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**Movement patterns of a Critically Endangered elasmobranch (*Dipturus intermedius*) in  
a Marine Protected Area**

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## 1 **Abstract**

2

- 3 1. Marine Protected Areas (MPAs) are widely used in marine management, but for mobile  
4 species understanding the spatio-temporal scale of management measures that is required  
5 to deliver conservation benefits depends on a detailed knowledge of species' movements  
6 that is often lacking. This is especially the case for species of skate (Rajidae) for which  
7 relatively few movement studies have been conducted.
- 8 2. In Scotland, the Loch Sunart to the Sound of Jura Marine Protected Area (MPA) has been  
9 designated for the conservation of the Critically Endangered flapper skate (*Dipturus*  
10 *intermedius*), but fine-scale movements within this area remain poorly understood.
- 11 3. A passive acoustic telemetry study which coupled acoustic tagging of 42 individuals and a  
12 static array of 58 receivers was conducted from March 2016–June 2017. Using acoustic  
13 detection time series, angler capture-recapture data and depth time series from archival  
14 tags, fine-scale movements of individuals were investigated.
- 15 4. Overall, 33 of the 42 tagged individuals were detected. Residency, site fidelity and  
16 transiency were documented. Residency around receivers, lasting from three months to  
17 more than 12 months, was documented in 16 acoustically detected individuals (48 %) and  
18 all life history categories but was most noticeable among females. Acoustic detections were  
19 associated with depth, salinity and season, but there was no evidence that individuals  
20 formed close-knit groups in the areas in which they were detected.
- 21 5. Taken together with historical occurrence records of flapper skate, the prevalence and scale  
22 of residency documented here suggest that the MPA is sufficiently large to benefit a notable  
23 percentage (38 [24–52] %) of skate found in the study area over monthly and seasonal  
24 timescales. This result strengthens the case for the use of MPAs to support the conservation

25 of flapper skate and other skate species that display similar movement patterns in areas of  
26 high local abundance.

27

## 28 **KEYWORDS**

29 detection, management, passive acoustic telemetry, Rajidae, residency

30

## 31 **1 INTRODUCTION**

32

33 Elasmobranchs are among the most threatened marine vertebrates (Dulvy et al., 2014;  
34 Pacoureau et al., 2021). One quarter of species are threatened with extinction, principally due  
35 to overfishing (Dulvy et al., 2014). The most threatened species are predominately large-bodied  
36 species in shallow, coastal areas (Dulvy et al., 2014). The decline of these species—especially  
37 those that are important predators—has potentially serious consequences for ecosystem  
38 structure, function and services (Stevens et al., 2000; Baum & Worm, 2009; Ferretti et al.,  
39 2010). Consequently, there is an urgent need for research into the efficacy of management  
40 approaches designed to reduce the pressures on these species.

41 In coastal marine ecosystems, spatial management approaches, such as Marine  
42 Protected Areas (MPAs), are a popular option for elasmobranch conservation (Ferretti et al.,  
43 2018; MacKeracher, Diedrich & Simpfendorfer, 2019). Their central objective is to reduce the  
44 pressures to which species or habitats of conservation concern are exposed. For mobile  
45 elasmobranchs, successful spatial management depends on the time that individuals in different  
46 life-history categories spend in protected areas, which is contingent upon the scale of  
47 movement in space and time with respect to these areas (Barker & Schluessel, 2005; Heupel &  
48 Simpfendorfer, 2005; Kinney & Simpfendorfer, 2009; Chapman et al., 2015).

49 A plethora of terms has been introduced to describe animal movements at different  
50 scales (Chapman et al., 2015). ‘Site affinity’ is a general term for site-attached behaviour that  
51 encompasses both prolonged and repeated periods of localized space use. The interpretation of  
52 ‘localized’ is context-specific, but affinity to specific sites such as MPAs is often of particular  
53 interest (Kinney & Simpfendorfer, 2009; Chapman et al., 2015). Prolonged periods of localized  
54 space use are usually distinguished by the duration over which they last, with ‘short-term  
55 residency’ lasting for three months and ‘long-term residency’ lasting more than one year.  
56 Repeated periods of localized space use interspersed with substantial movements away from  
57 an area are termed ‘site fidelity’. In contrast, a brief, unrepeated visit to an area is termed  
58 ‘transiency’.

