Intraspecific differences in movement, dive behavior and vertical habitat preferences of a key marine apex predator

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ABSTRACT: Understanding the patterns of large-scale movements of highly mobile marine predators is essential to understanding the impacts of anthropogenic pressures on the animals and the ecosystems they frequent. The broadnose sevengill shark *Notorynchus cepedianus* is one of the most important apex predators in temperate coastal areas around the world, yet little is known of its seasonal large-scale movements. Five male and five female sevengill sharks were equipped with pop-up satellite archival tags (PSATs) in a coastal embayment in southern Tasmania, that collected depth and temperature data during winter, when the animals leave the coastal embayment, resulting in a dataset covering a total of 818 d. Animal tracks indicated that males moved northwards into warmer waters, whereas females remained in southern waters. Three of the females stayed in the Tasmanian coastal areas while the other two left, with one of them moving into deeper waters of up to 360 m depth at the southern edge of the Tasmanian shelf before returning to the Tasmanian coast. These sex-specific differences in large-scale movement could potentially lead to the differential exploitation of the sexes when the sharks leave the protected areas where they were tagged. Both males and females switched between diel vertical migration and reverse diel vertical migration over the course of their tracks and displayed oscillatory vertical movements, probably linked to foraging. These vertical movements persisted throughout the tracks, suggesting that sevengill sharks foraged continuously during their migration rather than switching between transiting and foraging modes.

KEY WORDS: Broadnose sevengill shark · *Notorynchus cepedianus* · Pop-up satellite archival tag · Biotelemetry · Wavelet analysis · Sex-specific · Hexanchiformes

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INTRODUCTION

The patterns of large-scale movements of animals tend to be driven by the integration of a number of life-history requirements such as foraging, reproduction and dispersal (Kuhn et al. 2009). Understanding these patterns is essential to understanding the impacts of anthropogenic pressures on the animals, as well as the ecosystems they frequent (Dingle 1996). This is particularly true for higher order predators, which can exert considerable influence on ecosystem structure through the top-down regulation of prey species (Heithaus et al. 2007). Because of the potential for ecosystem-wide ramifications, the global decline in marine apex predator abundance is a growing concern (Baum et al. 2003, Myers & Worm 2003, Heithaus et al. 2008, Estes et al. 2011). This is particularly true for sharks, which are often slow growing, late maturing and have low fecundity, making them highly vulnerable to overexploitation (Compagno 1990).

Migratory behavior is a common trait in many shark species (Speed et al. 2010) and movements can range from short seasonal (Bruce et al. 2006) to transoceanic migrations (Bonfil et al. 2005). Understanding the complexities of this behavior is essential for the development of successful conservation and management measures (Speed et al. 2010). The broadnose sevengill shark *Notorynchus cepedianus* is a large (up to 3 m) demersal shark of the order Hexanchiformes (Barnett et al. 2012). It is one of the most important apex predators in temperate coastal areas around the world (Last & Stevens 2009) due to the high diversity of its diet, which includes marine mammals, chondrichthyans and teleosts (Cortés 1999, Ebert 2002, Barnett et al. 2010a). While not a target species, it is often caught as by-catch in commercial shark fisheries (Compagno 1984), and is targeted by recreational fishermen (Lucifora et al. 2005). Although the global fisheries status of the sevengill shark is not well known (Barnett et al. 2012), it is considered to be highly vulnerable to gillnetting gear and at high risk in terms of abundance and catch susceptibility (Walker et al. 2007).

Despite its importance as an apex predator in coastal marine systems, until recently, little was known about the species' ecology beyond dietary information (Ebert 2002, Braccini 2008, Barnett et al. 2010a) and it is therefore listed as data deficient on the IUCN Red List (Fowler et al. 2005). However, a number of recent studies carried out off the coasts of Patagonia (Lucifora et al. 2005), the west of the USA (Williams et al. 2011) and Tasmania (Barnett et al. 2010c) have shed light on the structure of the respective populations, and acoustic tracking studies off Tasmania (Barnett et al. 2010b, Barnett et al. 2011) and Washington State (Williams et al. 2012) have examined the fine-scale movement behavior and seasonal habitat use patterns of these animals.

All of these studies showed a marked increase in abundance in nearshore areas in spring and summer, followed by a near absence in winter with individuals showing strong site fidelity to certain coastal sites. Off Patagonia (Lucifora et al. 2005) and California (Ebert 1989), seasonal movement into nearshore areas has been attributed to pupping activity, whereas prey abundance was considered the main factor driving the seasonal use of coastal areas off Washington State (Williams et al. 2011) and Tasmania (Barnett et al. 2010c). Upon leaving the coastal areas in autumn, sexual segregation was evident from the migratory behavior of the sevengill sharks in Tasmania. Males moved distances of up to 1000 km northward into warmer waters off the east coast (Barnett et al. 2011)

or northwest to the central south coast of mainland Australia (A. Barnett unpubl. data), whereas some females stayed in coastal areas and others left for an unknown destination, possibly offshore (Abrantes & Barnett 2011). Sexual segregation is common in many shark species (Wearmouth & Sims 2008, Speed et al. 2010) and sex biased migration has been shown for other shark species such as the white shark *Carcharodon carcharias* (Domeier & Nasby-Lucas 2012). Sex specific differences in migratory behavior may have significant ramifications for conservation and management, if males and females are exposed to differential degrees of fishing pressure (Mucientes et al. 2009).

Pop-up satellite archival tags (PSATs), which transmit depth and temperature data from the tagged animal via a satellite link, have been successfully deployed on a number of different shark species to determine their dive behavior and habitat preferences (Nasby-Lucas et al. 2009, Hammerschlag et al. 2011).

In this study, we analyzed unpublished data on depth and temperature preferences from PSATs deployed on 5 male broadnose sevengill sharks by Barnett et al. (2011). We also deployed PSATs on 5 females in their nearshore Tasmanian summer habitat just before they were due to start their annual winter migration (Barnett et al. 2011) to investigate (1) sex specific differences in large-scale movement and (2) vertical habitat preferences and movement during the sharks' winter migration.

MATERIALS AND METHODS

Tagging of sharks

Ten pop-up satellite archival tags (MK10 PSAT, Wildlife Computers) were deployed on 5 male and 5 female broadnose sevengill sharks from 2008 to 2011. These tags measure external temperature, depth and light level at user-defined time intervals, detach from the animal after a pre-programmed deployment period (see Table 1) and transmit the collected data to the Argos satellite system. Satellite bandwidth is limited, so depth and temperature data are summarized for a specified summary period as histograms of time spent at a set of depth and temperature bins and as temperature-at-depth profiles. Since tags were deployed over 4 yr, data returns from initial tag releases informed the programming of subsequent tags to optimize sampling efficiency, resulting in different tag setups between years (Table 1).

