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Diel movement patterns of the Hawaiian stingray, *Dasyatis lata*: implications for ecological interactions between sympatric elasmobranch species

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Abstract The Hawaiian stingray, *Dasyatis lata*, is a common benthic elasmobranch in nearshore Hawaiian waters. Acoustic telemetry was used to track the movements of seven rays in Kaneohe Bay, Oahu, Hawaii. Rays were tracked continuously over 31–74 h periods. Geographical movements were analyzed to determine space utilization and rate of movement. Rays were found to utilize significantly larger activity spaces at night ($0.83 \pm 0.70 \text{ km}^2$) (mean \pm SD) than during the day ($0.12 \pm 0.15 \text{ km}^2$). Mean total activity space for rays tracked was $1.32 \pm 0.75 \text{ km}^2$. Rates of movement were also significantly higher at night ($0.34 \pm 0.30 \text{ km h}^{-1}$) than during the day ($0.15 \pm 0.22 \text{ km h}^{-1}$). Average straight-line swimming speed was $0.64 \pm 0.16 \text{ km h}^{-1}$, with a maximum observed swimming speed of 1.9 km h^{-1} . Tidal stage had no effect on rate of movement. Comparison with previously published data on juvenile scalloped hammerhead sharks, *Sphyrna lewini*, in Kaneohe Bay revealed a high degree of overlap in habitat use and time of activity, suggesting possible ecological interactions between these two species.

Introduction

Stingrays occupy an ecologically important niche as benthic predators in bays and lagoons (Smith and

Merriner 1985; Thrush et al. 1991; Gray et al. 1997). The feeding activities of rays in these areas can considerably modify physical habitat. These physical modifications can have substantial ecological impacts through the restructuring of invertebrate and algal communities and resuspension of benthic nutrients (Orth 1975; Karl and Obrebski 1976). Therefore, understanding the extent and frequency of movement patterns of stingrays relative to their habitat use would be beneficial in determining their impact on benthic communities.

Stingrays of the family Dasyatidae occur worldwide in a variety of habitats, and are becoming increasingly important as a fisheries resource, particularly in developing countries (Francis 1998). Many aspects of their biology (e.g., reproduction, diet, physiology) have been relatively well studied (e.g., Snelson et al. 1988; Gilliam and Sullivan 1993; Sisneros and Tricas 2000); however, little is known about the movement patterns of dasyatid rays. Using tag-and-recapture techniques, Schmid (1988) found that *Dasyatis sabina* had fairly restricted movements in a shallow tidal lagoon and showed some site fidelity. Conversely, other tag-and-recapture studies of this species suggest that they make onshore-offshore seasonal migrations (Schwartz and Dahlberg 1978; Lewis 1982). Although tag-and-recapture techniques are effective in quantifying dispersal rates and distances, they cannot resolve fine-scale diel movements, habitat utilization and activity patterns. To date, no studies have examined the fine-scale movements of any dasyatid ray, despite the ecological and commercial importance of this family (e.g., Orth 1975; Smith and Merriner 1985; Thrush et al. 1991; Francis 1998).

Dasyatis lata is a medium-sized (disc width $\sim 100 \text{ cm}$) benthic stingray reported only from Hawaii and Taiwan (Nishida and Nakaya 1990). Although *D. lata* is the most common batoid found in Kaneohe Bay, Oahu, Hawaii, little is known about its general biology, behavior, and feeding habits. Kaneohe Bay has an extensive soft bottom habitat supporting a variety of benthic fauna (e.g., teleost fishes, crustaceans, polychaete worms) (Smith and Kukert 1996). The bay is also a

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nursery ground of the scalloped hammerhead shark, *Sphyrna lewini*; the biology and nearshore ecology of which has been extensively documented (Clarke 1971; Holland et al. 1993; Lowe 2001, 2002; Bush and Holland 2002). Although *D. lata* and juvenile *S. lewini* are the most abundant, large benthic predators in the bay and are caught in the same locations, the degree to which these species interact ecologically and impact benthic communities is unknown.

