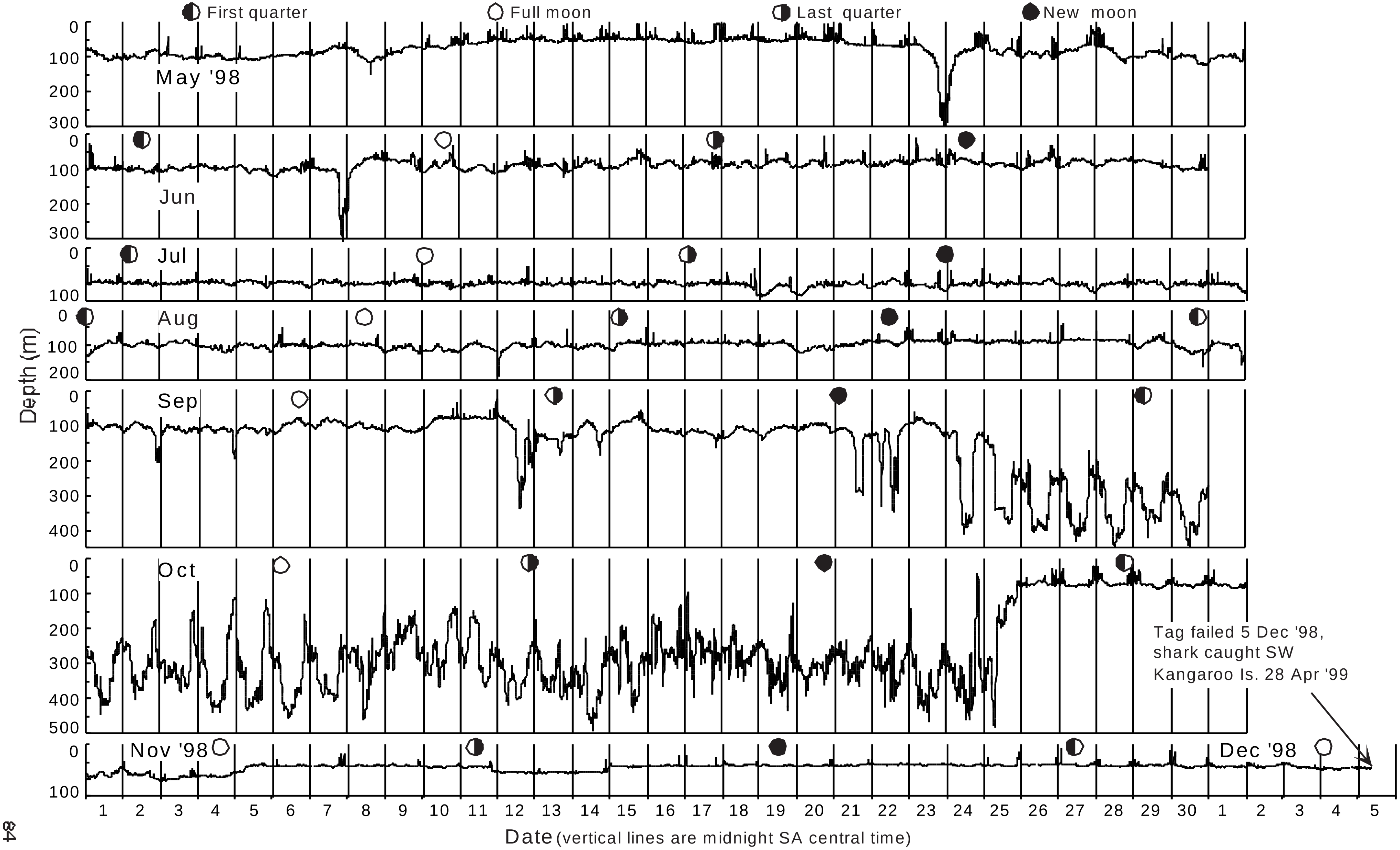


Fig. C7a. Female school shark 1259 depth profile.

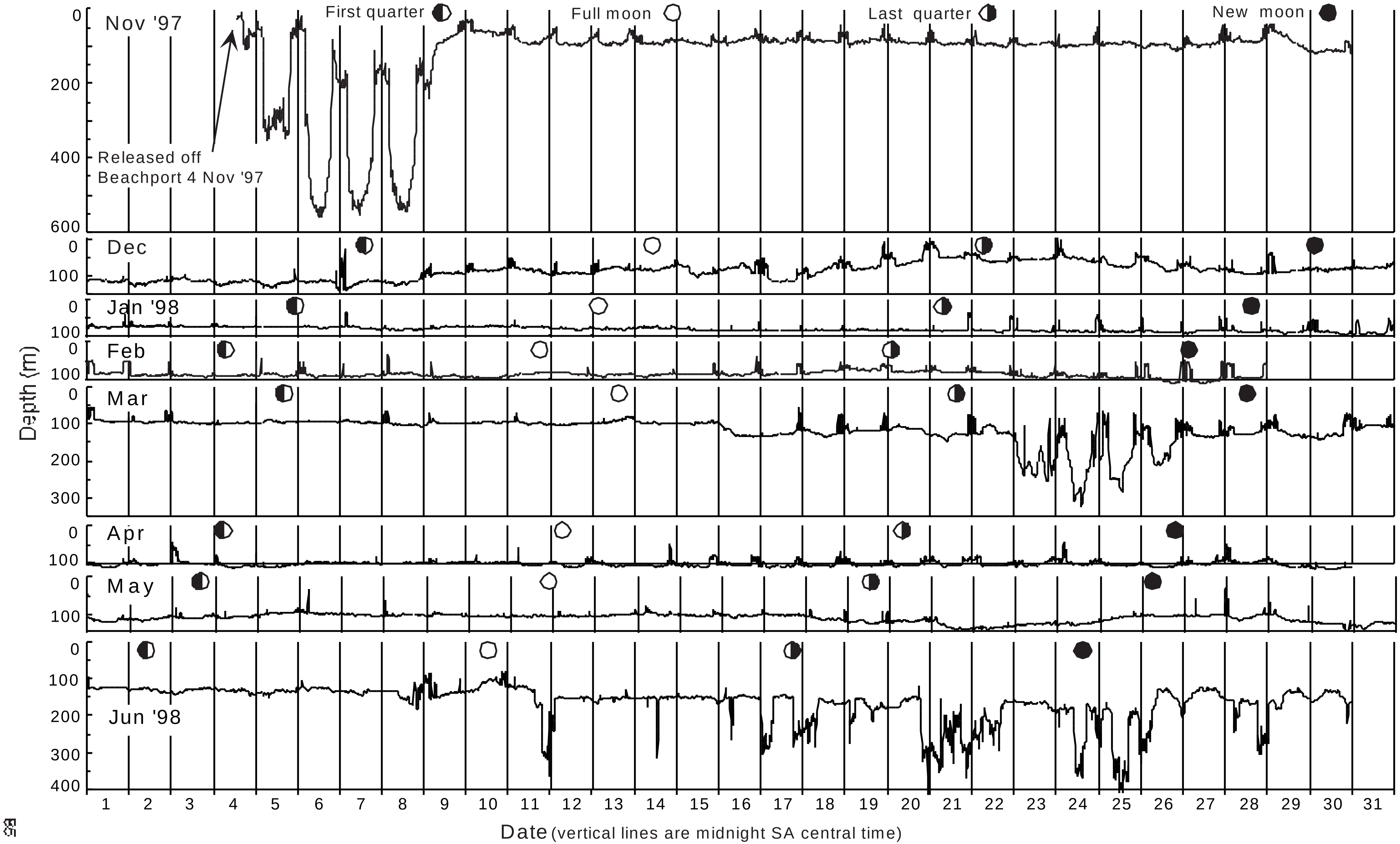


Fig. C7b. Female school shark 1259 depth profile.