Table 1. Data collection and summary set-up of the tags for the 3 deployment periods

	Temperature bins (°C)	Temperature sampling interval (s)	Depth bins (m)	Depth sampling interval (s)	Histogram summary period (h)	Deployment duration (d)
2008	0; 5; 10; 12; 14; 16; 18; 20; 22; >22	120	0; 2; 10; 20; 40; 60; 80; 100; 150; 200; 300; 500; 700; >700	30	24	180
2009	10; 11; 12; 13; 14; 15; 16; 17; 18; 19; 20; 21; 22; >22	120	0; 2; 10; 20; 40; 60; 80; 100; 120; 150; 200; 250; 300; >300	10	6	138
2010/2011	8; 9; 10; 11; 12; 13; 14; 15; 16; 17; 18; 20; 22; >22	60	0; 2; 10; 20; 40; 60; 80; 100; 120; 150; 200; 250; 300; >300	10	6	138

All tags were deployed in the Derwent Estuary/ Norfolk Bay, a system of coastal embayments on the southeast coast of Tasmania (see Fig. 1). Tagging was carried out at the beginning of the Austral winter (May and June), as seasonal longline sampling indicated migratory movement out of the coastal areas around this time (Barnett & Semmens 2012). Sharks were caught on bottom-set, baited longlines, lifted onto the tagging vessel and turned onto their back where they could be handled without the need for restraint. Aboard the tagging vessel, the hook was carefully removed from the shark's mouth, their eyes covered with a wet cloth to avoid injury, their sex identified and total length measured.

Tags were attached to the shark by implanting a stainless steel anchor, which was attached to the tag via a 100 mm long, nylon coated, multi-strand, stainless steel wire trace (2 mm diameter) into the dorsal musculature. A second anchor with a stainless steel wire loop attached to it, which was placed around the body of the tag, was implanted approximately 100 mm behind the first anchor to prevent excessive sideways movement of the PSAT.

Aseptic techniques were used during tag deployment and the entire procedure lasted approximately 3 to 5 min. Seawater was continuously pumped over the gills of the shark throughout the procedure. Prior to release, a povidone-iodine antiseptic was applied to the wounds to aid healing. All methods used were approved by the University of Tasmania Animal Ethics Committee (Approval No A0011590).

Data analysis

Data from the first 24 h of archival records were removed from the dataset to remove abnormal behavior associated with tagging stress, and records fol-

lowing tag detachment from the shark were also removed from the dataset.

Estimates of the movement paths of the individual sharks were obtained from state-space models (Patterson et al. 2008) using the approach outlined in detail by Pedersen et al. (2011). Movements are restricted to a discrete grid of locations; here, grid cells were of size 0.2° longitude/latitude bounded by 142 to 154°E and 45 to 25°S. The state-space observation model combined longitude estimates from the tag manufacturer's raw geolocation software (DAP Processor 3.0; Wildlife Computers) and Reynolds 10 d composite sea surface temperature (SST) using observation error parameters given in Pedersen et al. (2011). Additionally, we included depth data in the observation model by taking the difference between PSAT-observed maximum depth and the Terrainbase bathymetry product (see www.ngdc.noaa.gov/mgg/ topo/) and assumed that this had a logistic distribution model: $logit(h) = \beta_1 (PSAT_{depth} - Bathy_{depth}) + \beta_0$ where $PSAT_{depth}$ is the maximum depth for the given period from the PSAT data, $Bathy_{depth}$ is the bathymetric estimate of the depth throughout the spatial domain, and parameters $\beta_1 = 0.01$ and $\beta_0 = 0.02$.

This amounts to using an informative prior on the distribution of PSAT-observed maximum depth with respect to the spatial grid of bathymetry data. This formulation has the effect of only being informative for bathymetric depth values less than or approximately equal to the observed depth. In other words, the observed depth may be slightly greater than the bathymetry product but not drastically so and areas where the ocean is much deeper than the observed PSAT depth contribute practically zero information regarding location. Conversely, locations where observed PSAT depth is much deeper than the bathymetry are highly unlikely. Final movement tracks were given by the weighted average across the pos-

terior distribution of location on the state space (see Pedersen et al. 2011 for details).

To estimate the timing of movement away from the coastal tagging site, we defined departure as the first instance when recorded maximum depth dropped below 50 m or SSTs recorded by the tags (defined as any temperature values recorded at depths <5 m) fell outside of the range of monthly average SSTs ±1 SD, measured at the entrance to the Derwent estuary (Derwent Estuary Program).

To examine variations in preferred swimming depth throughout a shark's track, weighted mean depths for each data summary period were estimated from time at depth histograms as the sum of the product of the bin frequency and corresponding bin interval midpoint. As the temperature-depth data from the tags were quite sparse, temperature profiles along each track were constructed by applying a moving window of 72 h to temperature-at-depth data transmitted by the tags. For data from each window, the depth-temperature relationship was interpolated from the surface down to the maximum depth within the window using a polynomial B-spline (bs() function in R; R Development Core Team 2011).

To characterize the vertical movement behavior of the sharks, we analyzed the full archival records from the 4 recovered tags in 2 different ways. To determine diel changes in vertical movement activity, we separated the data series into daytime and nighttime periods based on timing of sunrise and sunset at the estimated position of the shark, obtained from a nautical almanac. We then counted the total number of ascents, defined as continuous decreases in swimming depth, uninterrupted by increases in depth greater than 0.5 m per 10-s sampling interval, in each period. The number of ascents at nighttime and daytime were then compared using a generalized linear model (GLM) with Poisson distribution for each shark.

To identify phases where sharks displayed diel vertical migration (DVM) or reverse diel vertical migration (rDVM), we separated each dataseries into 24-h periods from sunrise to the following sunrise, and then compared mean nighttime and daytime swimming depths of each 24-h period using the Mann-Whitney U-test with normal approximation (Sims et al. 2005). To ensure equal sample sizes despite differences in day and night lengths, nighttime swimming depths were randomly resampled to match the number of daytime observations. DVM periods were defined as 24-h periods where nighttime swimming depths were significantly (p < 0.05) shallower than daytime depths, periods where nighttime swimming depths were significantly (p < 0.05) greater than daytime depths were classified as rDVM periods.