We conducted an acoustic telemetry study to quantify the fine-scale movement patterns and habitat utilization of *D. lata* in Kaneohe Bay. Additionally, movement and activity patterns of rays in our study were compared with those of juvenile *S. lewini* previously tracked in Kaneohe Bay (Lowe 2002) to provide information for assessing ecological interactions between these two top-level predators.

Materials and methods

Study site

Kaneohe Bay (21°26'N, 157°47'W), located on the windward shore of Oahu, is the largest bay in the Hawaiian Islands (Fig. 1). The southern portion of Kaneohe Bay, where tracking was conducted, has scattered patch reefs separated by a substratum (average depth ~14 m) composed primarily of calcareous silt and mud (Smith et al. 1981).

Acoustic telemetry

Rays were caught from the deeper waters (12–16 m) adjacent to Coconut Island (CI) using handlines with barbless hooks. After capture, rays were brought onto the boat, measured, sexed, and tagged with a Peterson disc tag (1 cm diameter) through the posterior margin of the pelvic fin. An acoustic transmitter (Vemco, Nova Scotia, model V8–1L, 9 mm diameter x 24 mm, frequencies 65.5–76.8 kHz) was attached to the top of the Peterson disc tag with corrosion wire. Handling time did not exceed 5 min. Rays were then released at the site of capture.

Rays were tracked continuously for up to 74 h from a 6-m customized Boston Whaler using a hull-mounted, directional hydrophone (Vemco model V10) connected to an acoustic receiver (Vemco model VR60) as described in Holland et al. (1992). The boat was positioned above the ray and the location was determined with a handheld GPS every 15 min.

Movement analysis

Each track was plotted on a digital chart of Kaneohe Bay using ArcView GIS. Distances between successive positions were determined with the Animal Movement Analyst Extension (AMAE) (Hooge and Eichenlaub 1997) for ArcView GIS. We calculated rate of movement (ROM) by dividing distance between successive points by the sampling interval. Daytime and nighttime ROMs were categorized for each ray based on local times of sunrise and sunset (U.S. Naval Observatory data services). Pooled daytime and nighttime ROM data from all rays were compared using a Mann-Whitney *U*-test. To examine tidal influence, pooled ROMs were compared over periods of incoming, outgoing, high and low slack tides using a Kruskal-Wallis test. High and low slack tides were defined as the periods from one hour before to one hour after high and low tide.

Because the use of point-to-point estimates of ROM underestimate swimming speed (Gruber et al. 1988), a second measure of ROM was made by selecting only periods of straight-line swimming. Straight-line swimming was defined as instances where three or more consecutive positions had a cumulative angular concentration (*r*) of 0.9 or greater as determined by AMAE. Cumulative angular concentration is a relative index ranging from zero to one, where a value of zero represents completely random movements and a value of one represents a linear trajectory.

Daytime, nighttime, and total activity spaces of rays were determined using a 95% kernel utilization distribution (KUD) (Worton 1989). The KUD is a density-dependent model used to describe an animal's space utilization, and describes the probability of finding the animal within a given area (Seaman and Powell 1996). Pooled daytime and nighttime activity spaces of all rays were compared using the Mann-Whitney *U*-test. Total 95% KUDs of each ray were merged in ArcView to form a combined activity space indicating overall habitat utilization of all rays tracked in this study.

To examine possible ecological interactions of *D. lata* and *S. lewini*, the degree of habitat overlap between species was quantified. To make this comparison, total 95% KUDs of five previously tracked juvenile *S. lewini* (Lowe 2002) were merged in ArcView to yield a combined activity space for all sharks. Habitat overlap between *D. lata* and *S. lewini* was determined by overlaying the combined activity spaces of both species to measure the percentage and area of overlap.

Results

Seven Hawaiian stingrays, *Dasyatis lata*, ranging from 40 to 73 cm disc width, were continuously tracked for 31 to 74-h periods in August 2000 and January 2001 (Table 1). Ray no.6 was initially tracked for 50 h, relocated after 26 h and tracked for an additional 24 h.