59 Research on elasmobranch movements has increased in recent years, but most studies  
60 have focused on sharks (Heuter et al., 2004; Papastamatiou & Lowe, 2012; Chapman et al.,  
61 2015; Doherty et al., 2017; Doherty et al., 2019) and the movement patterns of batoids,  
62 especially skates (Rajidae), remain poorly understood (Flowers et al., 2016; Siskey, Shipley &  
63 Frisk, 2019). A number of studies have investigated skate movement using capture-recapture  
64 data (Little, 1995; Little, 1997; Walker, Howlett & Millner, 1997; King & McFarlane, 2010;  
65 Ellis et al., 2011; Peklova et al., 2014; Siskey, Shipley & Frisk, 2019; Bird et al., 2020;  
66 Simpson, Humphries & Sims, 2020). Yet while these data can demonstrate site affinity, more  
67 continuous monitoring is required to demonstrate residency (Hunter et al., 2005a). For  
68 example, archival tags record depth, temperature and other information at high resolution  
69 (Hussey et al., 2015; Siskey, Shipley & Frisk, 2019). These data can be informative about  
70 vertical movement patterns (Wearmouth & Sims, 2009; Peklova et al., 2014; Neat et al., 2015;  
71 Humphries et al., 2016; Pinto & Spezia, 2016; Humphries, Simpson & Sims, 2017) and  
72 movement over relatively large spatial scales (typically on the order of hundreds or thousands  
73 of kilometres) (Hunter et al., 2005a, 2005b; Farrugia et al., 2016; Pinto et al., 2016). However,

74 they are poorly suited to studying movement at fine spatial scales (from metres to tens of  
75 kilometres) because of the uncertainty inherent in geolocation algorithms based principally on  
76 depth, light levels and/or other oceanographic variables (Hunter et al., 2003; Seitz et al., 2006;  
77 Pedersen et al., 2008).

78 At fine spatial scales, passive acoustic telemetry is well suited to investigate movement  
79 patterns (Heupel, Semmens & Hobday, 2006; Hussey et al., 2015). This system comprises a  
80 static array of acoustic receivers which listen continuously for individual-specific acoustic  
81 transmissions from tagged individuals. Detections at receivers demonstrate occupancy and can  
82 provide the information on movement patterns in specific areas that is required to evaluate the  
83 potential benefits of MPAs to mobile species (Heupel, Semmens & Hobday, 2006; Neat et al.,  
84 2015; Lea et al., 2016). However, few studies have exploited this approach to monitor the  
85 movements of rajids (Morel et al., 2013; Neat et al., 2015; Sousa et al., 2019).

86 The Critically Endangered flapper skate (*Dipturus intemedius*) is one of the most  
87 threatened rajids. Formerly identified as the common skate (*Dipturus batis*), the flapper skate  
88 is now recognized as a distinct species and Europe's largest rajid (Iglésias, Toulhoat & Sellos,  
89 2010). They are considered largely benthic, with a broad diet comprising benthic and pelagic  
90 species, including crustacea, cephalopods, teleosts and elasmobranchs, which may be  
91 ambushed, actively hunted or scavenged (Steven, 1947; Wheeler, 1969). Once widespread in  
92 the North East Atlantic, flapper skate have been extirpated across much of their former range  
93 (Brander, 1981; Dulvy et al., 2000, 2006; Dulvy & Reynolds, 2002), though there are recent  
94 indications that population(s) may be starting to rebound (Rindorf et al., 2020). They are  
95 thought to prefer coastal habitats adjacent to deep basins, with a core depth range of 20–225  
96 m, but inhabit depths from 0–600 m (Dulvy et al., 2006; Wearmouth & Sims, 2009; Neat et al.,  
97 2015; Pinto & Spezia, 2016; Pinto et al., 2016; Thorburn et al., 2021).