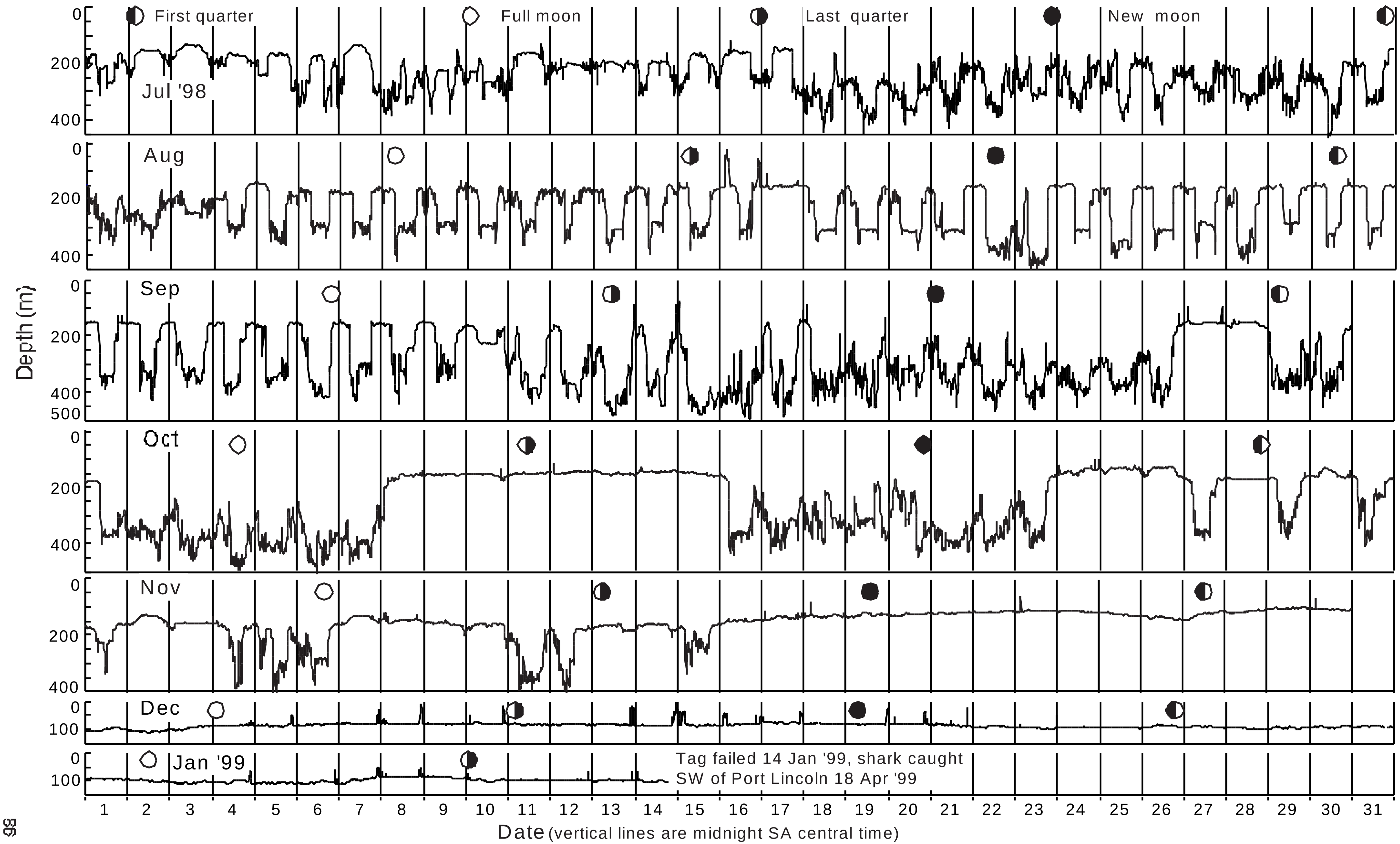


Fig. C8. Female school shark 98-073 depth profile.

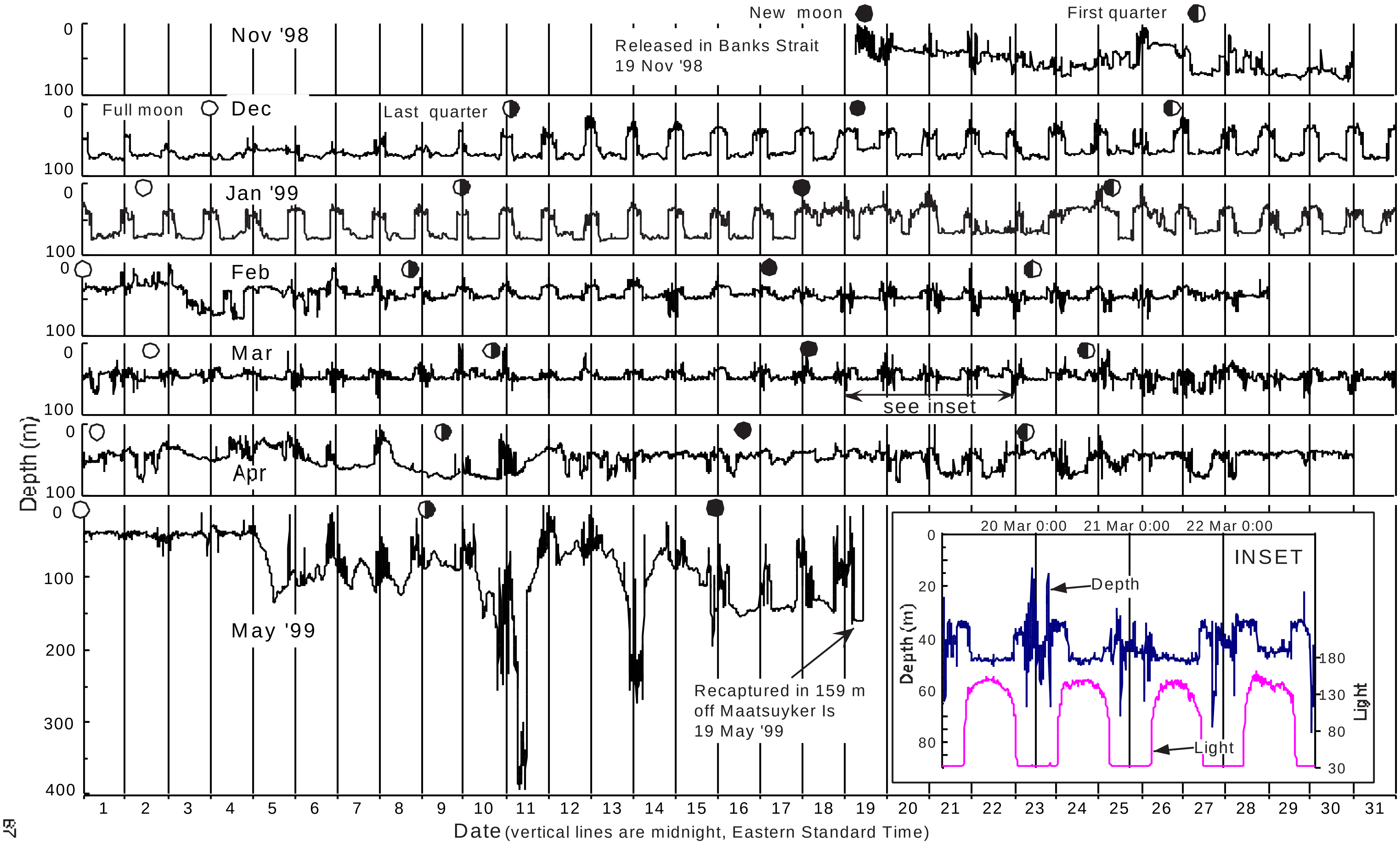


Fig. C9. Female school shark 98-085 depth profile.

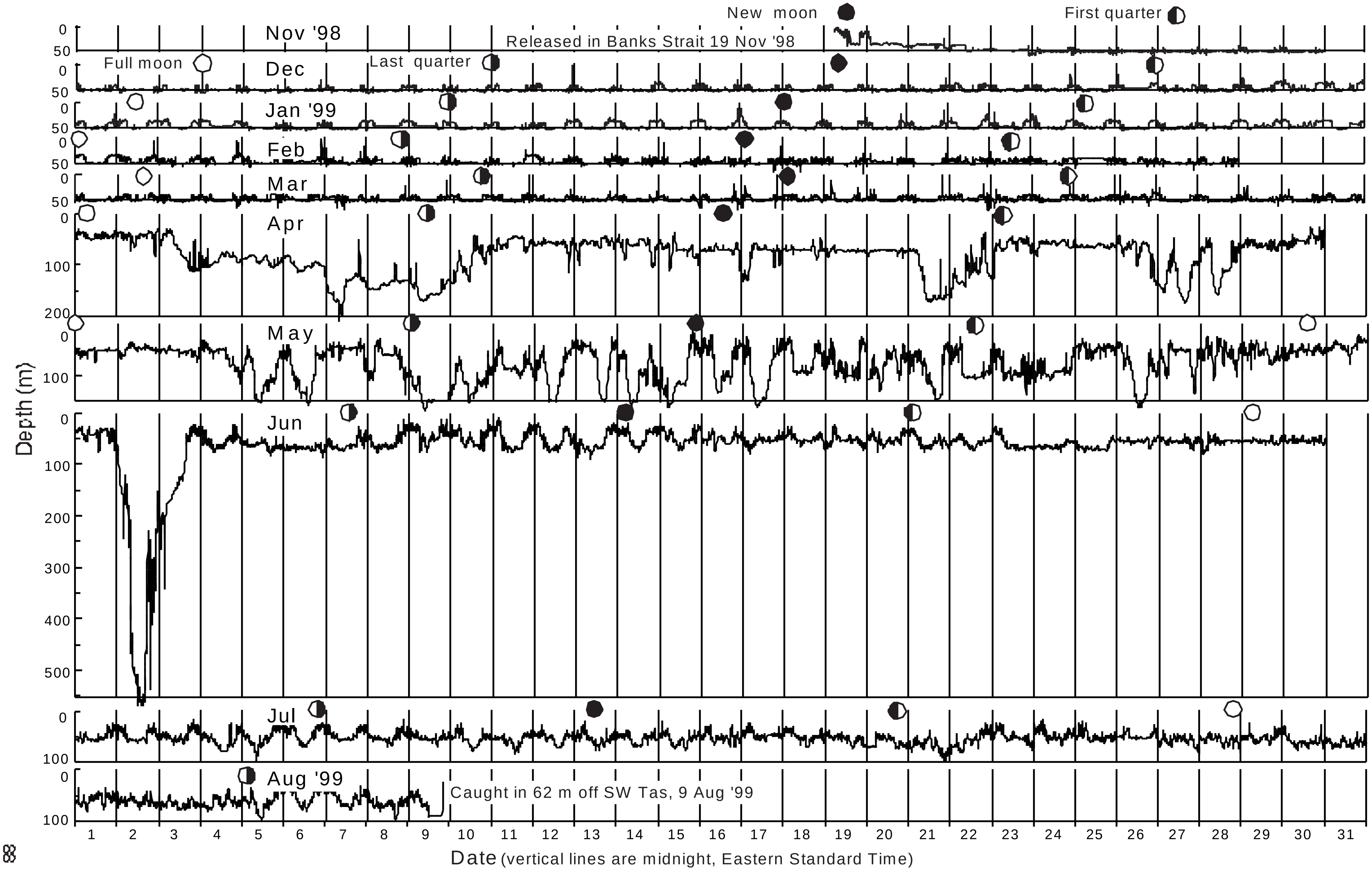


Fig. C10a. Female school shark 98-079 depth profile.