All rays tracked remained within the southern portion of Kaneohe Bay, showed limited daytime activity and often exhibited no detectable movement for extended periods of time. Nocturnal activity included more extensive movements throughout the southern portion of the bay, and rays rarely returned to the same daytime location (Fig. 1). That is, there was no evidence of fidelity to a predictable daytime refuging location.

The highest ROM (maximum ROM of 1.9 km h⁻¹) for all rays was observed for up to 2 h immediately following release. Because this increased ROM was likely due to handling stress, the first 2 h of each track were not included in ROM analyses. Pooled nighttime ROM (0.34 ± 0.30 km h⁻¹) (mean ± SD) was significantly higher than daytime ROM (0.15 ± 0.22 km h⁻¹) (Mann-Whitney *U*-test, *P* < 0.001) (Fig. 2). Tidal stage had no influence on ROM (Kruskal-Wallis test, *P* > 0.05). Straight-line ROM calculated from 17 separate straight-line swimming events from all rays indicated an average straight-line ROM of 0.64 ± 0.16 km h⁻¹.

Total activity spaces of rays tracked ranged from 0.62 km² to 2.77 km² with a mean of 1.32 ± 0.75 km². Increased nighttime ROM was accompanied by a larger activity space (Fig. 3), and most rays had greater activity spaces during nighttime periods (Fig. 4). Pooled nighttime activity space (0.83 ± 0.70 km²) was significantly larger than daytime activity space (0.12 ± 0.15 km²) (Mann-Whitney *U*-test, *P* < 0.001). Although we found

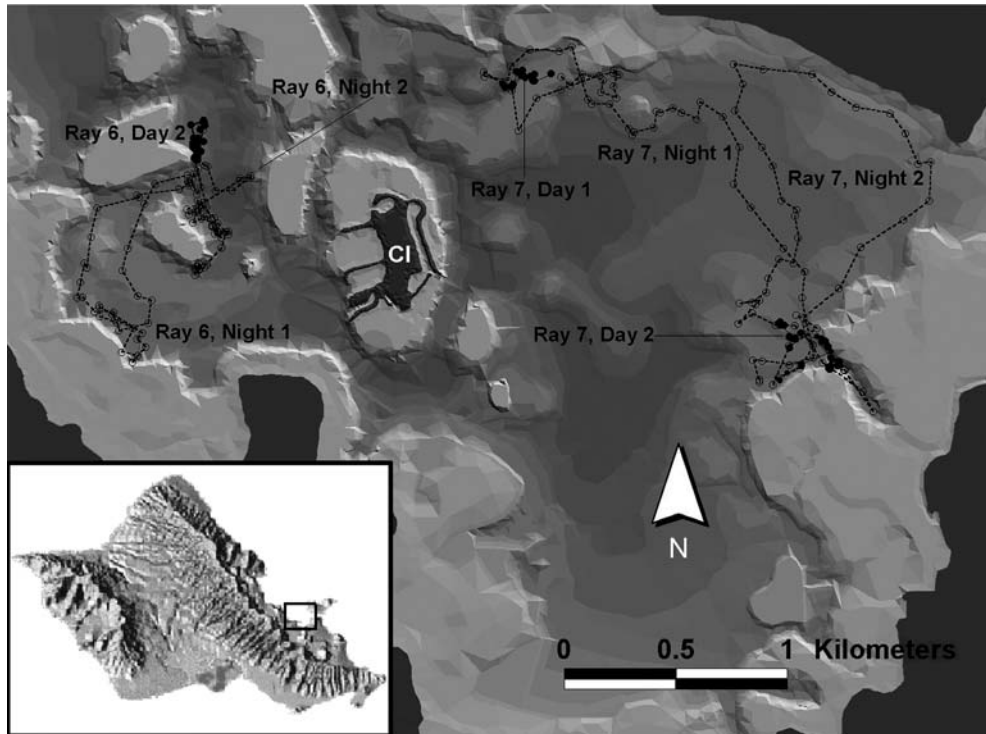


Fig. 1 Representative diel movement patterns of two *Dasyatis lata* tracked in Kaneohe Bay, Oahu, Hawaii. Daytime and nighttime movements of rays 6 and 7. *Solid circles and lines* represent daytime locations and movements of rays, respectively. Nighttime locations and movements are represented by *open circles and dashed lines*, respectively. The *inset* represents the location of southern Kaneohe Bay on Oahu, Hawaii

no significant difference in activity space size (Student's *t*-test, $P > 0.05$) between rays tracked during summer and winter months, rays tracked during summer months had significantly higher total ROMs than those tracked in the winter (Mann-Whitney *U*-test, $P < 0.001$).