98           On the west coast of Scotland, angler capture-recapture (CR<sub>A</sub>) records demonstrate that  
99 flapper skate show affinity to the Loch Sunart to the Sound of Jura Marine Protected Area  
100 (LStSJ MPA). This MPA was designated in 2016, in large part on the basis of historical CR<sub>A</sub>  
101 data recorded by Glasgow Museum and the Scottish Shark Tagging Programme from 1975–  
102 2015 that demonstrated skate are repeatedly caught throughout the area (Little, 1995; Little,  
103 1997; Wearmouth & Sims, 2009; Scottish Natural Heritage, 2014; Neat et al., 2015). However,  
104 movements between captures remain poorly understood. Extensive movements have been  
105 documented (Little, 1995) and the historical view was that skate move offshore over winter  
106 (Wheeler, 1969); yet an acoustic study of 20 tagged individuals in the Sound of Jura found that  
107 over 50 % were resident on a day-by-day basis for months at a time and identified three long-  
108 term, mature female residents (Neat et al., 2015). However, the extent of residency among  
109 other life-history categories and over time and space remains uncertain.

110           Seasonal movement patterns in particular have been identified as an important  
111 knowledge gap for management (Thorburn et al., 2021). In early spring, mating is thought to  
112 occur in inshore areas (Day, 1884), after which point a seasonal movement of males offshore  
113 over the summer has been suggested (Little, 1997). Following mating, it is thought that females  
114 may move into shallow water (25–50 m deep) to lay up to 40 eggs in areas with cobble or  
115 boulder substrate, possibly every other year (Little, 1995; NatureScot, 2021). There is  
116 circumstantial evidence for associations among pairs of individuals and single sex groups from  
117 angling (Little, 1995), but the extent to which individuals associate underwater remains  
118 unknown.

119           In this study, an acoustic and archival tagging programme was undertaken to improve  
120 our understanding of the movements of flapper skate in relation to the LStSJ MPA. The  
121 objectives were to investigate fine-scale movement patterns within the MPA and the roles of  
122 sex, maturity, habitat preferences and social interactions as drivers of these patterns.

123

## 124 2 MATERIAL AND METHODS

125

### 126 2.1 Study site

127

128 The LStSJ MPA occupies a 741 km<sup>2</sup> area on the west coast of Scotland (Figure 1).

129 Current management measures prohibit the use of fishing gear except in eight, seasonally

130 fished areas in which mechanical dredges and demersal trawls (excluding beam trawls),

131 without tickler chains, are permitted. The coastline and bathymetric environment are complex.

132 There are shallow-water (< 50 m deep) platforms, alongside glacially over-deepened basins (<

133 5 km<sup>2</sup> in area and > 150 m deep), numerous ridges and deep-water channels that range in width

134 from tens to hundreds of metres. The maximum depth is ~290 m (Howe et al., 2014) (Figure

135 S1). The predominant sediment type in the centre of the MPA is mud, while rock and coarser

136 sediments are found over smaller areas (Howe et al., 2014; Boswarva et al., 2018). There is

137 seasonal stratification in the upper 100 m of the water column over the summer and autumn,

138 with the temperature varying between 7.5 °C (March) and 16.0 °C (August). Salinity variation

139 in the upper layers (from 0.0–34.5 psu) is most strongly associated with proximity to sources

140 of freshwater input (i.e. river discharge and coastal lochs) and seasonal precipitation, which

141 peaks in winter. The flow regime is dominated by semi-diurnal tides that interact with the

142 bathymetry and incised coastline, with current speeds in narrow straights such as the Gulf of

143 Corryvreckan sometimes exceeding 8 knots.

144

### 145 2.2 Data collection

146



147 A passive acoustic telemetry array comprising 58 Vemco VR2, VR2W and VR2AR 69  
148 kHz receivers was deployed from March 2016–July 2017 in the MPA in water depths ranging  
149 from 5–180 m (Figure 1; Figure S1; Table S1). Each Vemco VR2 and VR2W receiver was  
150 deployed 25–50 m below the surface on a vertical line connecting a weighted ballast on the  
151 seabed to a surface buoy. Each VR2AR receiver was deployed 5–10 m above the seabed on a  
152 line from a weighted ballast.

153 Receivers were deployed in four main phases. The number of operational receivers  
154 ranged from 8–28 (median = 23) receivers. Receiver deployments clustered into eight sites  
155 (Figure 1). Most deployments concentrated in two sites—the Kerrera-Loch Spelve Gate and  
156 an area to the south—forming an area referred to as the ‘southern receiver curtain’ that spanned  
157 the deep-water basin between Kerrera and the Isle of Mull (Figure S1).