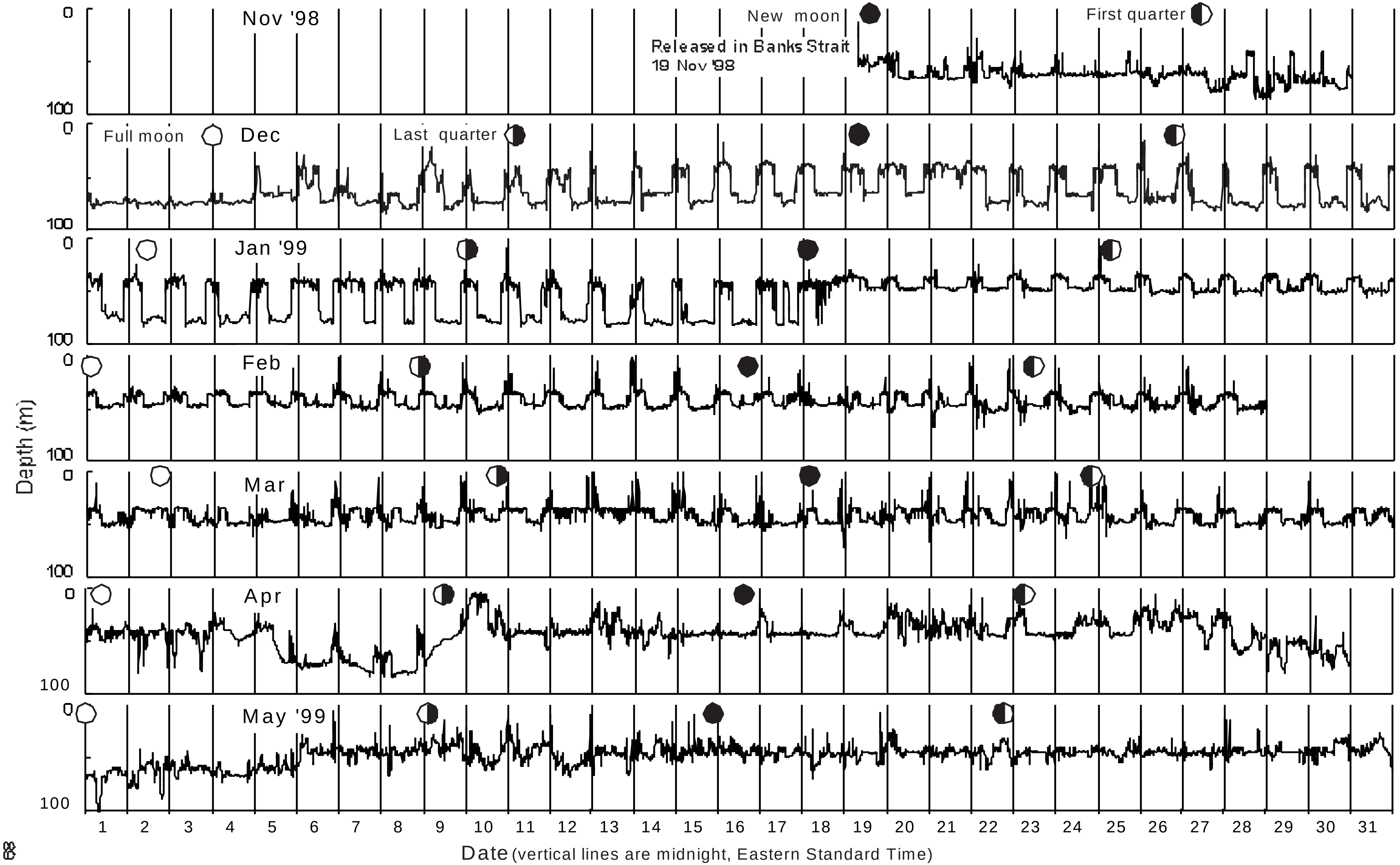


Fig. C10b. Female school shark 98-079 depth profile.

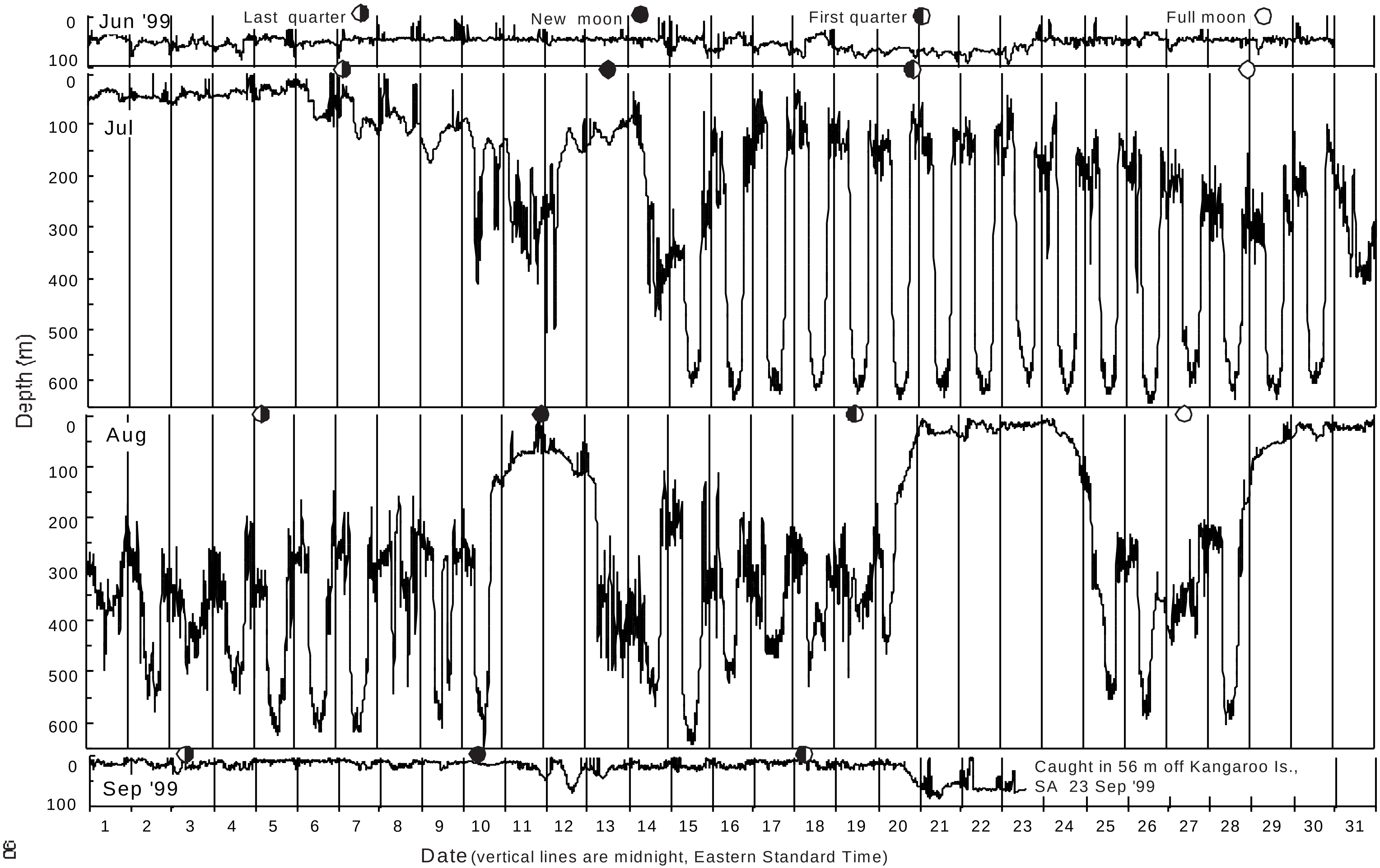


Fig. C11a. Female school shark 98-092 depth profile.

