INTRODUCTION

Anthropogenic alteration of the natural environment is a widespread and obvious phenomenon. There are numerous examples of the deleterious effect of artificial habitat changes on wildlife, such as the reduction in species diversity caused by dam constructions (Pringle 2000, Gehrke et al. 2002) or the range of animals affected by land-clearing (see examples in Vos & Chardon 1998, Crooks 2002, Lehman et al. 2006). However, a few animal populations are capable of adapting to and benefiting from anthropogenic changes, such as peregrine falcons *Falco peregrinus* nesting in high rise buildings (Gilbert 1989, Cade & Bird 1990).

The effects of human activities in the marine environment are less conspicuous than on land, but they are often extensive, particularly in coastal areas. While the local influence of anthropogenic habitat modification can be readily assessed for sessile organisms such as algae, seagrass and coral (e.g. Richmond 1993, Nyström et al. 2000, Duarte 2002), the effect on mobile marine animals is more difficult to determine. Ongoing miniaturisation of remote monitoring tools, such as satellite transmitters and diving loggers, is providing increased opportunities to identify how highly mobile animals use the marine environment (Ropert-Coudert & Wilson 2005) and to examine the influence of human alterations on them.

The little penguin is an ideal model for studying local oceanic alterations because it is part of a relatively short food chain (Cullen et al. 1992) and has a restricted foraging range during the chick-rearing phase.
of the breeding season (Collins et al. 1999). Little penguins are capable of acquiring only local resources at this time because they need to return regularly to their terrestrial nest site to feed their chicks (Chiaradia et al. 2007). This central place foraging behaviour facilitates the attachment and removal of data loggers, which allow their at-sea behaviour to be studied.

Although considered common, little penguins have been adversely affected by human settlement and activities in some places. Introduced mammalian predators and habitat loss have been the major causes of decline in this species on Phillip Island and south-eastern Tasmania in Australia, and the Otago region of New Zealand (Dann 1992a,b, Stevenson & Woehler in press). Other potential threats of anthropogenic origin also exist at sea, such as oil spills, over fishing, gill-netting, introduction of diseases to prey populations and dredging (Dann 1992b, Dann et al. 2000, Goldsworthy et al. 2001, Stevenson & Woehler in press).

A colony of little penguins resides on a breakwater wall constructed at St Kilda, 5 km from the centre of the city of Melbourne, Australia. The colony is close to both marine and terrestrial urban developments. This is the only established little penguin colony within Port Phillip Bay, which seems otherwise largely unsuitable for the establishment of penguin populations due to a lack of appropriate nesting sites, terrestrial threats from introduced predators and on-land habitat disturbance. Although extensive habitat alteration and other anthropogenic effects occur within this colony’s foraging range, the population has grown to approximately 1000 individuals (Z. Hogg unpubl. data) since the first breeding pairs were discovered in 1974 (Eades 1975). Population growth is attributed to the proximity of food resources in northern Port Phillip Bay, within 20 km of the colony (Cullen et al. 1996), but is also likely to be due in part to the general absence of predators. A secure fence prevents access to the breakwater by roaming dogs and foxes, which may otherwise decimate the colony.

We investigated the 3-dimensional foraging behaviour of little penguins at the St Kilda colony during the 2006–2007 breeding season in order to examine how penguins use a highly modified marine habitat. Using satellite transmitters and time-depth recorders, we assessed whether the penguins have adapted their foraging strategy to use bathymetric variations of the sea floor (including dredged shipping channels) that are present within their foraging range.

**MATERIALS AND METHODS**

**Study site.** The diving behaviour and foraging zone occupancy of little penguins were examined at St Kilda, Melbourne, Australia (37° 51’ S, 144° 57’ E, Fig. 1)
during November and December of the 2006–2007 breeding season. Penguins were monitored in their nests 3 times wk\(^{-1}\) to determine their stage of breeding and were permanently identified by either a passive integrated transponder (Trovan\(^\circledR\)) or a flipper band.