158 In drift tests of this array, detection probability,  $Pr(det)$ , was strongly associated with  
159 distance from receivers (Klöcker, 2019) (see Supporting Information §1). Near to receivers,  
160  $Pr(det) \sim 0.97$ ; but by 400–450 m  $Pr(det) \sim 0.50$ . In this study, the median value of 425 m was  
161 taken as an estimate of the detection radius around a receiver. Based on this estimate, over the  
162 course of the study, receiver detection radii covered  $\sim 3.93$ – $13.88$  km<sup>2</sup> (0.53–1.87 % of the  
163 MPA) (Figure S2). The maximum detection range observed in drift tests was 708 m.

164 Within the MPA, 42 skate were successfully caught and tagged from March–September  
165 2016 (Figure 1; Table S2) following the methods in Neat et al. (2015). Skate were captured  
166 using baited fishing lines with barbless hooks. Once captured, individuals were sexed and the  
167 total length (snout tip to tail tip) and disc width (wing tip to wing tip) of the dorsal surface of  
168 each skate were measured. Maturation status (immature, mature) was later defined using a  
169 model for maturation with total length (Iglésias, Toulhoat & Sellos, 2010). There was one  
170 individual (male 545: Table S2) for which one state was not considerably more probable than  
171 the other given its length, but post-hoc examination of photographs of this individual’s claspers

172 suggested it was mature. Together, sex and maturation status were taken to distinguish four  
173 life-history categories (immature females, mature females, immature males and mature males).  
174 Following measurement, individuals were tagged on the leading edge of the right wing with  
175 Vemco V13 or Thelma Biotel MP-13 coded acoustic transmitters, programmed to transmit an  
176 individual-specific acoustic signal at random intervals every 30–90 s over an 18-month battery  
177 life. Random transmission was used to minimize the probability of transmission collisions  
178 which can cause detection failure or false detections (Pincock, 2012; Simpfendorfer et al.,  
179 2015). Tag power output was 147 dB re 1 Pa and 153 dB re 1 Pa at 1 m for the V13 and MP-  
180 13 tags respectively. Forty of the individuals were also tagged with archival (Star Oddi milli-  
181 TD or CEFAS G6A) tags, programmed to record depth and temperature every two minutes.  
182 Individuals were given a passive integrated responder (PIT) tag, unless already tagged, and  
183 photographed as part of ongoing monitoring (Neat et al., 2015; Benjamins et al., 2018).

184 Tagging occurred in three phases at three sites: Kerrera, Insh and Crinan (Figure 1).  
185 Most individuals were tagged off Kerrera (25/42) or Insh (6/42) in March 2016. Later that  
186 spring, four large females were tagged off Crinan. In the summer, seven individuals, including  
187 6/7 of tagged immature males, were tagged off Insh. After tagging, individuals remained at  
188 liberty until they were recaptured and the tag removed or until the end of the study in June  
189 2017. During this time, the number of individuals at liberty varied through time from 3–33  
190 individuals (Figure S2).  $CR_A$  data from PIT and photo-identification records (comprising 1,771  
191 captures of 884 individuals between 2011–2018) were also obtained from NatureScot, the  
192 Scottish Association for Marine Science and Marine Scotland Science as a largely independent  
193 source of information on site affinity across a larger number of individuals, a longer timescale  
194 and a wider area.

195

## 196 **2.3 Data processing**

197

198 Data processing was implemented in R, version 4.0.2 (R Core Team, 2020). Raw  
199 acoustic data, comprising 206,377 detections, were quality controlled to ensure that no  
200 detections were retained from receivers or tags outside of their deployment periods or during  
201 servicing, or from unknown tags. Putative (type B) false detections were identified using the  
202 short interval criterion, with a time threshold of 1800 s, provided by the *glatos* package  
203 (Pincock, 2012; Simpfendorfer et al., 2015; Holbrook et al., 2020). Following Pincock (2012),  
204 all detections identified as potentially false ( $n = 1054$ , 0.72 %) were excluded.

205  $CR_A$  records were processed for analysis to include only capture events with all required  
206 information (individual identity, size, capture location and date). For each record, the  
207 probability that the captured individual was mature was predicted from its length, as previously  
208 described. To avoid including captures from individuals whose predicted maturation status was  
209 uncertain, capture records were only used from individuals for which the probability that they  
210 were either immature or mature exceeded 0.75.