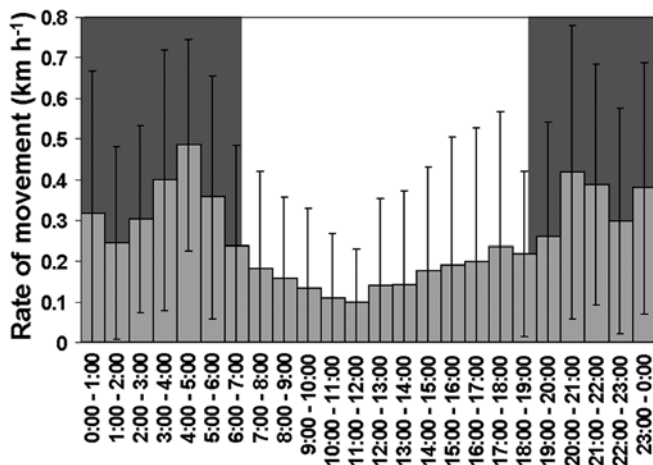


Fig. 2 *Dasyatis lata*. Mean (\pm SD) hourly rate of movement for all rays pooled over a diel cycle. The *shaded areas* represent approximate nighttime periods (averaged over all tracks)

Combined total activity space for *D. lata* was 6.7 km^2 , while the combined activity space for *S. lewini* was 5.1 km^2 . Collectively, both species occupied an area of 8.3 km^2 , of which 40% (3.3 km^2) of the combined area was shared (Fig. 5).

Discussion

This study presents the first measurements of rate of movement (ROM) for a benthic batoid species. Because point-to-point ROM estimates often underestimate swimming speed due to meandering movements, we calculated the ROM of tracked rays using swimming speeds derived from occasional periods of straight-line swimming. A geographic information system allowed determination of straight-line swimming behavior using a common linearity index, obviating subjective selection of data for inclusion in such analyses. Although this ROM is higher than expected for a supposedly 'sluggish' batoid, the range of ROM for *D. lata* was comparable to that of the Pacific angel shark, *Squatina californica* (nighttime ROM range: $0.54\text{--}1.8 \text{ km h}^{-1}$), which is also a demersal elasmobranch species (Standora and Nelson 1977). In addition, *D. lata* tracked during summer months exhibited higher ROM than those tracked in winter months. Water temperatures in Kaneohe Bay range from $\sim 19^\circ\text{C}$ in winter months to $\sim 29^\circ\text{C}$ in late summer months. Therefore, it is likely that the increased ROM in summer months is attributed to elevated water temperatures. Similar observations have been made for juvenile *S. lewini* in Kaneohe Bay (Lowe 2002).