At St Kilda, penguins forage inside Port Phillip Bay (Cullen et al. 1996), a bay of 1950 km\(^2\), with an average depth of 13 m and a maximum depth of 24 m (although some trenches at the entrance extend deeper). Several large shipping channels exist in the north and west of Port Phillip Bay, as well as the south where Port Phillip Bay joins Bass Strait (Fig. 1). The shipping channel ranges between 12–17 m depth and 180–240 m width.

**Deployment of satellite trackers and time-depth recorders.** Satellite tracking and time-depth recording devices were deployed separately on penguins. Although data from both devices on single birds could have proved useful, we considered the encumbrance resulting from their deployment together too great for a 1 kg bird. Only 1 penguin (O53F) was fitted with both devices, the time-depth recorder during incubation and satellite transmitter during chick-guard.

Satellite tracking was conducted on 13 birds from the chick-guard stage (chicks up to 2 wk old) using platform transmitter terminals (PTT, KiwiSat model 202 by Sirtrack, 60 × 31 × 20 mm, cross-sectional area 177 mm\(^2\), mass in air 43 g, antenna 18 cm spring mounted at 60\(^\circ\)). In parallel, miniature time–depth recorders (TDR, M190-DT by Little Leonardo 49 × 15 mm, cross-sectional area 177 mm\(^2\), mass in air 14 g) were fitted to 14 penguins, 9 at the egg incubation stage and 5 at the chick-guard stage. Little penguins typically make trips of up to 3 consecutive days at sea during egg incubation and just 1 day at sea during the chick-guard stage, but the duration may increase during poor breeding seasons (Chiaradia & Nisbet 2006). TDRs collected data every 1 s in the 0–190 m depth range with a 12-bit resolution and 0.1 m accuracy.

All devices were attached to the penguins’ feathers using waterproof tape (Tesa\(^\circledR\) 4651) (Wilson et al. 1997) along the mid-line of the lower back to minimise drag (Wilson & Culik 1994). We applied a thin strip of adhesive compound (Mastic, Denso) between the feathers and the device, to reduce friction and prevent loosening. All devices and adhesives were removed from the penguin upon its return to the colony after a foraging trip. Attachment and removal each took <5 min. Penguins were weighed to the nearest 20 g using a spring balance (Pesola 42500) before and after instrumentation.

**Data analysis.** Penguin locations from the PTTs and the accuracy of these locations were provided by CLS Argos and plotted using Elsa Pro software (CLS Argos, 2005). Only locations where accuracy was 1 km or better (Classes 1, 2 and 3) were included in the analysis. We filtered the locations in the R statistical program (R Development Core Team 2005) using TimeTrack, a custom designed software package (Summer 2006). TimeTrack uses the algorithms described by Mc-Connell et al. (1999) to filter out locations that result from unreasonable speeds for a particular species. Using the maximum swimming speed of 3.3 ms\(^{-1}\) reported by Bethge et al. (1997), none of the Class 1, 2 or 3 locations were eliminated. Time-in-area analysis was calculated by interpolation of locations at 10 min intervals between the predicted locations, assuming straight-line travel at an even speed between the 2 locations (Austin et al. 2003), and assigning time spent to 1 km\(^2\) grid-squares.

Bathymetry contours (at 5 m depth intervals) of Port Phillip Bay (provided by D. Ball, Primary Industries Research Victoria) were plotted using ArcView GIS version 3.0 (Environmental Systems Research Institute, 2004) and overlain with the time-in-area data.

G Power analysis (Faul et al. 2007) was used a posteriori to calculate the power of our sample size in describing the foraging area at 95% confidence interval. We used the number of grid-squares visited per penguin and conducted 50 permutations of adding the data from each penguin sequentially and in a random order. In this way, we derived a curve for the cumulative increase in grid-squares visited with each additional penguin. We then used the mean and standard deviations of the data to calculate the power of our sample size.