211

## 212 **2.4 Individual movement patterns**

213

214 Visual and statistical analyses were implemented using the *prettyGraphics*, *stats*,  
215 *robmixglm* and *mgcv* packages (Wood, 2017; Lavender, 2020a; R Core Team, 2020; Beath,  
216 2021). Undetected and detected individuals were compared in terms of their time at liberty, the  
217 location and timing of tagging, sex and size to investigate the drivers of acoustic detection. For  
218 undetected individuals,  $CR_A$  records were examined to evaluate the plausibility of different  
219 explanations for a lack of detections. For detected individuals, acoustic detection, depth and  
220  $CR_A$  time series were visualized to infer movement patterns. Over the acoustic study, ‘short-  
221 term residents’ were identified as individuals with ‘periods of detections, spaced less than 31

222 days apart, lasting for more than 3 months'. Long-term residents were identified as individuals  
223 with 'periods of detections, spaced less than 31 days apart, lasting for more than 12 months'.

224

## 225 **2.5 Collective spatio-temporal patterns**

226

227 The overall amount of time that males and females spent around receivers was  
228 investigated using Poisson generalized linear models of the total number of days with  
229 detections (hereafter, 'detection days') for each individual in relation to time at liberty, tagging  
230 location and sex (see Supporting Information §2). A robust regression framework was used to  
231 restrict the impact of influential observations. Models were fitted with and without a three-way  
232 interaction and compared using Akaike's Information Criterion (AIC).

233 Temporal trends in the use of areas around receivers for different life-history categories  
234 were investigated using a binomial generalized additive model (GAM) of the number of  
235 detected individuals in each life-history category per day, out of the total number that could  
236 have been detected in that category on each day, in relation to life-history category, time of  
237 year (Julian day), and the area surveyed by receivers at each time point, assuming a detection  
238 radius of 425 m (see Supporting Information §3.1). Time of year was implemented as a group-  
239 level smoother using a cyclic cubic regression spline with a basis dimension of  $k = 15$  and  
240 boundary knots at 0.5 and 366.5 (to account for the 2016 leap year). Tagging location was not  
241 included in the model since tagging locations were unbalanced across life-history categories.  
242 Seasonal patterns in  $CR_A$  time series were examined in a similar way using a negative binomial  
243 GAM of the number of individuals caught per unit time in relation to life-history category and  
244 a group-specific smoother for time (see Supporting Information §3.2). Time was expressed in  
245 months, rather than days, given the concentrated seasonal distribution of observations, with the  
246 boundary knots at 0 and 12. For this model, a basis dimension of  $k = 10$  was sufficient according

247 to the k-index diagnostic. Year was included as a factor, since CR<sub>A</sub> events have been recorded  
248 over three years. For these analyses of CR<sub>A</sub> records, the absolute patterns cannot be interpreted  
249 directly because capture effort is unknown; hence, the metric of interest is the relative  
250 differences among life-history categories, which should be independent of effort.

251 To summarize spatial movement patterns, the distribution of acoustic detections was  
252 mapped and CR<sub>A</sub> records were visually examined for evidence of skate presence beyond the  
253 array. The influence of tagging location and habitat preferences as drivers of the spatial  
254 distribution of acoustic detections was investigated by considering the number of days on  
255 which there were detections of each individual at each receiver (hereafter, the ‘detection  
256 count’) in relation to the distance between that individual’s tagging location and the receiver,  
257 and environmental conditions around receivers (see Supporting Information §4). Distances  
258 were calculated as the shortest distances between tagging locations and receivers, assuming  
259 skate move over the seabed, using the bi-directional Dijkstra algorithm provided by Larnet  
260 (2019), as implemented by the `lcp_over_surface` function with the ‘`cppRouting`’ method in the  
261 `flapper` package (Lavender, 2020b). Seabed bathymetry data at one arc-second resolution were  
262 sourced from Digimap for this analysis since available higher resolution data do not cover the  
263 whole area (Howe et al., 2014). Within each receiver’s 425 m detection radius, depth and  
264 hydrodynamic conditions (thermocline strength, bottom temperature, salinity and current  
265 speed) were identified as plausible environmental drivers of skate presence. For each receiver,  
266 depths were extracted from within its detection radius using the `raster` package (Hijmans, 2020)  
267 and hourly hydrodynamic model predictions over a one-year period were extracted from the  
268 West Scotland Coastal Ocean Modelling System (Aleynik et al., 2016) via the `fvcom.tbx`  
269 package (Lavender, 2020c) (see Supporting Information §4.1). Visualization suggested that  
270 detection counts were associated with depth, salinity and current speed; therefore, these  
271 variables were taken as candidate explanatory variables for model development. For each

272 variable, the average and variability around each receiver were summarized using the median  
273 and median absolute deviation respectively. Collinearity analyses showed moderate to strong  
274 correlations for these two statistics; therefore, only the average conditions were considered.  
275 Median depths and salinities were also strongly correlated, but both were retained for model  
276 development as variables of biological interest.