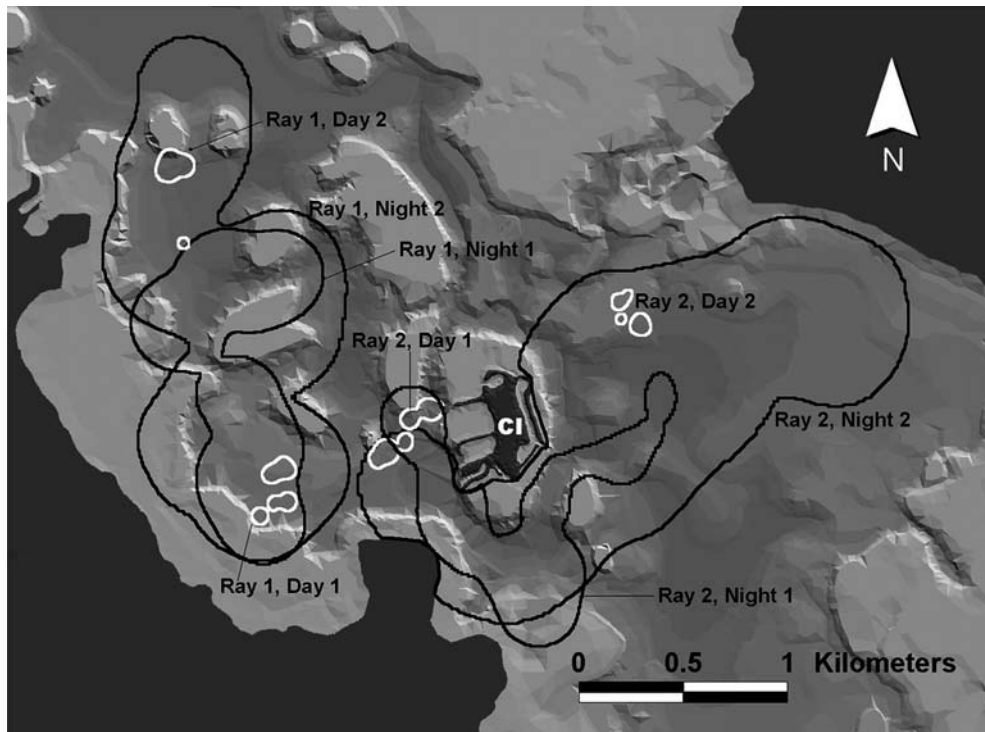


Fig. 3 *Dasyatis lata*. Representative plots of diel activity spaces of *D. lata* in Kaneohe Bay, Oahu, Hawaii. Daytime and nighttime activity spaces for rays 1 and 2. Black and white outlines represent nighttime and daytime activity spaces, respectively. White outlines clustered together belong to the same daytime period

D. lata showed clear diel movement patterns. Other studies that have examined fine-scale movements of batoids have also observed cyclicity in movement patterns. For example, acoustic telemetry studies of bat rays, *Myliobatis californica*, in Tomales Bay, California, suggest that their diel movement patterns are related to thermoregulation (Matern et al. 2000), while the move-

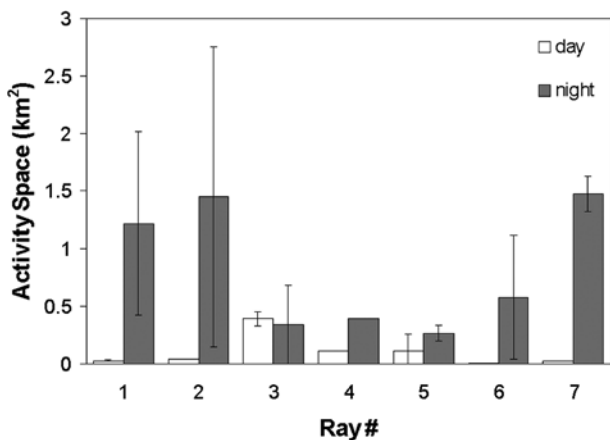


Fig. 4 *Dasyatis lata*. Mean (\pm SD) daytime and nighttime activity spaces for each of the seven rays tracked in Kaneohe Bay. Rays 1–4 were tracked during the summer, while rays 5–7 were tracked during the winter

ments of eagle rays, *Aetobatus narinari*, in Bimini, Bahamas, were associated with tidal stage (Silliman and Gruber 1999). Unlike bat and eagle rays, the movements of *D. lata* may be more influenced by light intensity, rather than water temperature or tidal stage. Eagle rays and southern stingrays, *Dasyatis americana* (Gilliam and Sullivan 1993), are thought to move and forage according to tide, due to increased availability of foraging habitat at high tide. However, for *D. lata*, no relationship between ROM and tide was observed. The differences in activity patterns between *D. lata* and these other species could be attributed to the different depths and magnitudes of tidal change of their respective habitats. Because both eagle and southern stingrays occur in relatively shallow lagoonal habitats, the shallow depth and slope of the habitat result in increased access to a greatly expanded foraging area during high tide. In contrast, Hawaiian stingrays are primarily found over silt/mud substratum in the deeper portions of Kaneohe Bay where tidal change is small, and thus, access to feeding habitat does not substantially increase during high tide.