Diving data were downloaded from TDRs and analyzed (surface-align and dive detection) using IGOR Pro version 5.0 (Wavemetrics). Based on the relative accuracy of the logger, we adopted a dive threshold of 1 m. Diving activity was defined by the following parameters: maximum depth, dive duration, bottom phase (calculated as the period in the dive between when vertical speed first drops below and last rises above 0.25 m s\(^{-1}\) vertical speed), depth amplitude within bottom phase (the difference between the maximum and minimum depths reached during the bottom phase), descent and ascent rates, and number of undulations in the dive profile (Kato et al. 2006, Ropert-Coudert et al. 2006). For analysis of these diving parameters, we filtered data to exclude dives without a bottom phase (15.4%). Predominately, they were shallow (86.5% were ≤5 m deep) and were likely to be dives performed during travel. Dive shapes were analyzed using MultiTrace Dive (Jensen Software Systems), excluding only dives <1 m. Based on observation of the dive profiles, demersal dives generally had descent rates ≥0.8 ms\(^{-1}\) and were performed at depths ≥6 m.

We conducted all other statistical analysis in SYSTAT Version 10 (SPSS). The statistical threshold was set at 0.05 and the values are presented as means with 1 SD.
RESULTS

Satellite tracking

The 13 penguins fitted with PTTs made either 1 or 2 d foraging trips and the total number of unfiltered locations of all classes was 279. After filtering, this was reduced to 11 penguins tracked from 98 Class 1, 2 or 3 locations, 10 of which performed single day trips and 1 (penguin O53F) performed a 2 d trip. By interpolating between satellite data, we calculated that the penguins spent time in 222 different 1 km² grid-squares within Port Phillip Bay. Time spent in each square ranged from 1 to 668 min.

Little penguins making 1 d trips from St Kilda remained in the north of the bay within 22 km of the colony (Fig. 2). They headed out in a south-westerly direction from St Kilda that included and crossed the shipping channels. Mean maximum distance from the colony on 1 d trips was 13.8 ± 4.1 km. Our sample size of 10 penguins had a power of 0.95 at 95% confidence interval to represent the foraging area within 1 d trip at the chick-guard stage.

On average, penguins on 1 d trips spent 10.8% of their time in the 1 km² grid-squares containing the shipping channels and 31.5% of their time <2 km from the northern shipping channel (i.e. the 1 km² grid-squares containing, and on either side of, the shipping channel). These grid-squares accounted for 9.3 and 22.5%, respectively, of all grid-squares visited on 1 d trips. The penguin that performed a 2 d trip travelled in waters <15 m deep to the western channel achieving a maximum distance from the colony of 51 km.

Dive behaviour

We retrieved TDRs from all penguins after 1 or 2 trips, except for 1 penguin at the incubation stage and 3 at the guard stage; these penguins had abandoned their nests. We do not think that nest abandonment was related to device attachment, because 57% of the monitored nests in the colony were abandoned prior to chick fledging, whether the birds had been part of this study or not. Reproductive success of the colony as a whole was poor during the 2006–2007 breeding season (T. J. Preston unpubl. data). Trip durations for retrieved dive loggers ranged from 1 to 11 d, with a total of 48 foraging days and 32 690 dives from 10 birds (Table 1).

Diving was exclusively diurnal, with dive depths being greatest during the middle of the day. Excluding dives <1 m, the total number of dives for an individual ranged from 422 to 6321 (Table 1). The maximum depth recorded was 26.5 m and the maximum dive duration was 79 s. Penguins dived to a mean depth of 8.4 ± 1.8 m, with a mean diving duration of 28.5 ± 3.8 s. Most (82.7%) dives were to depths of between 2 and 13 m (Fig. 3). Just under half (44.3 ± 4.6%) of all dives were made to a depth ±1 m of the previous dive.

Analysis of dives with a bottom phase (84.6%) found that the bottom phase accounted for almost half (49.7 ± 7.3%) of each dive time (Table 1). In 60.7 ± 7.0% of dives, at least half of the bottom phase occurred in the lowest depth quartile and these dives had either flat bottoms, several small undulations (<1 m amplitude) or ragged shapes (Fig. 4).