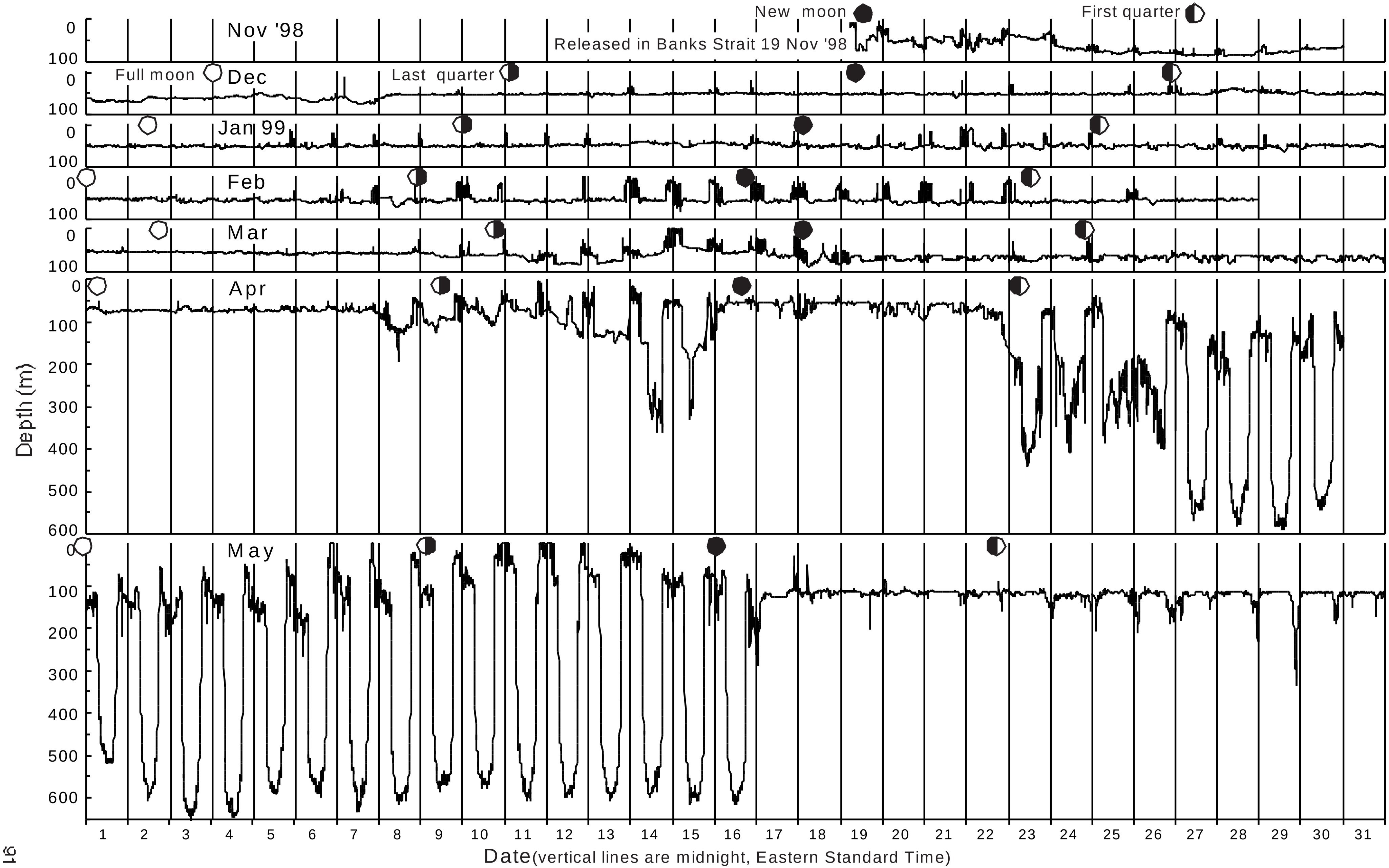


Fig. C11b. Female school shark 98-092 depth profile.

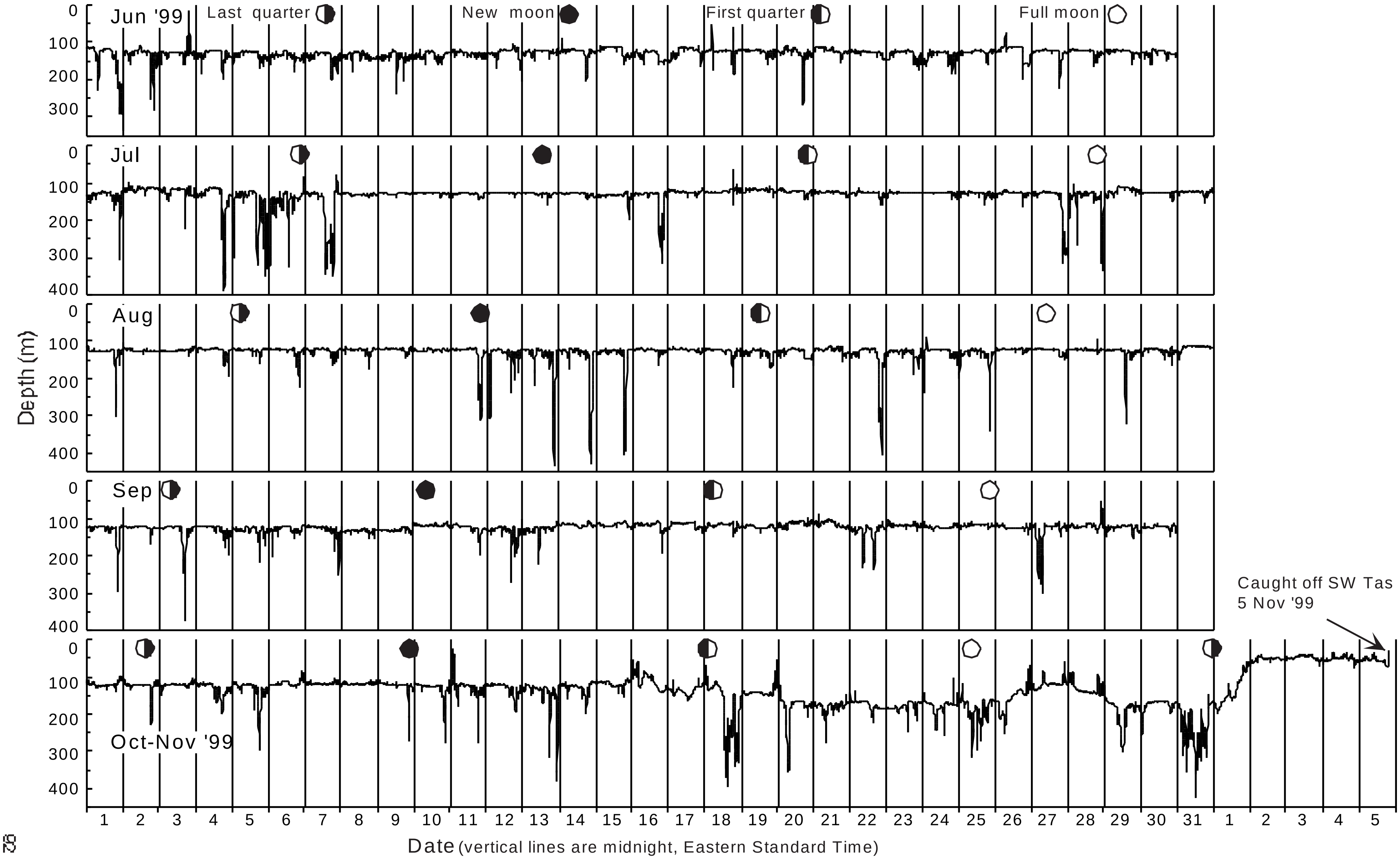


Fig. C12a. Female school shark 98-088 depth profile.

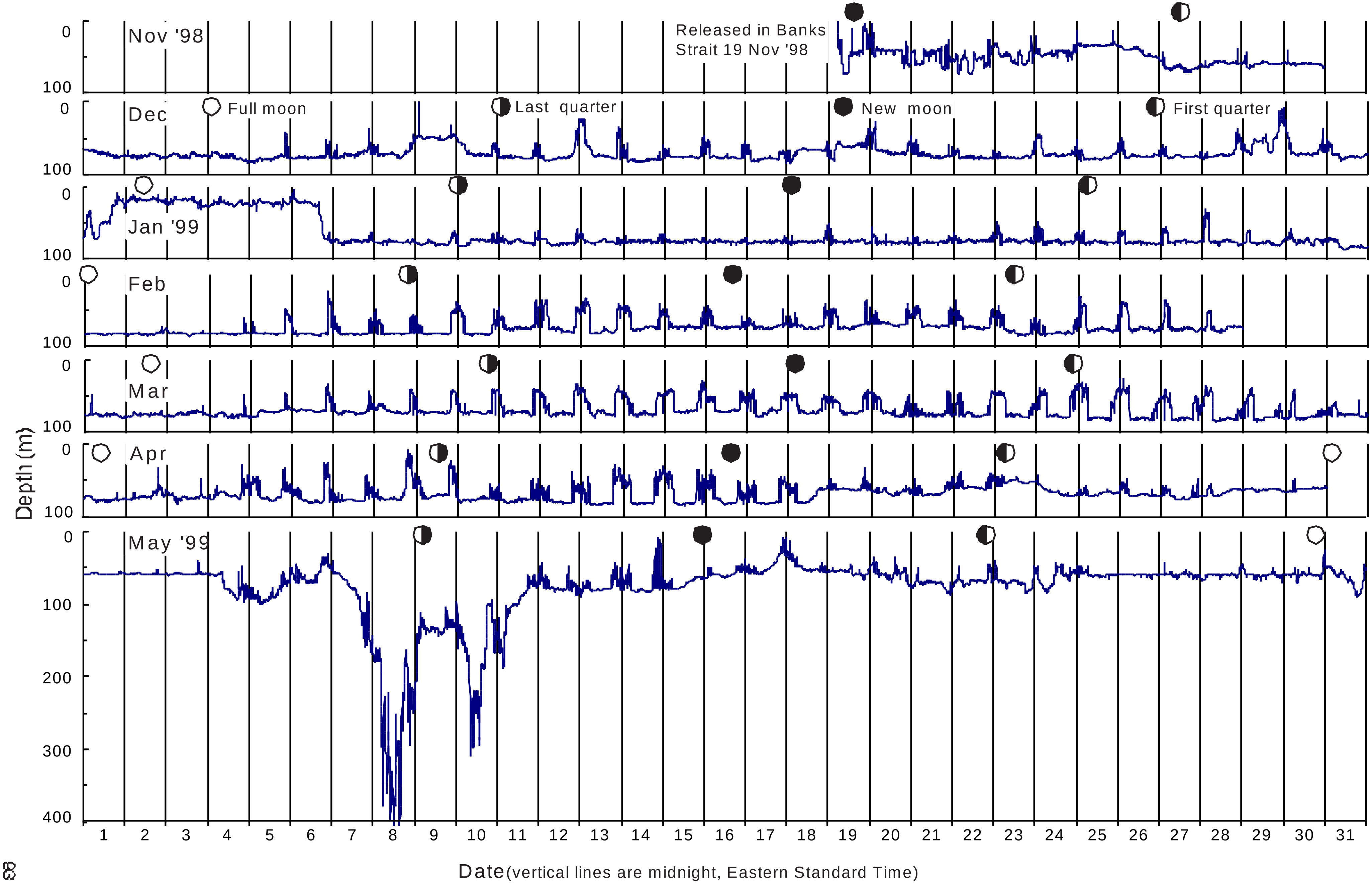


Fig. C12b. Female school shark 98-088 depth profile.