D. lata showed a consistent pattern of ROM, remaining relatively inactive by day and making extensive forays throughout the southern portion of the bay at night. This increased ROM spanned the entire nocturnal period, but peaked \sim 2 h before sunrise and after sunset (Fig. 2). Similar patterns in diel ROM have been described for various demersal elasmobranch species, such as juvenile *S. lewini* (Holland et al. 1993), horn sharks, *Heterodontus francisci*, swell sharks, *Cephaloscyllium ventriosum* (Nelson and Johnson 1970), *Squatina californica* (Standora and Nelson 1977), white-tip reef sharks, *Triaenodon obesus* (Nelson and Johnson 1980),

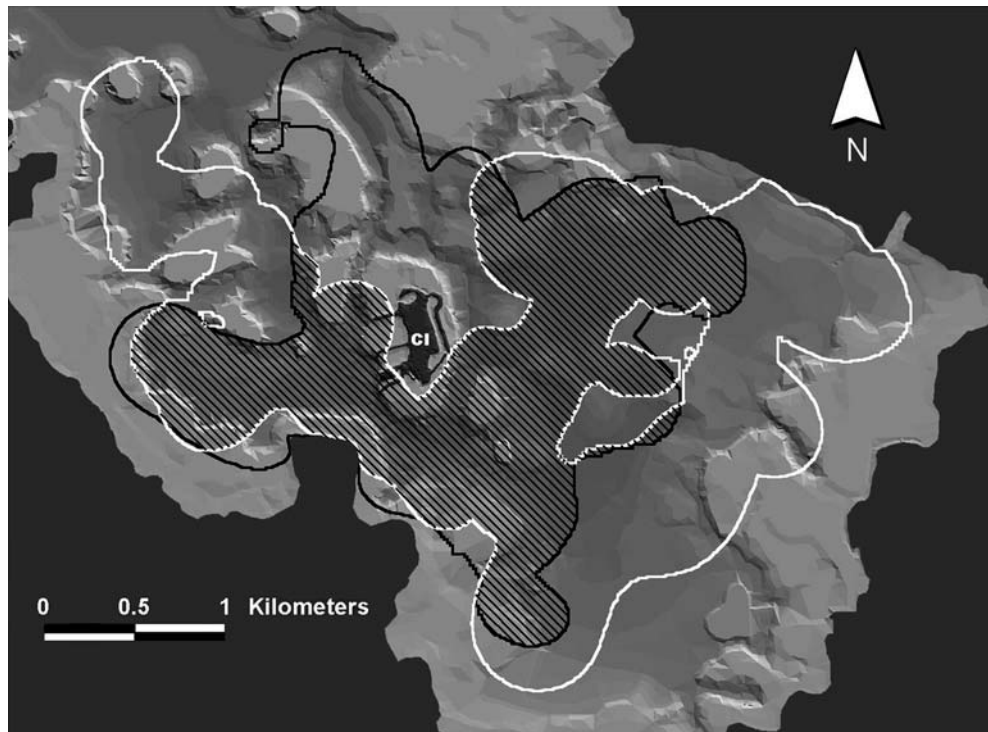


Fig. 5 *Dasyatis lata*. Combined activity spaces of seven *D. lata* (white outline) and five previously studied *Sphyrna lewini* (Lowe 2002) (black outline) in Kaneohe Bay, Oahu, Hawaii. The overlap (hatched area) between the two species covers 3.3 km²

and Pacific electric rays, *Torpedo californica* (Bray and Hixon 1978), all of which forage at night.