As location and diving data was collected separately, it was not possible to identify definitively which dives were made inside the shipping channels. However, penguins in the present study did exhibit some unusual dive profiles that contained a flat bottom phase usually followed, but sometimes preceded, by a rapid change in depth (Fig. 5). Many of these dives appeared to be made midwater, as indicated by the surrounding dives and low descent rates, but 248 were considered demersal. Of these, 180 correspond with the depth profile of the shipping channels (outside channel...
6–10 m, inside 11–17 m, depth between outside and inside ≥3 m). These dives could have been made by the penguins entering or leaving the shipping channels. The remaining dives were deeper and all made by penguins on trips >1 d that may have travelled to deeper trenches at the mouth of the bay.

**DISCUSSION**

Many studies of penguin behaviour at sea now combine both location and diving information for the same bird (e.g. Pütz et al. 1998, Charrassin et al. 2004, Ryan et al. 2004, Sokolov et al. 2006, Mattern et al. 2007); this allows direct correlation between behaviour of the animal and bathymetry of the area. Unfortunately, the instruments required to combine this information are still too large to be deployed on little penguins. Accordingly, our data on location and diving behaviour were collected separately. We have no reason to believe, however, that over a comparable time-frame the penguins fitted with TDRs foraged in different areas to those fitted with PTTs. The foraging area of all PTT-carrying birds on 1 d trips were similar and the diving depths recorded by TDRs on single day trips were within the ranges of depths over which PTT-bearing birds foraged. Time spent at sea is a determining factor in how far penguins can travel from the colony, and those penguins at sea for >1 d may have travelled further than the 1 d foraging area described.

Attachment of external devices to penguins is known to affect their foraging performance (Wilson et al. 1986). Decreasing the device size and judicious placement on the lower back minimises the effects (Ropert-Coudert et al. 2007). In the present study, we used the smallest devices available to us. The difference in cross-sectional area between the TDRs and PTTs, as well as the presence of an aerial (cf. Wilson et al. 2004), may have resulted in differences in diving capabilities, but it is unlikely that this will lead to a difference in foraging area used by penguins fitted with PTTs compared with those fitted with TDRs. Aban-

<table>
<thead>
<tr>
<th>Penguin</th>
<th>Breeding stage</th>
<th>Trip duration (d)*</th>
<th>Total no. of dives</th>
<th>Diving depth (m)</th>
<th>Dive duration (s)</th>
<th>Bottom phase duration (s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>B14M</td>
<td>Incubation</td>
<td>1, 7</td>
<td>5533</td>
<td>8.1 ± 3.9</td>
<td>25.1 ± 11.7</td>
<td>46.7 ± 19.9</td>
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<tr>
<td>B33M</td>
<td>Incubation</td>
<td>1</td>
<td>561</td>
<td>7.9 ± 4.6</td>
<td>26.3 ± 14.5</td>
<td>47.0 ± 20.9</td>
</tr>
<tr>
<td>C93F</td>
<td>Incubation</td>
<td>7</td>
<td>5365</td>
<td>9.9 ± 4.6</td>
<td>34.0 ± 13.5</td>
<td>48.9 ± 17.4</td>
</tr>
<tr>
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<td>Incubation</td>
<td>6</td>
<td>3532</td>
<td>9.7 ± 5.2</td>
<td>29.2 ± 13.8</td>
<td>43.8 ± 19.7</td>
</tr>
<tr>
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<td>6</td>
<td>4116</td>
<td>8.5 ± 4.6</td>
<td>27.8 ± 15.3</td>
<td>46.6 ± 21.6</td>
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<tr>
<td>O63M</td>
<td>Incubation</td>
<td>11</td>
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<td>11.0 ± 5.8</td>
<td>31.4 ± 16.0</td>
<td>39.3 ± 19.3</td>
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<tr>
<td>L24F</td>
<td>Incubation</td>
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<td>422</td>
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<td>23.1 ± 15.1</td>
<td>53.3 ± 18.9</td>
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<tr>
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<td>23.1 ± 12.5</td>
<td>56.2 ± 20.0</td>
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<td>O03F</td>
<td>Chick-guard</td>
<td>1</td>
<td>922</td>
<td>5.6 ± 2.8</td>
<td>24.5 ± 9.8</td>
<td>65.7 ± 17.0</td>
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<tr>
<td>O74M</td>
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<td>2</td>
<td>2118</td>
<td>10.0 ± 4.4</td>
<td>31.1 ± 15.1</td>
<td>49.9 ± 19.1</td>
</tr>
</tbody>
</table>