To determine the dominant periodicity of dive behaviors through time, we compared the power of 24, 12 and 6-h periodicities using wavelet analysis for the complete time series of vertical movement from 4 tags that were recovered. Wavelet analysis is the local time-scale decomposition of a signal, which allows the estimation of the spectral characteristics of a signal as a function of time (Cazelles et al. 2008). Hence, it does not assume stationarity of the signal, an assumption that needs to be addressed using ad hoc windowing procedures when using more traditional methods such as Fast Fourier Transform (Cazelles et al. 2008). Wavelet analyses using a Morlet wavelet transform were carried out in R with the 'biwavelet' package (Gouhier & Grinsted 2012).

RESULTS

Tagged males ranged from 208 to 234 cm total length (TL), tagged females ranged from 152 to 233 cm TL (Table 2). Male sevengill sharks mature at

Table 2. *Notorynchus cepedianus*. Information for tagged broadnose sevengill sharks. *Recovered archival tags

| ID	Sex	Total length (cm)	Deployment date (dd/mm/yyyy)	Days at liberty	Straight line displacement (km)	External temperature range (°C)	Maximum depth (m)
F1	F	233	10/05/2011	136	<10	8.0–13.0	50
F2*	F	190	10/05/2011	136	<10	8.4–13.0	64
F3	F	152	10/05/2011	24	<10	11.0–13.2	48
F4	F	154	10/05/2011	13	54	11.6–13.8	56
F5*	F	189	10/05/2011	135	96	11.0–14.4	360
M1*	M	234	30/04/2010	153	891	12.8–18.2	210
M2	M	216	03/06/2009	94	887	11.0–16.6	192
M3	M	214	05/05/2009	29	356	12.4–16.4	280
M4*	M	208	30/04/2008	47	424	11.6–15.2	175
M5	M	211	02/05/2008	51	708	11.0–15.6	208
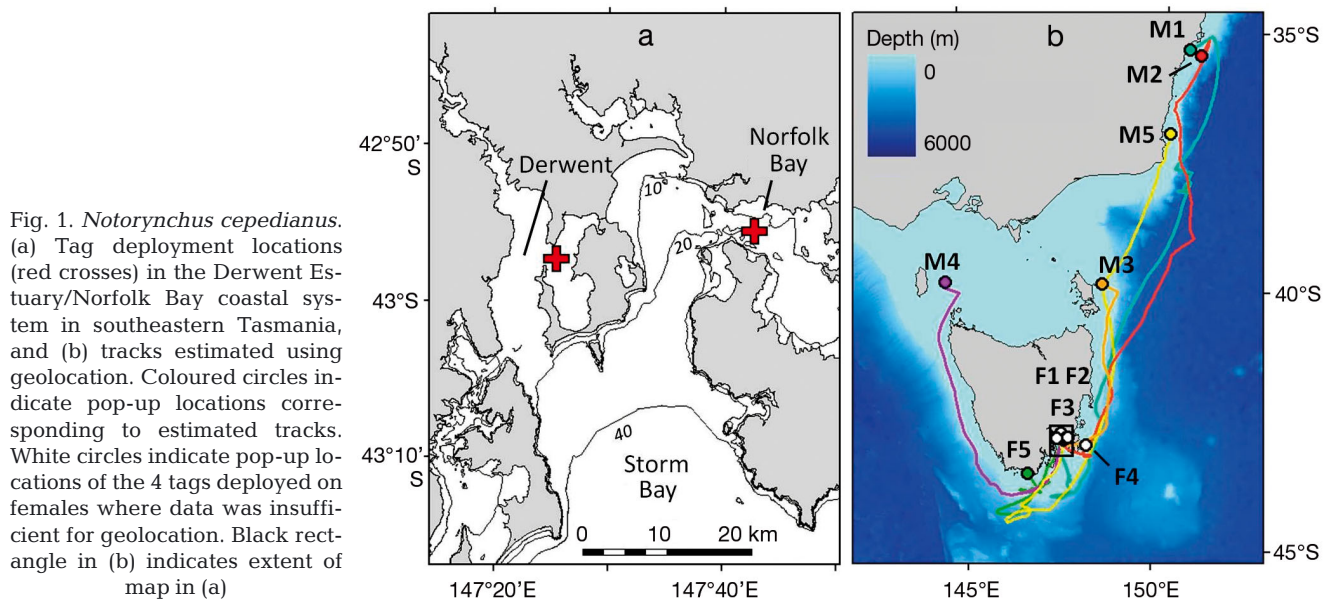
Fig. 1. *Notorynchus cepedianus*. (a) Tag deployment locations (red crosses) in the Derwent Estuary/Norfolk Bay coastal system in southeastern Tasmania, and (b) tracks estimated using geolocation. Coloured circles indicate pop-up locations corresponding to estimated tracks. White circles indicate pop-up locations of the 4 tags deployed on females where data was insufficient for geolocation. Black rectangle in (b) indicates extent of map in (a)

approximately 150 to 180 cm TL (Barnett et al. 2012), which means all tagged males were adults. Females, on the other hand, grow larger than males and mature at approximately 220 cm TL; hence, only one of the tagged females was an adult at the time of tagging.

Mean time at liberty was 75 d (SD = 50 d) for males and 89 d (SD = 64 d) for females (Table 2). Out of the 5 tags deployed on male sharks, only 1 tag stayed on the shark for the programmed amount of time (see Table 1), with all other tags detaching prematurely, whereas for females, 3 of the 5 tags remained attached to the sharks for the programmed amount of time. Four tags, two deployed on males and two deployed on females (Table 2) were recovered after detachment and the complete data records (unbinned depth and temperature measurements at 10 to 120 s sampling intervals; see Table 1) were available for analysis.

Large-scale movement

All tagged males left the Tasmanian coastal area and moved northward. Four of the males moved up the east coast of Tasmania (M1, M2, M3, M5) and one moved up the west coast (M4) (Fig. 1). For 3 of the males (M1, M4, M5), the averaged movement track did not head north immediately after leaving the coastal tagging site, but initially headed south to the edge of the Tasmanian shelf. Two of the tags deployed on males popped-up in the Bass Strait (those with the shortest time at liberty) and the remaining 3 off the east coast of mainland Australia (Fig. 1).

