ABSTRACT: The giant devil ray *Mobula mobular* is the only mobulid species regularly present in the Mediterranean Sea. The spatial ecology and biology of this species are poorly known, and given its high bycatch mortality, low reproductive capacity, and limited range, it is listed as Endangered (A4d) on the IUCN Red List. Most of the information concerning this species has been obtained through bycatch data and opportunistic sightings. To inform conservation and management actions, it is necessary to conduct research on the behavior of giant devil rays. This study is the first attempt to systematically describe the diving behavior of this species. Three specimens were tagged with popup satellite tags in the Messina Strait (central Mediterranean Sea) during summer 2007. Two tags were programmed to detach after 120 d and 1 after 60 d. The data revealed that these fish dove to depths between 600 and 700 m. However, they spent most of their time (81.5%) between the surface and 50 m, in waters with temperatures between 20 and 29°C. The preference for shallow depth and warm surface waters exposes this species to threats such as accidental captures in driftnets and surface longlines.

KEY WORDS: Giant devil ray · *Mobula mobular* · Diving behavior · Satellite tag · Mediterranean Sea
swordfish pelagic driftnets (Muñoz-Chapuli et al. 1993). Giant devil rays have also occasionally been reported as bycatch from longlines (Orsi Relini et al. 1999), purse seines, trawls (Bau- chot 1987), pelagic trawls (Scacco et al. 2009), trammel nets (Bradai & Capapé 2001), and traditional fixed tuna traps (Boero & Carli 1979).

The giant devil ray is included in Annex II (‘List of endangered or threatened species’) of the Protocol concerning Special Protected Areas and Biological Diversity in the Mediterranean of the Barcelona Convention, enforced in 2001. Given presumed high bycatch mortalities, its limited reproductive capacity (Wourms 1977), and range, 

*Mobula mobular* has been listed as Endangered (A4d) by IUCN (Notarbartolo di Sciara et al. 2006).

Information concerning the ecology and the behavior of this species is very scarce and has largely been obtained from opportunistic observations. No systematic effort has been made to study this species in its natural environment. Considering the high impact of human activities throughout the whole Mediterranean basin, it is important to understand their spatial ecology to identify and protect critical habitat. Our study represents the first attempt to describe the diving behavior of giant devil rays in the Mediterranean Sea. Although the tagging of only 3 animals cannot lead to any conclusive information on the behavior of this species, it provides useful data on which to base further studies.

**MATERIALS AND METHODS**

During summer 2007, 3 giant devil rays, visually estimated by experienced fishers to have a DW between 2.5 and 3 m, were tagged with Mk10-PAT (pop-up archival transmitting) tags (Wildlife Computers). Tagging took place in the Messina Strait (Fig. 1), central Mediterranean Sea, where the presence of giant devil ray aggregations during spring and summer is well documented (Celona 2004). The operations were conducted onboard a ‘felucca’, a traditional local fishing boat, characterized by a 25 m long gangway and a 25 m high mast, specifically built and equipped to catch swordfish with harpoons (Fig. 2). Giant devil rays were sighted from the mast while they were swimming slowly very close to the surface (<1 m deep), sometimes in a group. They were approached and tags were applied using a 4 m long aluminum pole (Fig. 2). Tagging data are summarized in Table 1.

Tags were secured to the animals with tethers and medical grade nylon anchors (Prince & Goodyear 2006) inserted 16 cm deep into the dorsal musculature of the wing. Tags were programmed to detach from the animals after 120 d (2 ind.) and 60 d (1 ind.).

MK10-PAT tags were programmed to automatically summarize and transmit depth and water temperature data in four 6 h intervals (starting at 00:00 GMT; local
For each of these temporal intervals, tags were set to record the time spent in 14 unequal depth categories, from surface to 1000 m (0, 10, 20, 50, 100, 150, 200, 300, 400, 500, 600, 700, 800, 1000 m), and in 14 water temperature intervals of 1°C increments (from 13 to 25°C and >25°C). After detaching, tags surfaced and started transmitting the collected data, as time at depth and time at temperature histograms, via the Argos system, which also calculates the geographic position of transmitting tags. The four 6 h intervals were selected considering the limited performance of Argos in the Mediterranean Sea (Gaspar & Malardé 2007) and represent a tradeoff between the need for a low number of intervals, necessary to maximize the chances of retrieving full day data sets, and the need for a high number of intervals, necessary for maintaining higher accuracy when describing giant devil ray diving behavior throughout the day. In addition to the time and depth histograms, tags generated and transmitted daily profiles of depth and temperature (PDTs), recording maximum and minimum temperatures at 8 depth intervals.

Because animals were tagged in the same period, they were all adults. Given the small sample size, data from the 3 tags were pooled.

To evaluate whether diving behavior is influenced by sunlight, depth data were grouped in two 12 h periods, from 06:00 to 18:00 h and from 18:00 to 06:00 h; these intervals, even if they are not strictly correlated to the time of sunset or sunrise, comprise most of the day and night, at least during summer.

Differences in the average time spent at different depth and temperature intervals between day and night were tested with a Student’s t-test, and differences in the 6 h intervals were tested with an analysis of variance (ANOVA). Means ±SD are given in the text.

**RESULTS**

During the tagging procedure, the 3 giant devil rays did not show any avoidance behavior towards the approaching boat, but they reacted to tagging with a fast burst and a vertical dive.

All tags detached at the pre-established time, 298, 337, and 278 km from where the animals were tagged. The first animal moved south while the other 2 moved north (Fig. 1, Table 1). The average number of data packages transmitted by tags and successfully received by the Argos system was 196 ± 39 (SD).