*Two values denote 2 trips made by the same penguin.
A preponderance of nests during the 2006–2007 breeding season was high (57%) for all breeding pairs in the colony. Interestingly, though, the breeding success of birds that carried devices was actually higher than the colony average (colony 29.5%, TDR or PTT carried by at least 1 parent on 1 trip: 38.0 and 44.5%, respectively).

The distribution of tracked penguins at the chick-guard stage from St Kilda was concentrated in the north of Port Phillip Bay, similar to the non-breeding distribution recorded by radio tracking (Cullen et al. 1996). This foraging area is inclusive of the northern shipping channels that lie to the west of the colony. The limited foraging range of little penguins caring for young chicks was reflected in the low maximum distance travelled from the colony, which was slightly lower than the value reported for little penguins on 1 d trips from Phillip Island (Collins et al. 1999).

The west of Port Phillip Bay was used by 1 penguin in our study that spent 2 d at sea and travelled between shipping channels in the north and west. Little penguins from Phillip Island (Fig. 1) are known to occur in both the north and west of Port Phillip Bay (Collins et al. 1999), which suggests high prey availability and highlights the importance of these areas to both populations. Penguins have also been observed in the central part of Port Phillip Bay, but it was not identified whether they came from St Kilda, Phillip Island or elsewhere (Port of Melbourne Corporation 2007). We can expect that little penguins from St Kilda, if not restricted in their foraging trip duration, might also sometimes forage in the west of the bay.

Little penguins commonly dive to mid-levels of the water column (Bethge et al. 1997, Chiaradia et al. 2007), but demersal diving has also been reported in this species (Ropert-Coudert et al. 2006). Penguins in the present study appeared to use both mid-water and demersal diving strategies, as suggested by the length and shape of dive profiles (Fig. 4, Table 1). Penguins dived to ±1 m of the previous dive depth on a mean of 44.3% of occasions, comparable with rockhopper penguins Eudyptes chrysocome employing a mixture of benthic and pelagic dives, to within ±10% of the previous dive depth around 53% of the time (Tremblay & Cherel 2000). Given the shallow nature of Port Phillip Bay and reasonable natural variations in the sea floor topography, we considered that a threshold of ±1 m was more appropriate than ±10% for this study.

The mean bottom phase duration of penguins from St Kilda was similar to that reported for demersal diving little penguins from Penguin Island, Western Australia (Ropert-Coudert et al. 2006). In contrast, little penguins from other colonies that engage primarily in mid-water or shallow-water diving spend less time in the bottom phase of the dive (Chiaradia et al. 2007). Penguins in present study could move from the shallow area around their colony (<5 m) to the deepest part of the bay (>20 m), a distance of approximately 20 km, in around 3 h (based on average swimming speed, Bethge et al. 1997). Subsequently we saw frequent changes in the depth profile throughout the day, which makes differentiation between demersal and mid-water dives difficult.

Little penguins from St Kilda have an unusual monospecific diet of anchovy (Engraulis australis; A. Chiaradia unpubl. data), with apparently few supplementary or alternative prey species in the diet (T. J. Preston unpubl. data). Anchovy is generally regarded as a shallow water pelagic species, occurring in the top 20 m of the water column (Kailola et al. 1993). Penguin species including the Humboldt Spheniscus humboldti and African Spheniscus demersus that feed on pelagic schooling fish, including anchovy, have been found to seize prey from below, as the fish are easier to locate as a silhouette rather than from the side or above (Wilson & Duffy 1986, Wilson et al. 1989), and this is likely to be the case for penguins at St Kilda that feed almost exclusively on anchovy.