The only female with a large enough displacement to make geolocation informative (F5) showed a southward movement to the shelf edge similar to that shown by some of the males, but spent a larger amount of time there before returning to the Tasmanian coast instead of moving north. Another female left the coastal tagging site (F4) and moved up the east coast of Tasmania where the tag popped up; however, time at liberty was too short for geolocation. For the 3 remaining females (F1, F2, F3), tags popped up at the tagging site (Fig. 1), and maximum depth and SST analyses indicated that while leaving the shallow tagging site in Norfolk Bay for deeper parts of the coastal embayment, they did not leave the Tasmanian coastal area (Fig. 2b).

Temperature preferences

Temperatures experienced by the tagged sharks ranged from 8 to 18.2°C (Table 2). The coldest temperatures of all tagged individuals were experienced by the females that remained in the Derwent Estuary/Norfolk Bay area throughout the winter (Fig. 2b). These individuals (F1, F2, F3) spent the majority of their time in waters between 10 and 12°C and did not experience temperatures above 14°C (Fig. 3a). The 2 females that did not stay in the Derwent Estuary/ Norfolk Bay over winter (F4 and F5) left the estuary in June, before temperatures dropped below 11°C (Fig. 2). This resulted in markedly different time at temperature histograms for these 2 females, with over 90% of time spent in waters between 12 and 14°C
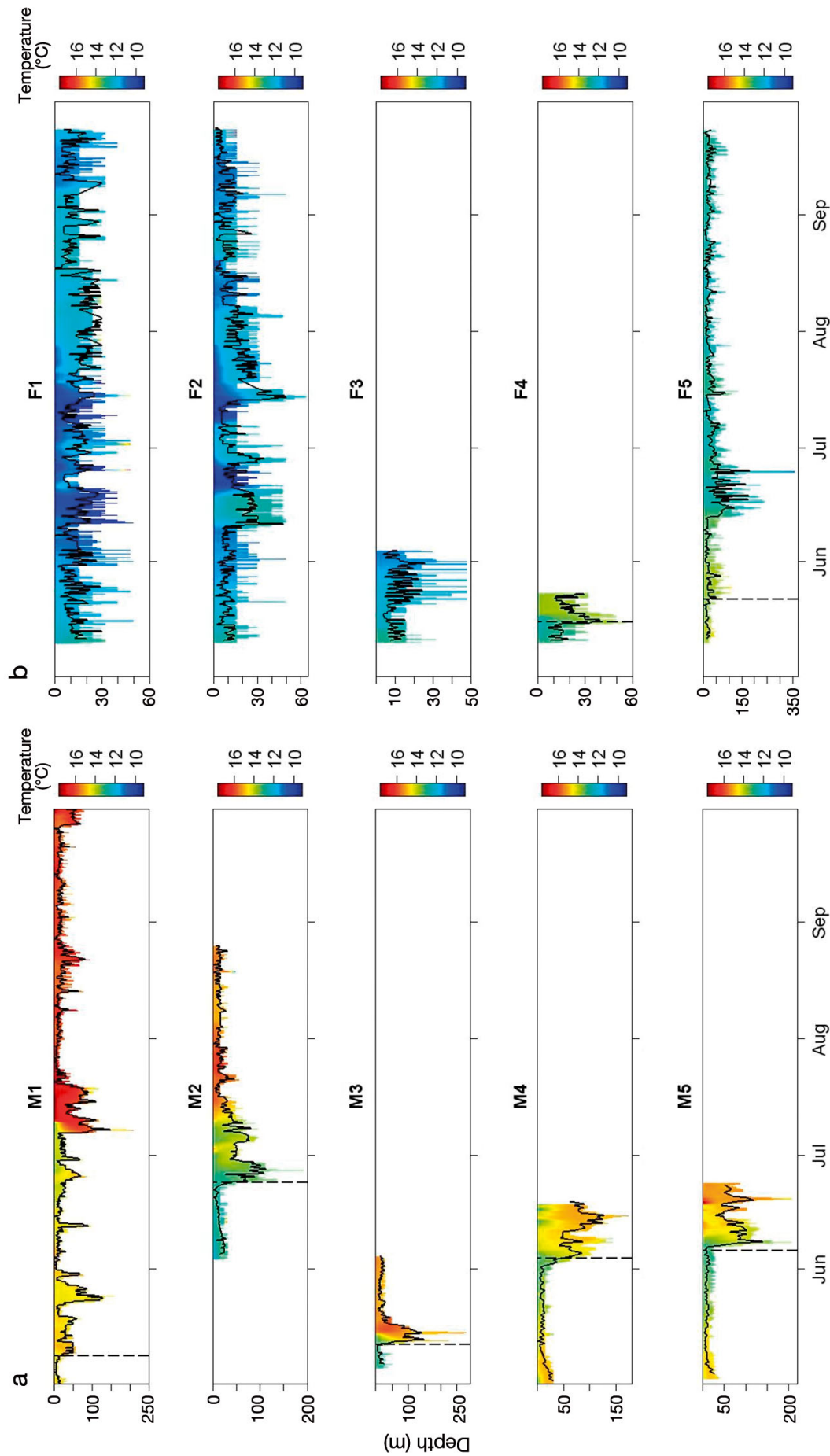
Fig. 2. *Notorynchus cepedianus*. Mean swimming depth and interpolated temperature/depth profiles for (a) 5 tagged male sevengill sharks and (b) 5 tagged female sevengill sharks. Temperature/depth profiles were created by applying linear interpolation to up to 8 temperature-at-depth readings transmitted by the tag for each summary period. Black line indicates weighted mean swimming depth; profile colours indicate temperature in °C. Vertical dashed lines indicate timing of departure from the Tasmanian tagging site where applicable. Bottom edge of the temperature profile is equivalent to maximum swimming depth
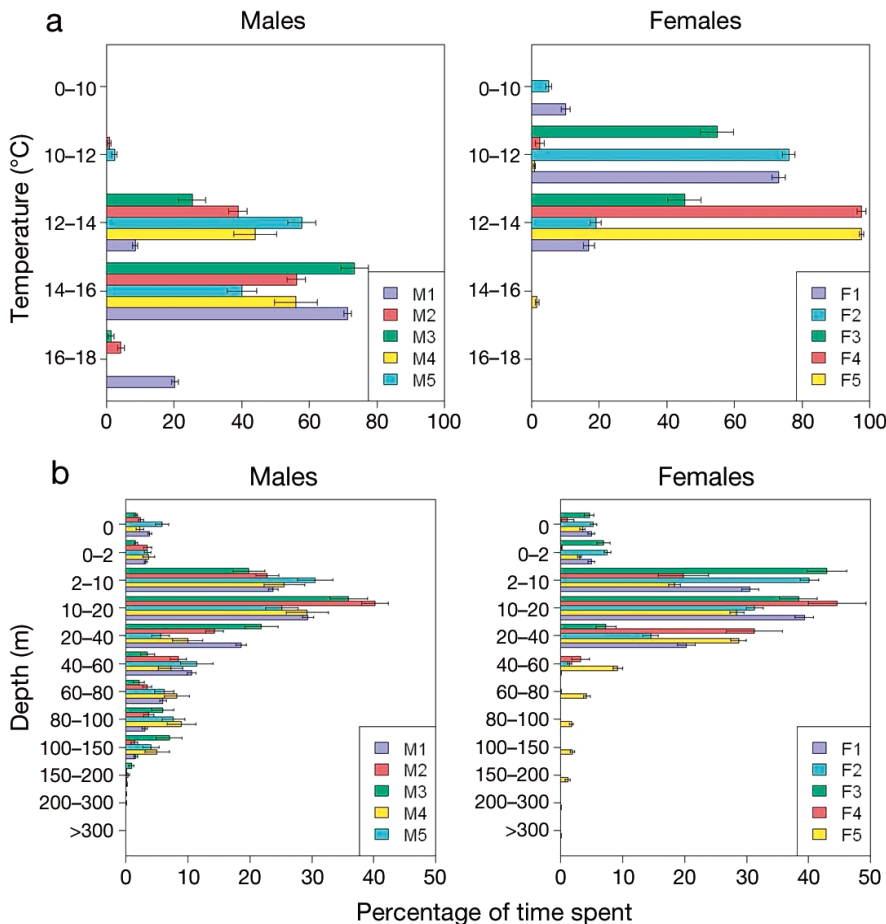
Fig. 3. *Notorynchus cepedianus*. Time spent at (a) temperature bins and (b) spent at depth bins outlined in Table 1. Bins were standardized across tags to the highest common resolution and histograms averaged over the tag deployment period. Error bars indicate ±1 SE