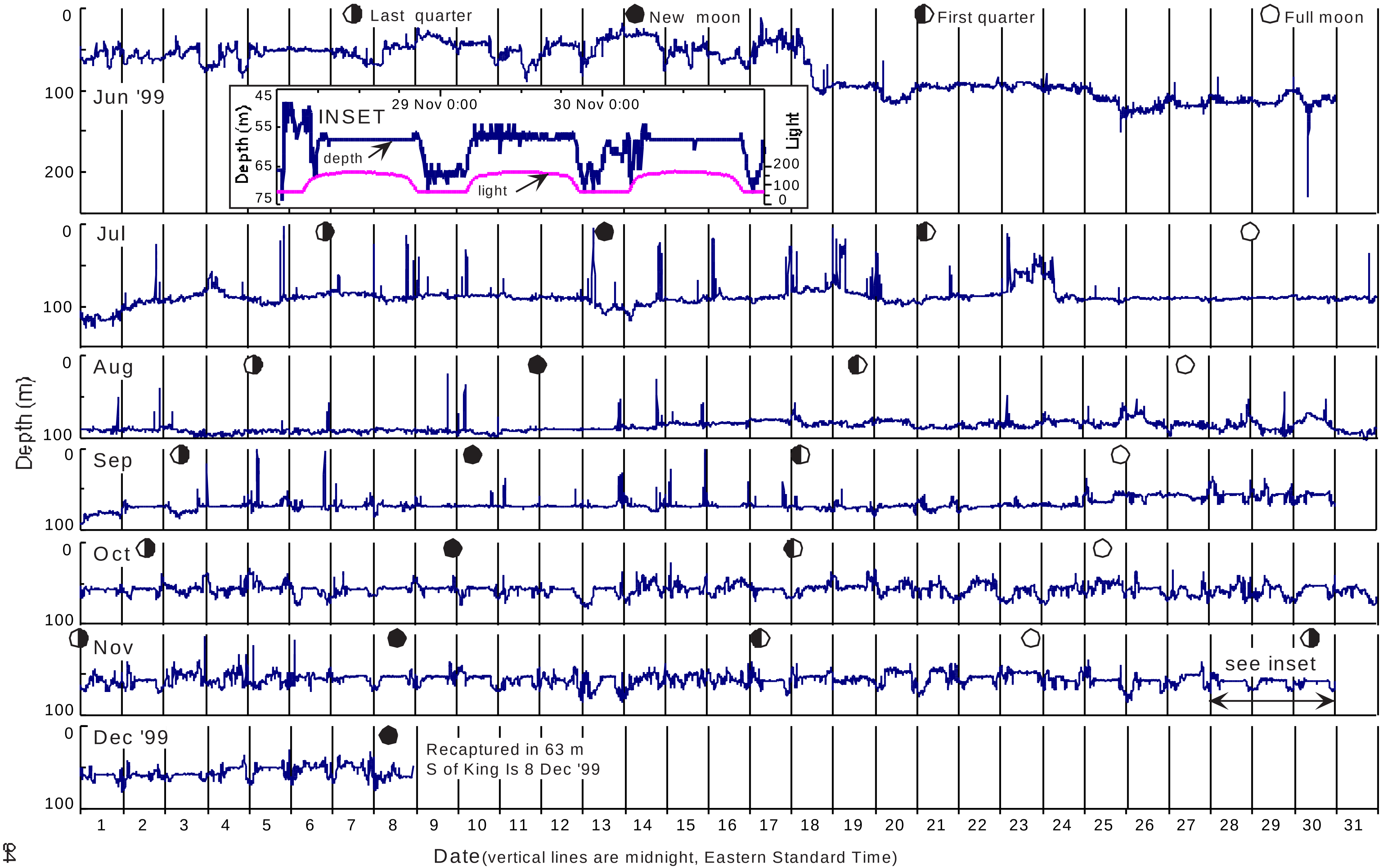


Fig. C13a. Male school shark 98-081 depth profile.

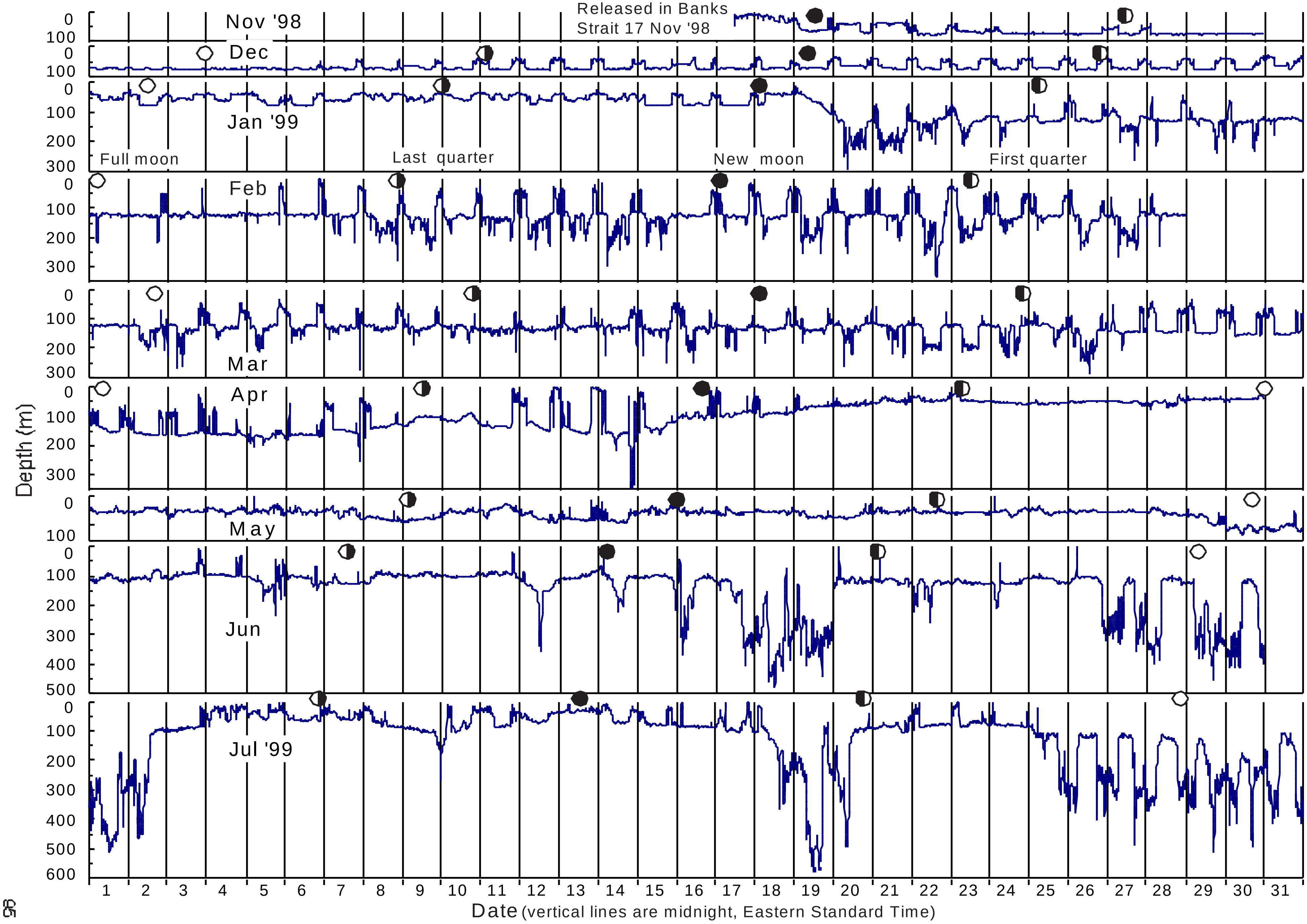
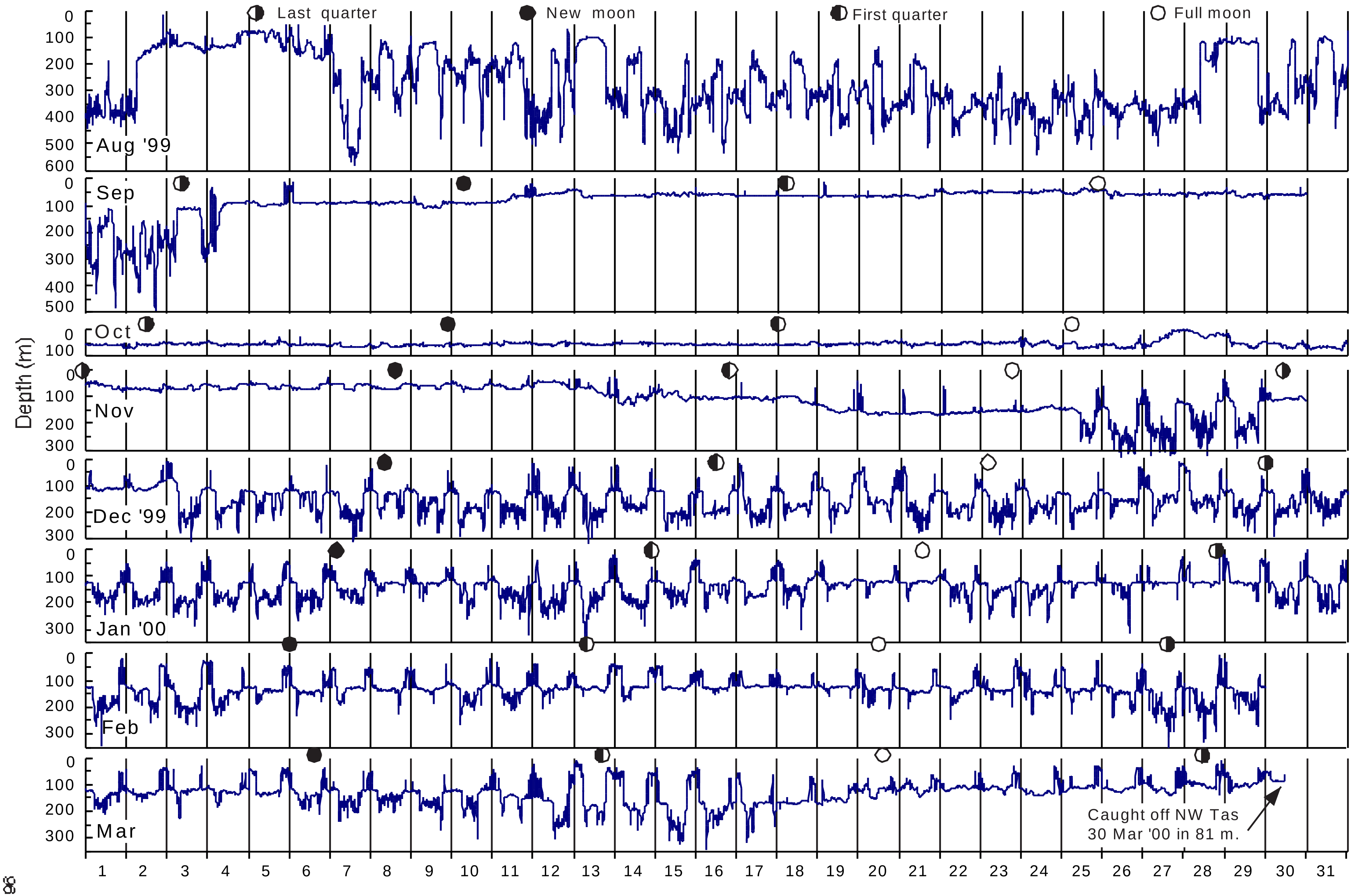