Based on these movement patterns, it is likely that *D. lata* actively forages at night. Kaneohe Bay has a relatively depauperate benthic fauna dominated by small burrowing polychaetes (Smith and Kukert 1996). Larger prey, such as alpheid shrimp (e.g., *Alpheus malabaricus*), gobies (e.g., *Oxyurichthys lonchotus* and *Hazeus nephodes*), and portunid crabs (e.g., *Podophthalmus vigil*) are also present, but in lower abundance and densities (Bush and Holland 2002). Therefore, the greater nocturnal activity exhibited by *D. lata* may be related to exploitation of this dispersed food resource. The daytime inactivity of *D. lata* could be due to the nocturnal nature of benthic prey or may be a mechanism for avoiding predators;

Kaneohe Bay is frequented by a variety of elasmobranchs that may prey upon *D. lata*, including adult *S. lewini* and tiger sharks, *Galeocerdo cuvier* (C. Lowe, personal observation).

The increased nighttime activity of *D. lata*, coupled with a lack of refuging behavior, results in these rays exhibiting large nighttime activity spaces. A majority of the rays' overall activity space was over silt/mud substratum, with up to 30% of the positional fixes located within 20 m of the edge of patch reefs. These movements are similar to those of juvenile *S. lewini* observed by Holland et al. (1993) and Lowe (2002). It is thought that the silty bay floor boundary surrounding the patch reefs provides nocturnal cover for many reef associated fishes, such as scarids, labrids, and gobiids, which are more energetically valuable than benthic invertebrate prey (Bush and Holland 2002; Lowe 2002). Therefore, the concentrated movements of these rays and juvenile *S. lewini* around the bases of these reefs may be related to higher concentrations of more energetically valuable prey.

The results from the present study show a high degree of overlap between activity spaces occupied by *D. lata* and juvenile *S. lewini*, and a similar sized average activity space for both species (Fig. 5). Although this indicates that rays and juvenile *S. lewini* utilize the same habitats and approximately the same amount of space, they may be partitioning resources in these habitats by being active at different times. A comparison of activity times of the two species, however, indicates that both are active and possibly foraging simultaneously. Holland et al. (1993) and Lowe (2002) found higher nighttime ROM for juvenile *S. lewini*, which they hypothesized

Table 1 Summary of sexes, size, and tracking dates and durations of seven Hawaiian stingrays, *Dasyatis lata*, tracked in Kaneohe Bay

Ray no.	Sex	Disc width (cm)	Dates tracked	Hours tracked
1	M	44.3	3–5 Aug 2000	65
2	M	40.3	11–13 Aug 2000	52
3	F	62.7	13–15 Aug 2000	46
4	M	68.5	16–18 Aug 2000	31
5	F	45.2	11–13 Jan 2001	58
6	F	73.0	15–20 Jan 2001	74
7	M	52.0	21–23 Jan 2001	54

was attributed to foraging. Examination of stomach contents of these sharks confirms that, although opportunistic, they are feeding primarily at night on benthic invertebrates and teleosts (Bush and Holland 2002). Because *D. lata* is also more active at night, it is likely that they are primarily foraging at this time; however, this is speculative without more detailed knowledge of the feeding habits of *D. lata*. Dasytid rays, in general, appear to be opportunistic feeders that favor benthic invertebrates and teleosts (Struhsaker 1969; Snelson and Williams 1981; Thorson 1983; Capape and Zaouali 1992; Gilliam and Sullivan 1993).

If *D. lata* and *S. lewini* are feeding on the same benthic prey, they may be partitioning these resources according to prey size. *D. lata* found in the bay have larger mouths than juvenile *S. lewini* and therefore may be able to handle larger prey items. Alternatively, it is also possible that prey are not limited in Kaneohe Bay, and there is no need for the partitioning of resources. However, Bush and Holland (2002) and Lowe (2002) found that juvenile *S. lewini* may be starving in Kaneohe Bay either due to limited prey availability or to slow development of foraging skills. Clearly, a detailed study of *D. lata* feeding habits is needed to test any of these hypotheses. In addition, to further investigate ecological interactions between these dominant predators in Kaneohe Bay, future studies should also focus on the abundance and energetics of *D. lata* as well as the availability of prey species in Kaneohe Bay.

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