and no time spent in waters below 10°C. (Fig. 3a). Males also left the Derwent Estuary/Norfolk Bay before temperatures dropped below 11°C; however, timing of departure varied (Fig. 2a) both within and between years. These animals spent the majority of time in temperatures between 12 and 16°C, with hardly any time spent below 12°C (Fig. 3a) and only one male spending considerable amounts of time in waters warmer than 16°C (M1).

External temperature records obtained from recovered tags showed very little temperature variation with depth for parts of the tracks of sharks M1, M4 (Fig. 4a) and F5 (Fig. 4b), even as the sharks dove to depths in excess of 100 m, indicating a relatively well mixed water mass. Shark F2, on the other hand, which stayed in the Derwent Estuary/Norfolk Bay area throughout the winter, experienced variations in external temperature of up to 4°C with coldest temperatures experienced during sporadic ascents close to the surface (Fig. 4b), indicating the presence of a colder surface layer.

Depth preferences

Despite the fact that females that stayed in the coastal areas over winter reached much shallower maximum depths than males or females that left the coastal areas (Fig. 2), both groups spent the majority of their time between 2 and 40 m of depth (Fig. 3b). For large parts of their tracks, the males and the females that left coastal areas had mean swimming depths of about 20 m, which were similar to those of the females that remained in coastal waters, yet their mean swimming depth also dropped below 50 and 100 m on several occasions (Fig. 2) and time-at-depth histograms showed that these animals spent a considerable amount of time in depths from 40 to 150 m.

Archival records for the 4 recovered tags showed that these sharks displayed both DVM and rDVM over the course of their tracks (Table 3). For these animals, apart from the female that remained in the Tasmanian coastal area (F2), DVM was more frequent than rDVM and was evident for longer consecutive periods (Table 3). Furthermore, most of these animals displayed 2 distinct behaviors: a shallow phase, characterized by regular trips to the surface, and a deep phase, with no trips to the surface for over 24 h (Fig. 4). During the shallow phase for males M1 and M4, DVM was evident throughout, with a strong 24-h periodicity in vertical movement (Fig. 5), as the shark stayed near the surface for most of the night and at depths of 10 to 20 m during the day (Fig. 4a). During the deep phase, both DVM and rDVM behavior were evident, as well as periods with no significant difference between daytime and nighttime swimming depths. Overall, changes in depth were much less regular during these phases.