Fig. C13b. Male school shark 98-081 depth profile



16 APPENDIX D: ARCHIVAL TAG MOVEMENTS

1. Beachport releases

Shark 1394. (Fig. D1)

This shark moved quickly west from 140°E reaching 133° by late November. It continued west, but more slowly, reaching 131.4° by the end of December, before returning east a little irregularly until it was caught at 135° on 19 March 1998.

Shark 1259. (Fig. D2)

This shark moved quickly west reaching 131.5°E in early January 1998, before returning east, reaching 133° by early March. It then made a temporary (~ 3 weeks) westward excursion to 130° before resuming its easterly movement, reaching 137.5° by the first week in June. It stayed at ~137-138° until the first week in November, when it turned west arriving at ~133.5° in early December. It remained at these longitudes until the tag failed on 14 January 1999. It was recaptured in April 1999 at 134.3°E, a similar longitude to that in April 1998.

Shark 1346. (Fig. D3)

This fish stayed deep until late January1999, so longitudes are uncertain although they appeared to have been centred around ~141°E. At the beginning of February when it came into shallow water, it was at ~145°; it moved slowly west reaching 143° by mid- April, before moving west more rapidly to reach 138.5° by the end of April. It stayed at these longitudes (the estimates are poor because of a period in deep water from June–August) until late September, when it moved east, reaching 146° by the end of October. It stayed at these longitudes until the tag failed in early December. It was caught at 138.6° on 28 April 1999, so at some stage, possibly as late as April (it moved west the previous April) it must have moved west.

Fig. D1. Daily and weekly-median position estimates, and maximum daily depth for school shark 1394 (female, 151 cm TL)

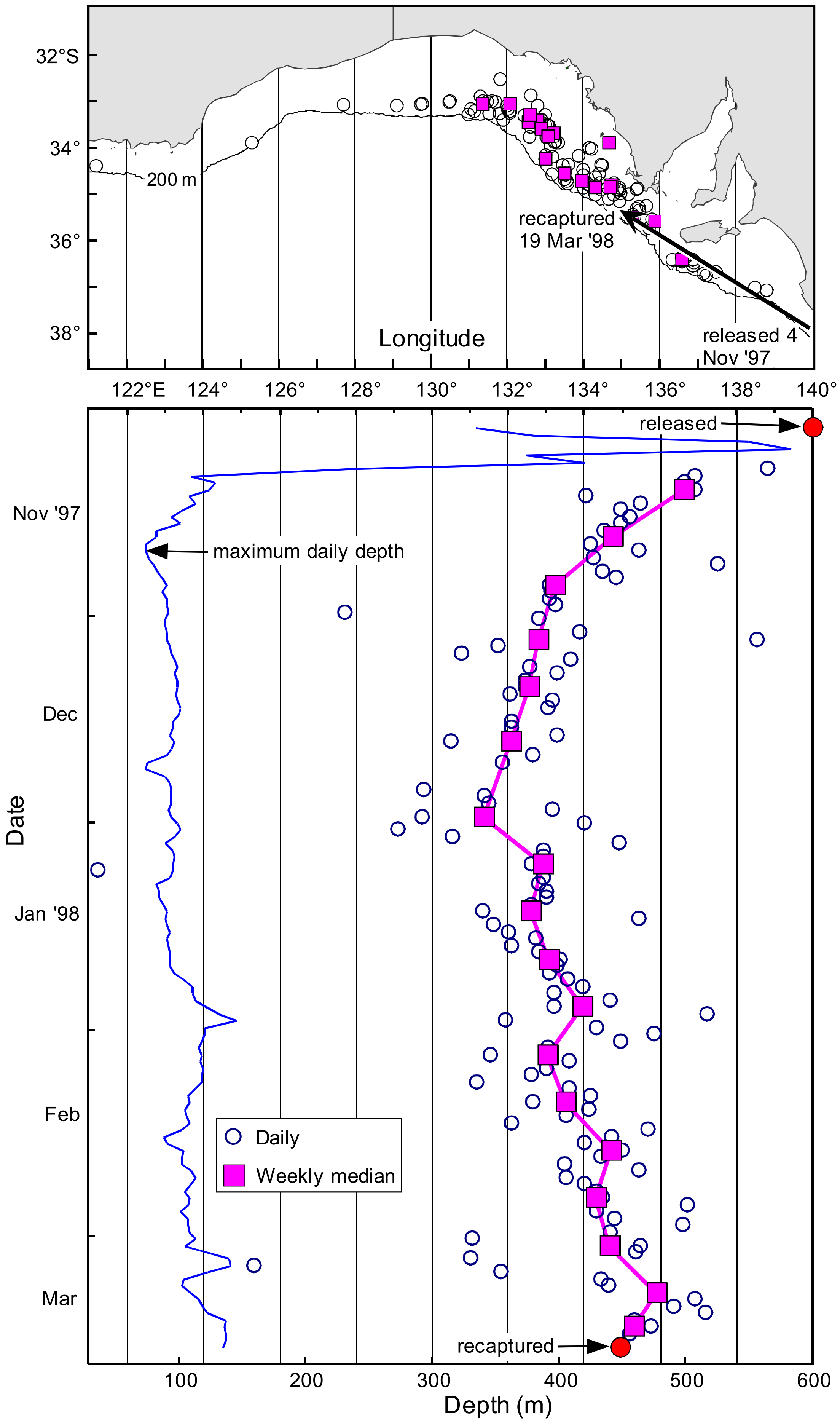


Fig. D2. Daily and weekly-median position estimates, and maximum daily depth for school shark 1259 (female, 128 cm TL).