Little penguins from St Kilda had some unusual dive profiles that displayed a sharp increase in depth during the bottom phase (Fig. 5). Unpublished accounts of these types of dives in Snares Eudyptes robustus (T. Mattern pers. comm.) and Magellanic penguins Spheniscus magellanicus (R. Wilson pers. comm.) suggest that these dives are made mid-water, as do the characteristics of many of the dives made in this study. However, benthic diving yellow-eyed penguins Megadyptes antipodes are also known to make dives of similar shape (T. Mattern pers. comm.). The surrounding dives to consistent depth and the high
The proposed dredging to increase the depth of shipping channels by approximately 3 m is much larger in scale than the routine dredging that has taken place since the channels were first constructed in the 1860s. The main immediate potential effect of the dredging on little penguins in the vicinity will be the increased water turbidity, the extent and concentration of which are likely to vary at any one time and place. In all, the dredging will produce suspended sediment above 5 mg l⁻¹ that is predicted to spread over an area approximately 4 km wide and 18 km long before it settles, immediately surrounding and east of the shipping channels in the north of Port Phillip Bay (Port of Melbourne Corporation 2007). This area overlaps approximately 30% of the penguin foraging range described in this study and is situated between the penguin colony and their main foraging area to the west of the shipping channels. The reactions of little penguins to turbidity are unknown, but they are considered visual predators (Cannell & Cullen 1998, Ropert-Coudert et al. 2006) and as such it is unlikely that they will be able to forage within highly turbid areas of the suspended sediment plume, particularly in the area of the channels where the suspended sediments originate from the sea floor. Whether the penguins will travel across the densest areas of the plume or swim around them in order to reach clear foraging areas is not known.

Much of the recruitment biology and spawning dynamics of the anchovy inside Port Phillip Bay is uncertain, but the north of the bay, including areas to be affected by the dredging plume, has been identified as a spawning ground for this species in several studies (Blackburn 1950, Jenkins 1986, Neira & Tate 1996). Spawning takes place from September to March, peaking in January (Jenkins 1986), which coincides with the scheduled dredging in the north of the bay (Port of Melbourne Corporation 2007). The foraging behaviour of anchovy may be affected by the turbidity plume, as they are generally regarded as visual predators (Chiappa-Carrara & Gallardo-Cabello 1993). Physiological effects of the suspended sediment on anchovy, particularly eggs and larvae, may result in high levels of mortality (Wilber & Clarke 2001), decreasing recruitment and ultimately leading to a decline in the population size. Reduction of available cape anchovy Engraulis capensis has been implicated in the breeding failure of African penguins Spheniscus demersus (Crawford & Dyer 1995, Crawford 1998), and a widespread decline of pilchards Sardinops sagax was associated with high levels of adult mortality and very low breeding success in little penguins from Phillip Island (Dann et al. 2000). Similar levels of breeding failure and adult mortality may be expected for the St Kilda little penguin colony if there was a significant reduction or an absence of anchovies and alternative food sources as a result of the dredging. The population of >52,000 little penguins at Phillip Island may also be affected by the channel dredging, as radio-tracking has determined that they use Port Phillip Bay extensively in winter and spring (Collins et al. 1999) and anchovy is a major prey component of their diet (Cullen et al. 1992).

The St Kilda colony of little penguins appears to have adapted to and benefited from some artificial environmental modifications in the past; construction of a breakwater wall provided a suitable nesting habitat and shipping channels reduced the prey escape field. However, this adaptation to artificial environmental modifications now puts little penguins in a precarious position where significant changes in their spatially limited marine habitat, such as the proposed dredging, have the potential to severely affect this population.

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Industries Research Victoria, Queenscliff, provided the bathymetry data for Port Phillip Bay. Funding for satellite tracking was provided by Toyota Australia, The Penguin Foundation and Dan Costa. Diving study was supported by a grant from BHP-Billiton. The study site was accessed with permission from Parks Victoria and the St Kilda Breakwater Wildlife Management Co-operative Area committee. Research was conducted under animal ethics permit BSCI/2006/12 from the Monash University AEC and wildlife permits 10003374 and 10003848 from the Department of Sustainability and Environment, Victoria. Picture in Fig. 1 accessed from Google Earth™.

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