For the 2 females whose tags were recovered, vertical movement behavior differed considerably. Female F2, which remained in the shallow Tasmanian coastal area, displayed shallow phases as well as deep phases (Fig. 4b). During the shallow phase,
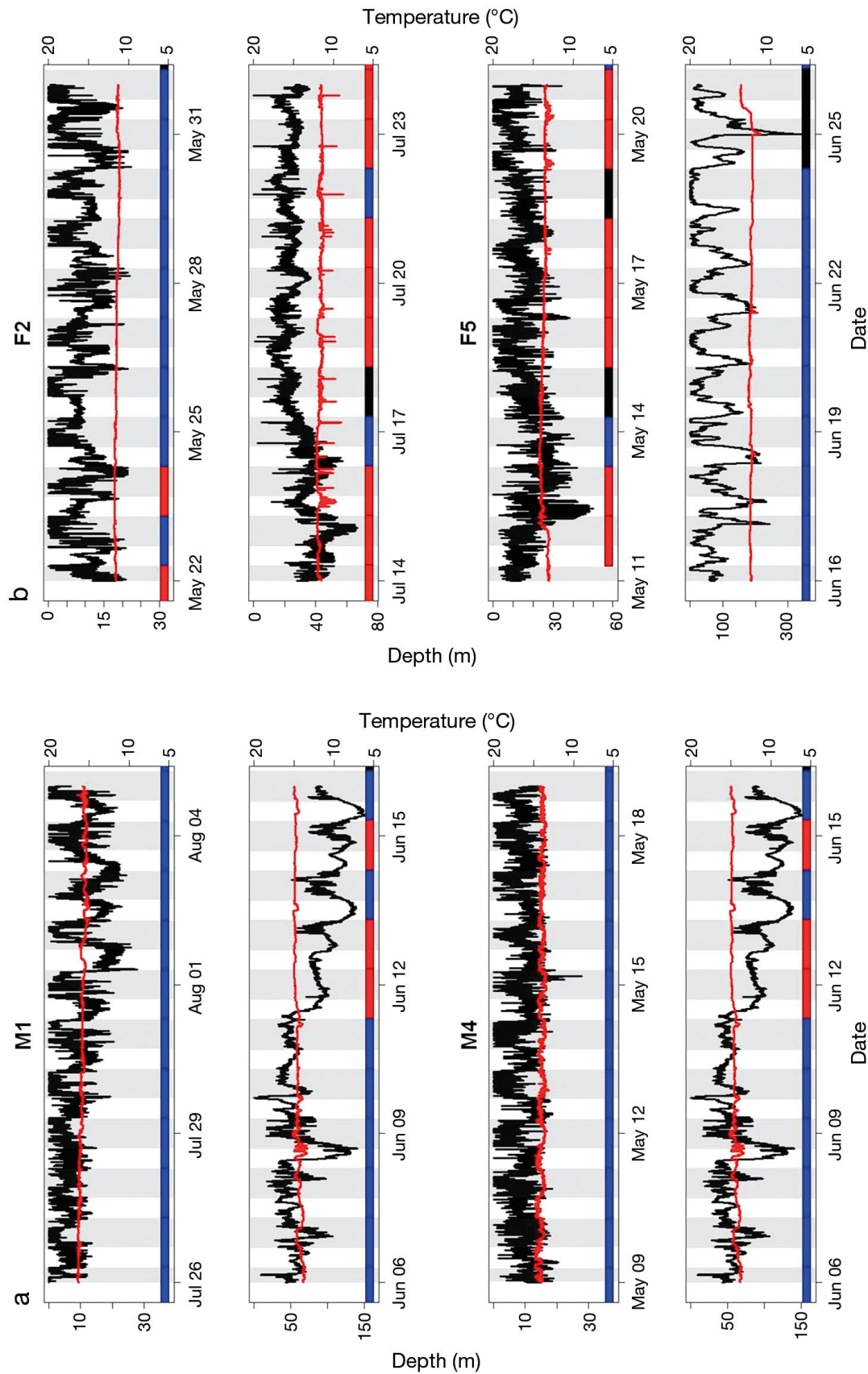
Fig. 4. *Notorynchus cepedianus*. Vertical movements for two 10 d periods from (a) 2 male and (b) 2 female broadnose sevengill sharks. One of the females left the coastal areas over winter (ID: F5) and one stayed (ID: F2). Top panels show 10 d example of swimming depth (black line) and temperature (red line) during shallow swimming phases, bottom panels show 10 d example of depth and external temperature during deep swimming phases. Vertical grey bars indicate nighttime. Colour bar at the bottom edge indicates vertical behavior for each 24-h period (blue = DVM, red = rDVM, black = no difference between daytime and nighttime swimming depth). For female F5, which did not exhibit a deep phase, periods with small and large vertical movement range are shown

Table 3. *Notorynchus cepedianus*. Diel vertical migration (DVM), reverse diel migration (rDVM) and periods of no difference between daytime and nighttime swimming depths for the entire deployment periods of the 4 recovered tags

| ID | DVM | | rDVM | | No difference | |
	Total %	Maximum consecutive period (d)	Total %	Maximum consecutive period (d)	Total %	Maximum consecutive period (d)
M1	56	14	41	8	3	1
M4	73	19	25	3	2	1
F2	42	9	53	15	5	2
F5	64	17	29	8	7	2

DVM behavior was dominant, whereas rDVM was more prevalent during the deep phase and overall rDVM was more frequent for this animal (Table 2). However, even though overall swimming depths were shallower in the day during the rDVM phase, absolute minimum depths were often reached during single ascents in the night (Fig. 4b). In contrast to the males and the female that stayed in the Tasmanian coastal area, the female that left (F5) did not exhibit a deep phase, as it showed regular returns to the surface throughout its track. It did, however, display periods with larger and smaller vertical movement range (Fig. 4b). During the period with small vertical movement range, rDVM was evident as well as phases with no diel differences in swimming depth, during which the power of the 24-h periodicity was greatly reduced (Fig. 5). During the period with large vertical movement range, on the other hand, strong DVM behavior was evident and the animal returned to the surface every night, even after spending the day at great depths, making vertical movements of up to 360 m in a 24-h period.

In addition to vertical migrations, all sharks also showed a diel pattern in vertical movement activity
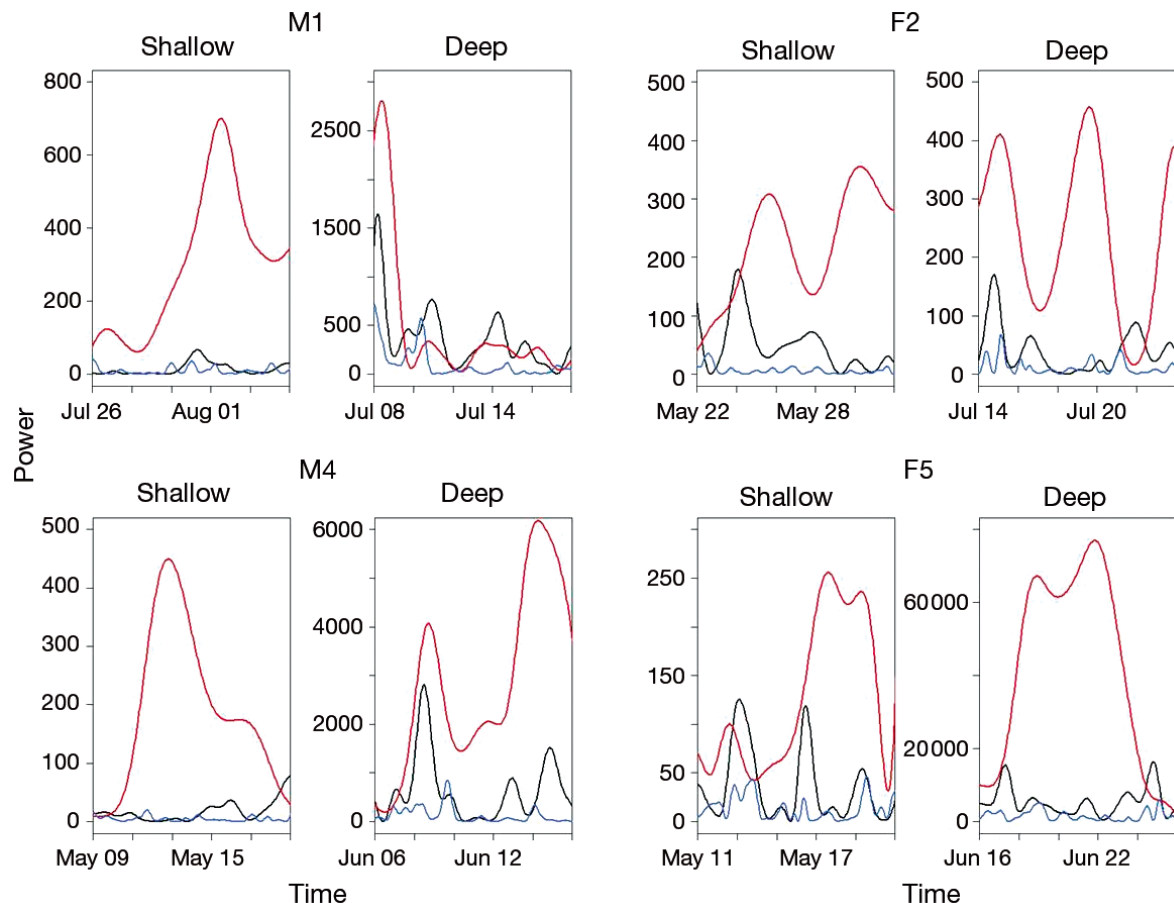