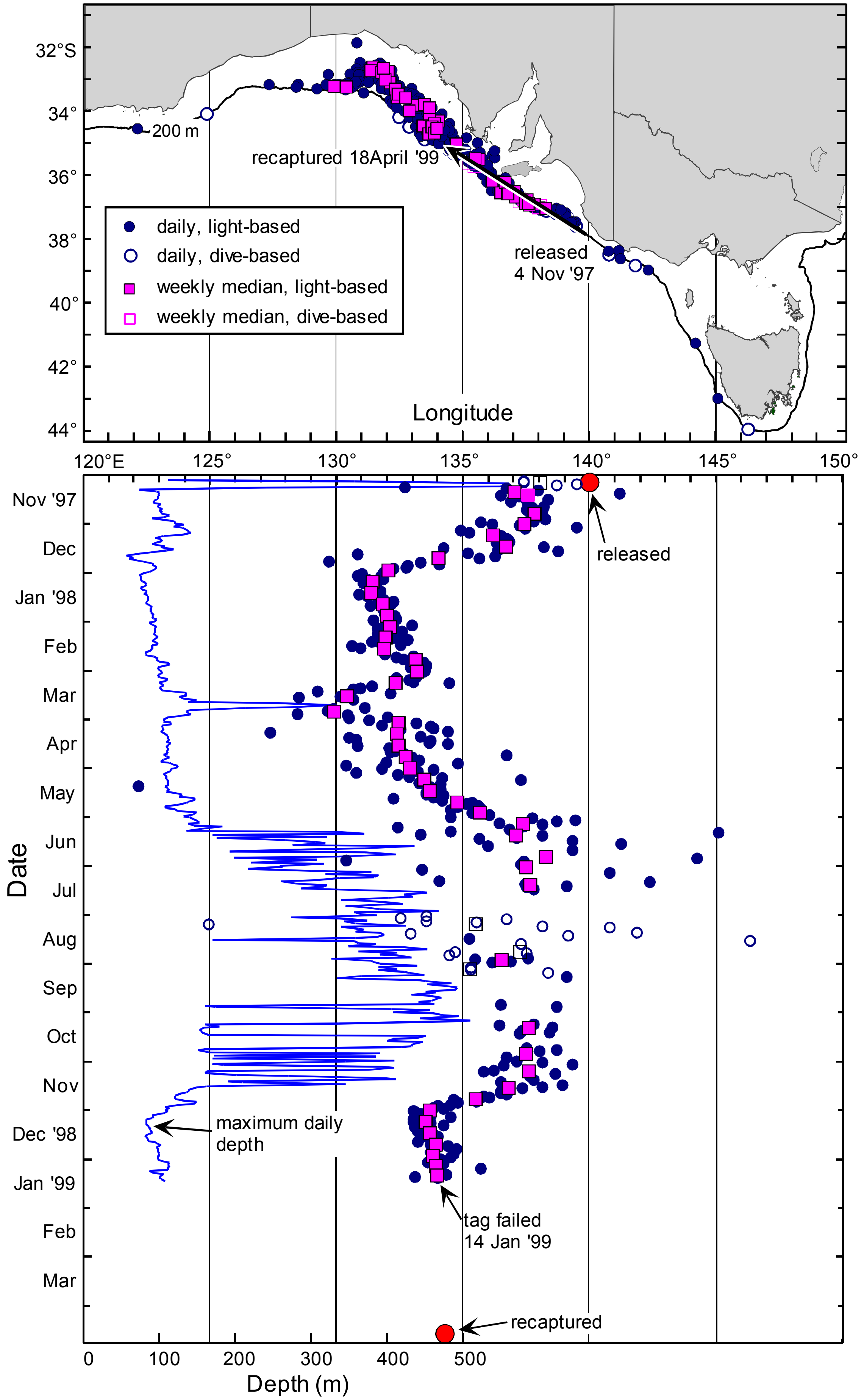
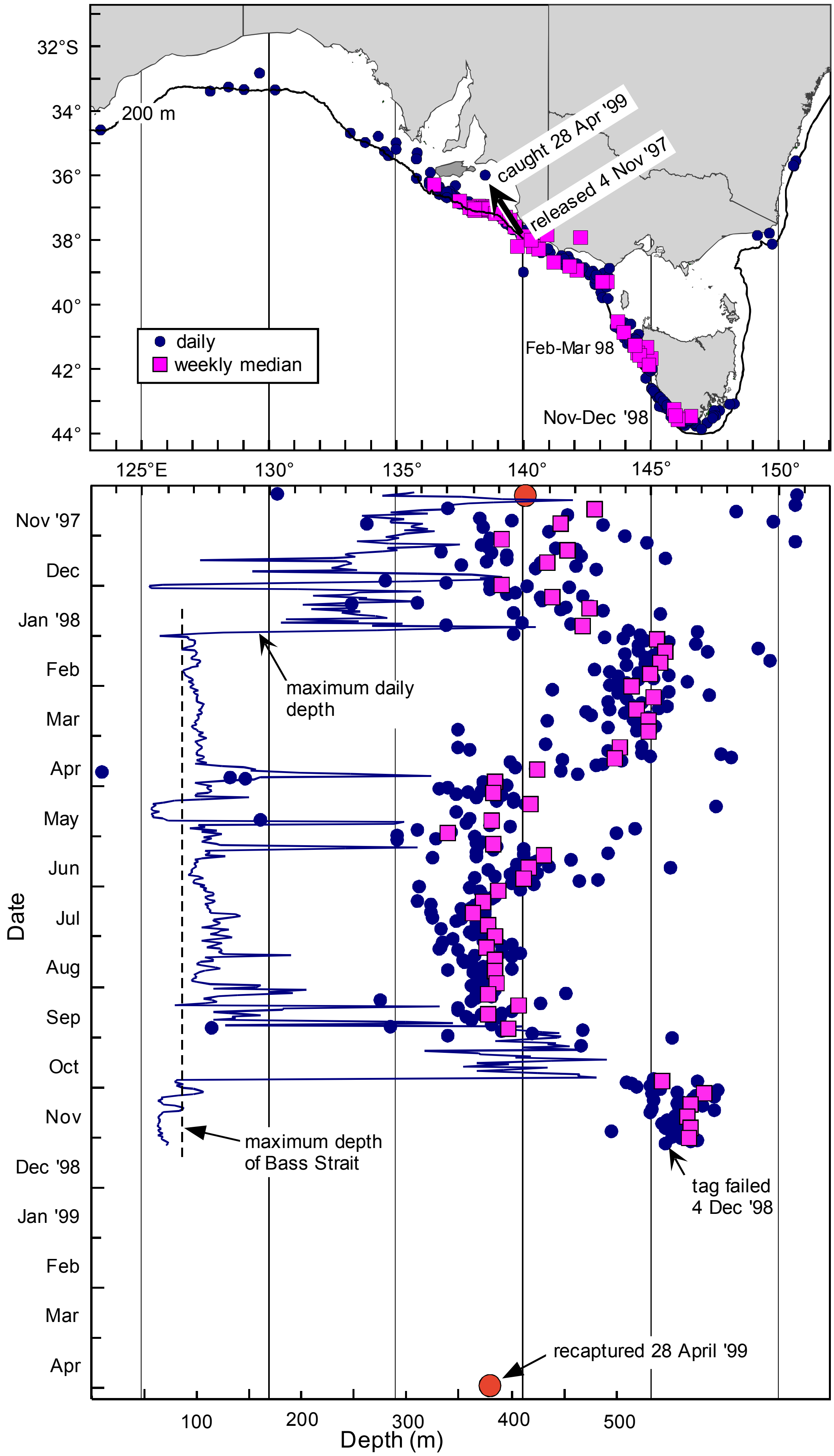


Fig. D3. Daily and weekly-median position estimates, and maximum daily depth for school shark 1346 (male, 131 cm TL).



2. Tasmanian releases

Shark 98-073. (Fig. D4)

This shark stayed in shallow water at 148-149° from release on 19 November until mid-May (6 months). It was caught to the west off Maatsuyker Island on 19 May, and had been in deep water on several days (Fig. B8), consistent with movement across southern Tasmania.

Shark 98-085. (Fig. D5)

This shark stayed at 148-149° from 19 November 1998 until late March 1999 (~4 months). It then moved west (in water > 86 m) to 145-147° where it stayed for about 4 months until caught on 8 August 1999.

Shark 98-079. (Fig. D6)

This shark stayed at 148-149° from 19 November 1998 until the end of March 1999 (~4.5 months). It then moved west, staying in < 86 m, consistent with moving through Bass Strait, reaching 144.5-145.5° by mid-April. It remained at these longitudes until mid-July (~ 3months), before disappearing into deep water for about 5 weeks, reappearing at 140-139° in SA in late August, where it remained until caught on 23 September 1999.

Shark 98-088. (Fig. D7)

This shark moved west immediately after tagging, so it must have done so in Bass Strait– the depths are consistent. It reached 144.7°E (level with the western tip of NW Tas) in mid-December. It then returned east reaching longitudes of 146.5–147.5° by mid-January. It could have done so in Bass Strait (the depths are consistent), but it had reached sufficiently far west in mid-December that it could have rounded the NW tip of Tas and commenced its easterly return by following the west coast southwards. However, the shallow depths imply that it would have had to remain close to the coast all this time (the depth plots in Fig. C12a are what we expect from a fish following the bottom all the time). In April it moved west again, reaching ~ 145° late in the month. At this longitude it was able to access water 400m deep in early May, placing it on the Tas south-west coast. However, the weekly median longitudes in April-May indicate that it is unlikely that it could have moved out of Bass Strait around the NW tip of Tas and down the west coast to reach deep water. This implies that it had moved inshore down the west coast in December-January, and spent January–April off the south coast of Tas, before moving north-west to King Island longitudes in July-September. It is possible that it spent its last few months in western Bass Strait, near where it was caught in December 1999.

Fig. D4. Daily and weekly-median longitude estimates, and maximum daily depth for school shark 98-073 (female, 132 cm TL).