The time at temperature and time at depth histograms transmitted by tags indicated that giant devil rays spent most of their time at depths between 0 and 50 m (average = 81.5 ± 20%; Fig. 3) and in water with temperatures between 20 and 29°C (maximum temperature registered in the PDTs; average = 78.5 ± 21%; Fig. 4). PDTs transmitted by the tags confirmed the presence of a clear thermocline close to a depth of 50 m in the study area (Fig. 5).

Occasionally, giant devil rays dove below the thermocline, reaching a maximum depth between 600 and 700 m (Fig. 3). The rays spent the majority of their time near the water surface (i.e. in the first 10 m depth) during both day (49 ± 25% of their time) and night (47 ± 25%). No statistically significant differences were noted in use of surface waters between day and night.
However, significant differences were found in their vertical distribution between day and night in the depth range of 0 to 50 m (above the thermocline). At night, 88 ± 12% of their time was spent above the thermocline, and during the day, 75 ± 24% of their time was spent in the same depth range (Student’s $t$, $F_{1,57} = 3.19, p < 0.001$). The analysis conducted for thermal data confirmed the preference of giant devil rays for warmer water with temperature between 20 and 29°C at night, with an average proportion of 86 ± 12%; during the day, this proportion was 75 ± 25% (Student’s $t$, $F_{1,31} = 3.19, p < 0.05$).

Giant devil rays spent significantly more time in the first 50 m of the water column from 18:00 to 00:00 h (ANOVA, $F_{3,54} = 6.84, p < 0.001$), while in the morning from 6:00 to 12:00 h, they spent significantly more time at greater depth (Table 3).

**DISCUSSION**

The felucca represents an optimal platform for sighting and tagging giant devil rays. Specimens swimming at the surface or basking can easily be spotted from the top of its mast (Fig. 2) and can be readily approached for tagging through its extremely long gangway. The nylon anchor darts yielded good retention on this species with no premature releases. As such, we judged the overall tagging procedure applied in this study to be relatively efficient compared with other studies on different species (De Metrio et al. 2001, Sedberry & Loefer 2001).
The presence of giant devil ray aggregations in the Messina Strait is a well documented seasonal event occurring annually between late spring and summer (Celona 2004). Celona (2004) hypothesized that the local availability of high densities of prey may be a factor in the attraction of giant devil rays to the area. Indeed, we noted that 1 animal caught in this area had a full stomach. As confirmed by our observation of the tagged animals, giant devil rays move away from the Messina Strait in the middle of fall; however, the swimming direction was not limited to north as anecdotally reported by local fishers (Celona 2004). The Messina Strait could represent an aggregation area where animals from different parts of the Mediterranean Sea congregate during late spring for feeding and/or breeding purposes. Strong site fidelity has been recently described for the giant manta ray *Manta birostris* in the Komodo Marine Park, Indonesia, and in several other locations (Dewar et al. 2008).

Giant devil rays, like other mobulids, are considered epipelagic (Brito 1991) as confirmed by this study. However, in our study area, this species also showed dives in very deep mesopelagic waters, down to 600 m, even if only for a limited time. Deep dives have also been described for the Mediterranean fin whale *Balaenoptera physalus* that can dive deeper than 500 m (Panigada et al. 1999) when feeding on northern krill *Meganysthelasma norvegica* that can dive deeper than 500 m (Panigada et al. 1999) when feeding on northern krill *Meganysthelasma norvegica* (Sardou et al. 1996) can induce this species to dive at these depths.

Giant devil rays do not follow the typical diving pattern of large planktivorous sharks like the basking shark *Cetorhinus maximus* (Sims et al. 2005) or the megamouth shark *Megachasma pelagios* (Nelson et al. 1997), which both show a definite vertical migration timed to meet the upwards vertical migration of zooplankton. Giant devil rays spent most of the time in the upper layers and executed deep dives that were not correlated to the time of day.

In mobulids, the general mechanisms regulating body temperature have not been identified (Alexander 1996), even though a counter-current heat-exchanger has been identified at least in the Chilean devil ray *Mobula tarapacana* (Alexander 1995). Therefore, the preference for warmer superficial water noted in this study supports the existing hypothesis that the giant devil ray’s basking behavior is an adaptation for increasing its body temperature (Alexander 1996).

However, the preference for superficial waters exposes giant devil rays to accidental captures in driftnets or surface longlines. Our observations corroborate the hypothesis that these gears are amongst the main threats for giant devil rays in the Mediterranean Sea (Notarbartolo di Sciara et al. 2006).

Further studies are needed to elucidate the biology of giant devil rays, including long-range movements within and outside the Mediterranean Sea, and potential changes in winter behavior as described in basking sharks (Sims et al. 2003).

### LITERATURE CITED


### Table 3. *Mobula mobular*. Average ± SD proportions (%) of time tagged giant devil rays spent above and below 50 m during 4 time intervals (*significant difference at p < 0.05*)

<table>
<thead>
<tr>
<th>Depth intervals (m)</th>
<th>Depth (m)</th>
<th>Time intervals (h)</th>
<th>00:00–06:00</th>
<th>06:00–12:00</th>
<th>12:00–18:00</th>
<th>18:00–00:00</th>
</tr>
</thead>
<tbody>
<tr>
<td>0–50</td>
<td>77 ± 11</td>
<td>70 ± 25</td>
<td>85 ± 17</td>
<td>96 ± 4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>50–700</td>
<td>23 ± 11</td>
<td>30 ± 25</td>
<td>15 ± 17</td>
<td>4 ± 4*</td>
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</tbody>
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