Fig. 5. *Notorynchus cepedianus*. Change in power over time for the 6-h (blue line), 12-h (black line) and 24-h (red line) periodicity in swimming depth for the example periods in Fig. 4, determined using wavelet analysis of mean hourly swimming depth from recovered archival tags. Absolute power is dependent on the magnitude of the oscillation. Hence, scales are much larger for deep than for shallow periods for animals that left the shallow coastal areas (all except F2)

Table 4. *Notorynchus cepedianus*. Diel changes in vertical movement activity for the entire deployment periods of the 4 recovered tags. Standard deviation in brackets

	Daytime mean number of ascents	Nighttime mean number of ascents
M1	7.5 (7.5)	20.6 (15.7)
M4	4.9 (3.2)	24.9 (10.7)
F2	10.4 (7.6)	18.7 (10.5)
F5	11.6 (6.0)	18.5 (8.6)

(Table 4) with the number of ascents made during the night significantly greater than during the day for all animals (GLM, p < 0.05).

DISCUSSION

This study has provided new insight into the migratory behavior and vertical movements of a relatively poorly studied apex predator of great ecosystem importance. We found behavioral differences in the winter migration of male and female broadnose sevengill sharks tagged in Tasmania. All males left the coastal tagging site in the Derwent Estuary/Norfolk Bay between mid-May and the end of June to move northwards into warmer waters, covering minimum distances of up to 880 km. Some of the females remained in the Derwent Estuary/Norfolk Bay for the entire winter, in waters with temperatures as low as 8°C, while others left the coastal tagging site and in one case moved into deeper waters at the southern edge of the Tasmanian shelf. Females that remained near the tagging site left Norfolk Bay and moved into deeper parts of the embayment, possibly into Storm Bay, the area at the entrance to the Derwent Estuary/Norfolk Bay (Fig. 1), which has been suggested to be the winter habitat of juvenile school sharks *Galeorhinus galeus* (Stevens & West 1997), one of the prey species of sevengill sharks (Barnett et al. 2010a).

Barnett et al. (2011) also found that females spent the winter near the entrance to the Derwent Estuary; hence, our results further support both sex specific and within female differences in migratory patterns previously proposed for sevengill sharks in Tasmania from acoustic tracking and stable isotope analysis (Abrantes & Barnett 2011, Barnett et al. 2011).

Sex specific differences in long-distance movement in the sevengill shark were also detected in animals tagged in the Pacific Northwest of the USA. However, in that region roles appeared to be reversed, with long distance coastal movements into warmer waters carried out by female sharks (Wil-

liams et al. 2012). Sex specific differences in seasonal migration could be due to one or a combination of differences in thermal tolerance, seasonal spatial resource partitioning or reproduction (Springer 1967, Wearmouth & Sims 2008).

Migrations driven by changes in water temperature have been reported for numerous shark species (Speed et al. 2010). It is possible that the sexual dimorphism in the body size of sevengill sharks might cause sex specific differences in thermal tolerance, as has previously been reported for other elasmobranch species (Wallman & Bennett 2006), with the larger females being able to withstand lower temperatures. However, all but one of the tagged females in this study were smaller than males and the study from the west coast of the USA where the migratory pattern for males and females was reversed seems to contradict this hypothesis (Williams et al. 2012). Further deployments of archival tags in different parts of this species' range are required to better understand the thermal tolerances of male and female sevengill sharks.

It is also possible that differences in migratory behavior are due to seasonal resource partitioning caused by diminished foraging resources in winter, when the main chondrichthyan prey species are absent from coastal areas (Barnett et al. 2010a). Intraspecific differences in seasonal migration driven by resource partitioning have been shown for various ungulate species such as the Yellowstone pronghorn *Antilocapra americana* (White et al. 2007) and moose *Alces alces* (Ball et al. 2001) and tend to emerge when migrants and non-migrants in a population receive approximately equal payoffs (Swingland & Lessells 1979). While differences in migratory behavior in those species were not sex specific, it is possible that the subtle sexual dimorphism in body size of sevengill sharks can lead to sex specific resource partitioning. In order to reach the body size required for gestation of embryonic young, females may have greater energetic demands than males, leading to the evolution of differential migration, as has been suggested for the scalloped hammerhead shark *Sphyrna lewini* (Klimley 1987). This hypothesis requires the assumption that it is energetically advantageous for the females to remain in coastal areas over winter, with males being forced to pay the cost of migration due to the diminished prey resource.

The most common driver of sex specific migrations in sharks, however, is generally thought to be the difference in reproductive requirements of males and females (Sims et al. 2001). In contrast to sevengill shark populations in Argentina and California (Ebert

1989, Lucifora et al. 2005), sevengill sharks do not appear to use the Tasmanian coastal areas as mating sites, pupping grounds or nursery areas, as only limited numbers of fresh mating scars were detected on females and neonates are not present in these areas (Barnett et al. 2010c). Therefore, it has to be assumed that both mating and pupping primarily occur outside of the Tasmanian tagging area. The areas on the east coast of mainland Australia frequented by the tagged males are unlikely to be used for mating, however, as sevengill catches in shark control beach nets in New South Wales are overwhelmingly male (Barnett et al. 2011). Hence, Barnett et al. (2011) hypothesized that mating may occur at the entrance to the Derwent estuary in autumn, prior to the males' departure. It is also possible that mating occurs in the area at the southern edge of the Tasmanian shelf which was frequented both by one of the females and some of the males; however, further research is required to ascertain the significance of this area to the sharks.