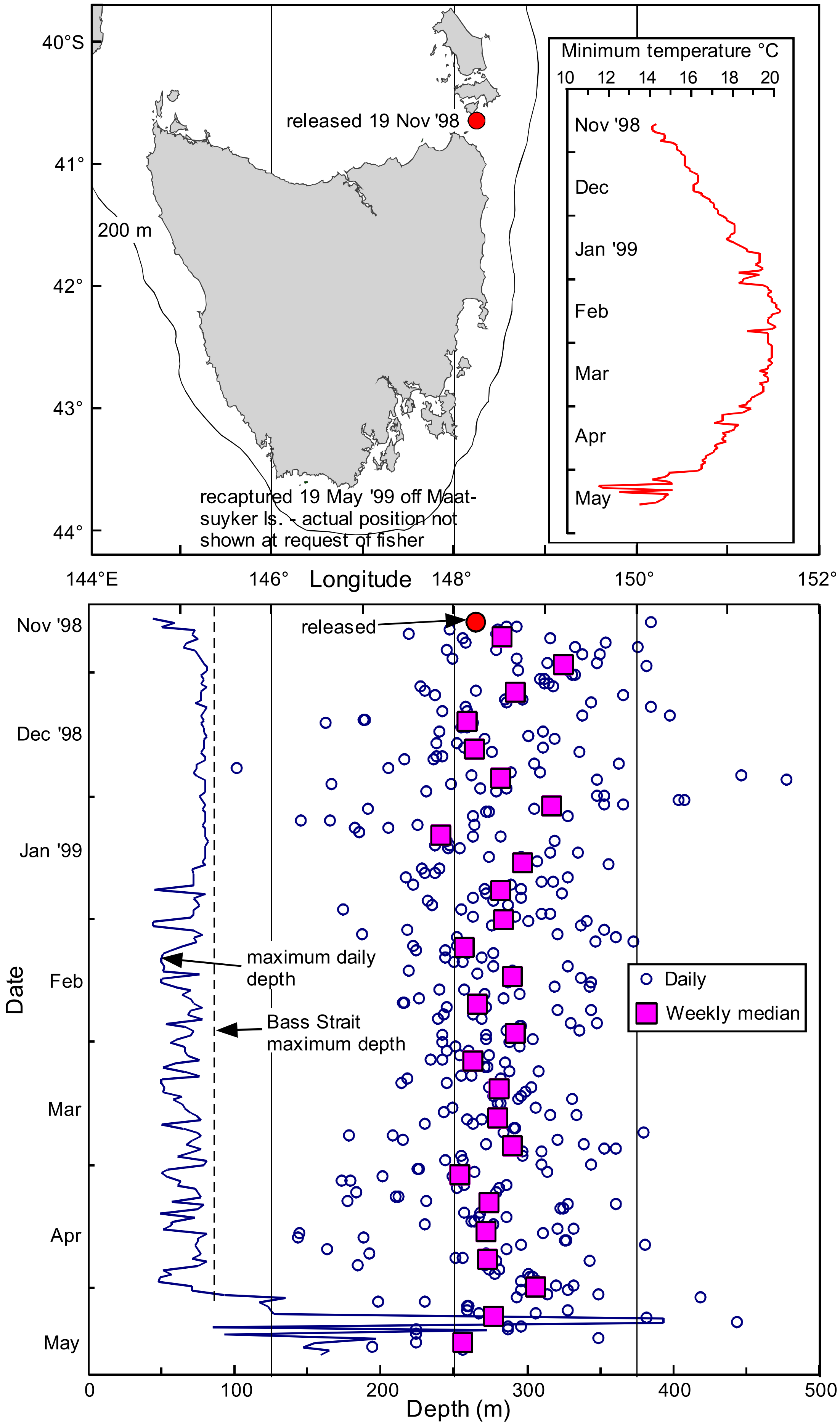


Fig. D5. Daily and weekly-median longitude estimates, and maximum daily depth for school shark 98-085 (female, 140 cm TL)

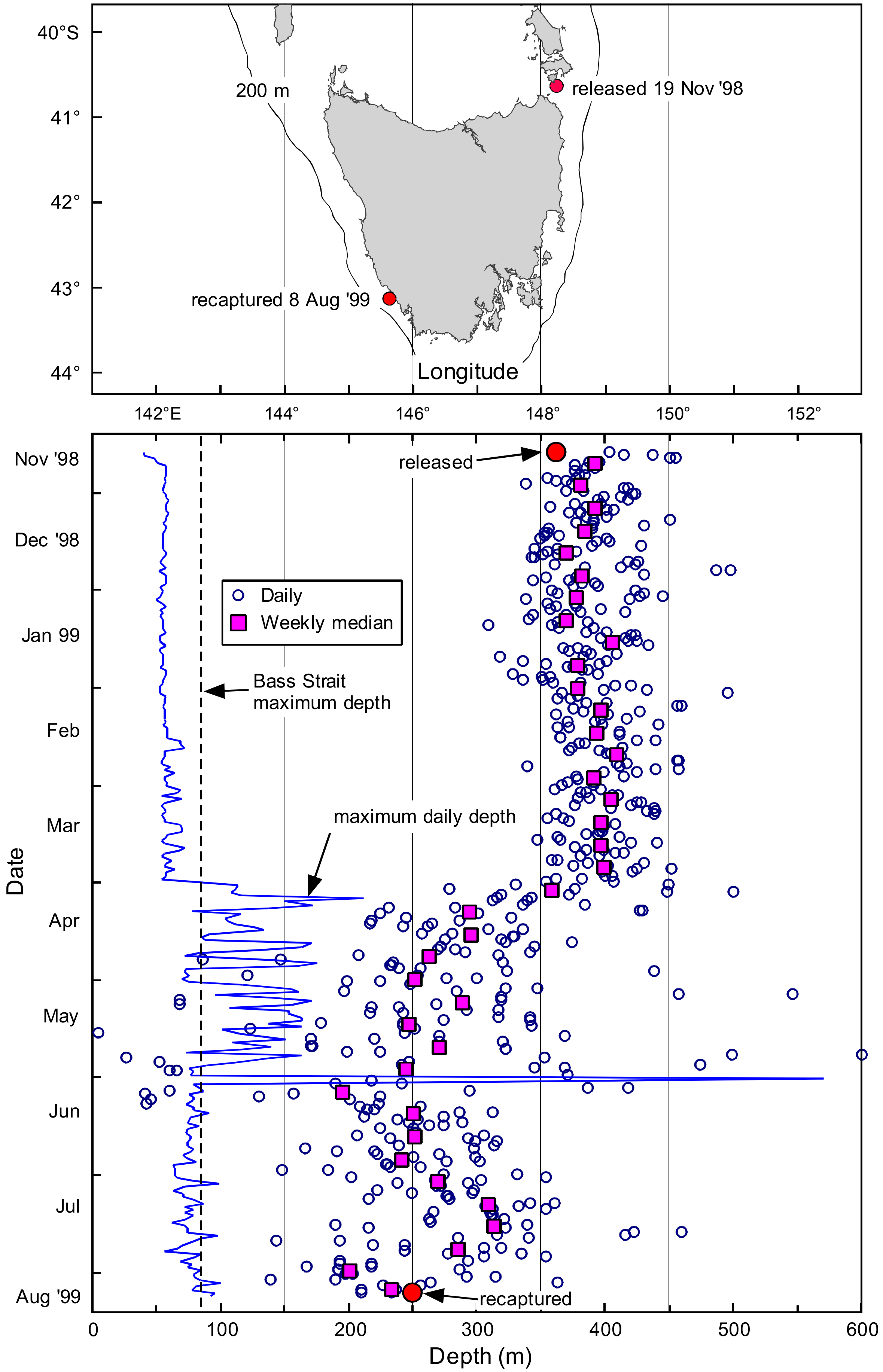


Fig. D6. Daily and weekly-median longitude estimates, and maximum daily depth for school shark 98-079 (female, 128 cm TL).

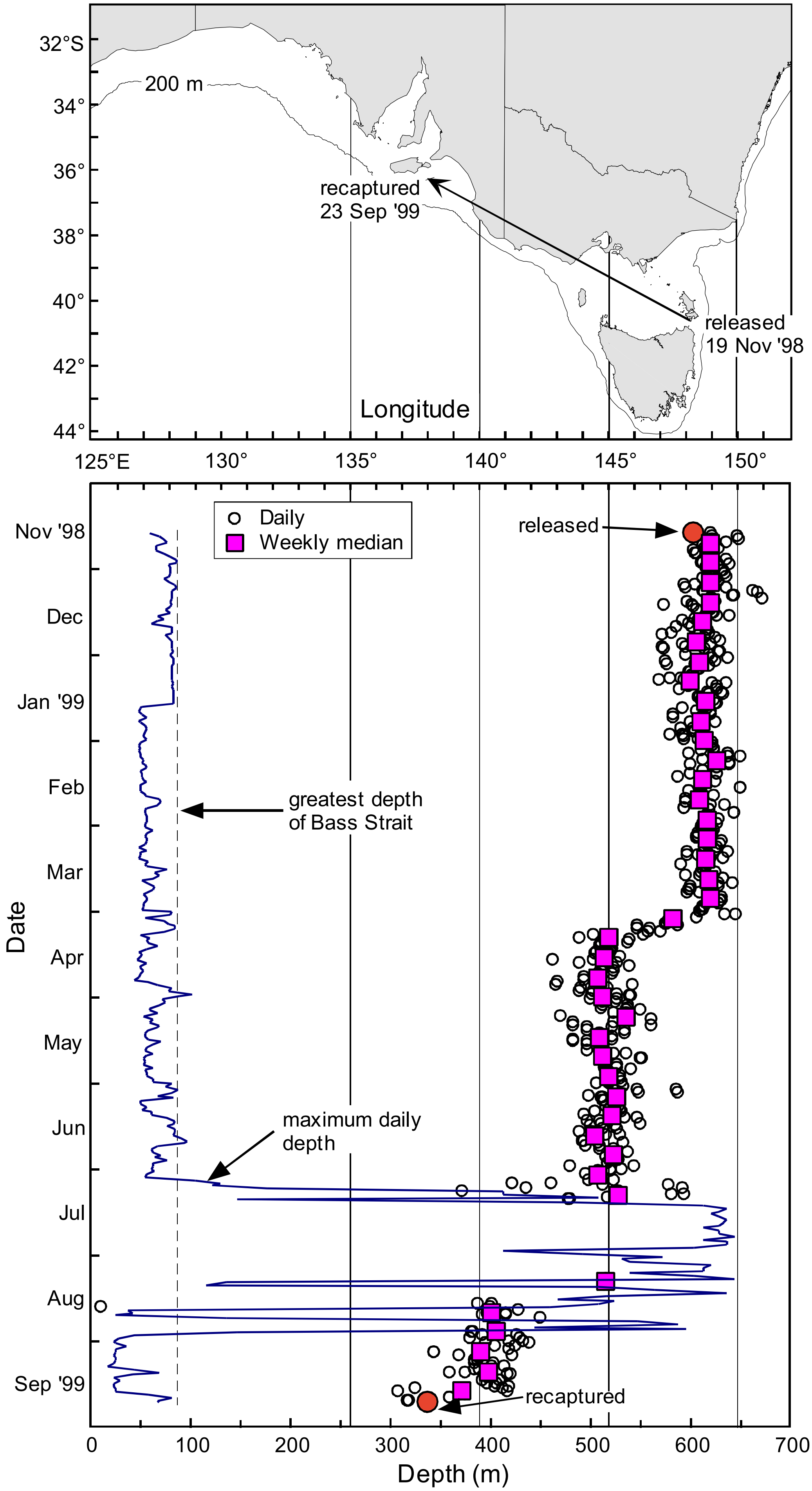


Fig. D7. Daily and weekly-median longitude estimates, and maximum daily depth for school shark 98-088 (female, 151 cm TL).