In other shark species, long-distance movements into warmer waters by females may be driven by reproductive requirements (e.g. porbeagle shark *Lamna nasus* [Campana et al. 2010], grey reef shark *Carcharhinus amblyrhynchos*, lesser spotted dogfish *Scyliorhinus canicula* [see Sims 2005 for review]) and it might be driving the migratory movement of the female sevengill sharks in Tasmania and also in the Pacific Northwest of the USA (Williams et al. 2012). The biennial reproductive cycle of sevengill sharks (Ebert 1989) would hereby explain why only some of the tagged females left and others remained at the coastal site. However, based on length at maturity data from other regions (Barnett et al. 2012), 4 of the 5 females tagged in this study are considered subadults, so the link between reproductive and migratory behavior cannot be established from this study.

Whatever the reason for the differences in migratory behavior, it potentially has significant ramifications for the management of this species, as males and females are likely to be subjected to different rates of fishing mortality during the winter. Neither sex spent large amounts of time in the designated shark nursery protected areas in the Derwent Estuary/Norfolk Bay, although females do so more than males (Barnett et al. 2011). Outside of these areas, fishing pressure is unlikely to be uniformly distributed between southern Tasmania and the east coast of Australia. This may cause differential exploitation of the sexes, as has been suggested for the shortfin mako *Isurus oxyrinchus* in the South Pacific (Mucientes et al. 2009).

Sex specific differences were also evident in the characteristics of vertical behavior of male and female sevengill sharks. Both sexes displayed DVM as well as rDVM throughout much of their tracks. Diel changes in swimming depth are relatively common in sharks (Speed et al. 2010) and are generally linked to thermoregulation (e.g. Carey & Scharold 1990, Sims et al. 2006) or foraging (e.g. Nakano et al. 2003). Because archival records showed that the behavior was evident in well-mixed water masses, with relatively homogeneous temperatures, thermoregulation can be discounted as the reason for vertical migration. Hence, foraging is the most likely driver of vertical migration behavior for sevengill sharks in Tasmania.

For male sharks, DVM was more common than rDVM, particularly when in shallow coastal areas. Similar to the bluntnose sixgill shark *Hexanchus griseus* (Andrews et al. 2009), Greenland shark *Somniosus microcephalus* (Stokesbury et al. 2005) and Pacific sleeper shark *Somniosus pacificus* (Hulbert et al. 2006), DVM behavior became less pronounced as male sharks moved offshore into deeper waters. On some occasions, the male sevengill sharks sporadically shifted to rDVM (see Fig. 4a). This may be due to sharks switching to a different foraging strategy when in transit mode or feeding on different prey species with different vertical movement behavior.

The female that left the coastal areas for deeper offshore areas also predominantly displayed DVM with sporadic bouts of rDVM behavior, particularly in the Tasmanian coastal area. However, in contrast to the males, DVM was also evident and highly pronounced in deeper waters offshore, with large diel changes in swimming depth and vertical movements to depths of up to 360 m (see Fig 4b). This is the deepest record for this species, which had previously only been reported to depths of up to 200 m (Barnett et al. 2012).

The female sevengill shark that remained in the Derwent Estuary/Norfolk Bay area predominantly displayed rDVM during the winter period with intermittent bouts of DVM. Due to the diverse diet of the sevengill sharks (Cortés 1999, Ebert 2002, Barnett et al. 2010a), these shifts in behavior are possibly a response to shifts in available prey species in the coastal areas during winter. Switching between DVM and rDVM has previously been linked to different habitats in the plankton-feeding basking shark (Sims et al. 2005), but a direct link between these behaviors and shifts in the dominant prey species at a fixed location has not yet been established for a predatory shark species. A dietary study on sevengill

sharks in the Tasmanian coastal area during winter as well as further deployment of archival tags to increase sample sizes beyond the 4 tags recovered in this study could shed further light on this subject.

In addition to shifts between DVM and rDVM, the shark that remained in the Derwent Estuary/Norfolk Bay area also displayed considerable changes in the diel depth range and mean depth (see Fig. 4b). These changes might be due to movement in and out of shallower areas or changes in either nighttime light intensity through cloud cover and lunar phases, as has been reported for school sharks (West & Stevens 2001) and juvenile white sharks (Weng et al. 2007), or changes in surface temperature and salinity through increased freshwater flow at the surface. The possible influence of surface temperature is supported by the fact that one of the sharks reduced its nightly returns to surface waters in the coastal area to sporadic, short ascents when the surface layer was up to 4°C cooler than the water underneath.

In addition to vertical migration, sevengill sharks also showed a diel change in activity with vertical movement increasing during the night for all sharks. This nightly 'yo-yo-ing' behavior has previously been reported for this species from acoustic tracking data in shallow habitats (Barnett et al. 2010b) and yo-yo-ing behavior, in general, is relatively common in sharks (e.g. Heithaus et al. 2002, Andrews et al. 2009). It may be used to detect and ambush prey in low light conditions (Carey & Scharold 1990, Barnett et al. 2010b), to reduce energetic cost of travel (Weihs 1973) or to detect magnetic gradients as a means of navigation (Carey & Scharold 1990). As sevengill sharks exhibited yo-yo-ing behavior throughout their tracks, in both shallow and deep water and during both resident and transit phases, it is likely to be primarily employed as a foraging strategy as has previously been reported for tiger sharks *Galeocerdo cuvier* (Nakamura et al. 2011).

This suggests that sevengill sharks foraged throughout their tracks rather than switching between commuting and foraging modes, as has been reported for other marine species such as leatherback turtles (James et al. 2005) and salmon sharks (Weng et al. 2008). Hence, migratory behavior did not seem to include a suppression of responses to foraging resources as Dingle (1996) suggested. While this type of behavior has been described as ranging rather than migrating for other species (Kuhn et al. 2009), the strong fidelity of sevengill sharks to their summer feeding sites in Tasmanian coastal areas (Barnett et al. 2011) means that their movement most likely falls somewhere between the two.

As the first comprehensive analysis of pop-up satellite archival tag data from broadnose sevengill sharks, this study presents the deepest swimming depth recorded for this species, shows complex shifts in vertical movement behavior and demonstrates differences in the large-scale movement of the males and females of this species, differences that could potentially lead to the differential exploitation of sexes when the sharks leave the protected areas on the Tasmanian coast.

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