277 These exploratory analyses led to four competing models for the spatial pattern (SP) of  
278 detections, which were compared qualitatively and using AIC:

- 279 • Model SP1 was a negative binomial GAM of the number of detections of each  
280 individual at each receiver, offset by overlap (in days) between each individual's time  
281 at liberty and each receiver's operational period, in relation to a fixed effect of life-  
282 history category and smooth functions of distance, median depth, the median absolute  
283 deviation in depth, median salinity and current speed. Smooth functions were  
284 implemented using thin plate regression splines with a basis dimension of  $k = 10$ .  
285 Individual was included as a random effect. This model was termed Model SP1 (see  
286 Supporting Information §4.2.1).
- 287 • To allow for potential differences in relationships by life-history category, a model with  
288 group-specific smoothers was fitted (Model SP2) (see Supporting Information §4.2.2).
- 289 • Since depth and salinity were strongly correlated, models with only one of each of these  
290 variables were also evaluated (Models SP3 and SP4) (see Supporting Information  
291 §4.2.3).

292 To investigate the occurrence of social interactions among flapper skate and their  
293 potential influence on spatial patterns,  $CR_A$  records were used to quantify the extent to which  
294 specific pairs of individuals have been caught together (i.e. in the same location and on the  
295 same day) through time. Using acoustic detections, the total number and percentage of  
296 detections 'shared' among all pairs of detected individuals ( $n = 1056$ ) was also examined using

297 the `make_matrix_cooccurrence` function in the `flapper` package (Lavender, 2020b). ‘Shared’  
298 detections were defined as detections at the same receiver within 90 s of each other (the upper  
299 limit for the delay between sequential acoustic transmissions). Among the individuals who  
300 shared a high proportion of detections, overlapping acoustic and depth time series were visually  
301 examined further for evidence of coupled movement patterns.

302

### 303 **3 RESULTS**

304

#### 305 **3.1 Movement datasets**

306

307 The processed passive acoustic telemetry dataset comprised 205,323 detections from  
308 33 individuals. Archival time series were retrieved from 15 acoustically tagged individuals and  
309 totalled 2,709,676 observations. The processed  $CR_A$  database comprised 1,026 records of 555  
310 individuals. This included individuals in all life-history categories, though few records for early  
311 life stages.  $CR_A$  events were distributed from 3<sup>rd</sup> March 2016 until 30<sup>th</sup> October 2018 and  
312 occurred exclusively within MPA boundaries. Per capita, the number of  $CR_A$  records ranged  
313 from 0–12 (median = 1).

314

#### 315 **3.2 Individual movement patterns**

316

317 Nine successfully tagged individuals were undetected by receivers. Undetected  
318 individuals were at liberty for a similar duration (3–449, median = 385, days) to detected  
319 individuals (71–452, median = 398, days). Summary statistics suggest that detection may have  
320 been affected by capture location, season or individual characteristics but the relative  
321 importance of these variables is difficult to disentangle. Most individuals tagged near to the

322 array (off Kerrera and Insh) in winter and summer were detected while none of the four  
323 individuals (all large females) tagged off Crinan in spring were detected. One of the individuals  
324 tagged in Crinan (546) was re-captured (twice) in the same area during the study, suggesting  
325 its absence from the array may have been caused by residency in this area. In total, large ( $\geq$   
326 198 cm) females accounted for seven undetected individuals. In contrast, the two undetected  
327 males were smaller ( $\leq 175$  cm) than average. Tag shedding or removal probably contributed  
328 towards the lack of detections for at least one male (245) that was recaptured without its tags  
329 (Table S2). However, there was no evidence for transmitter malfunction among recovered tags,  
330 nor any CR<sub>A</sub> records of undetected individuals beyond the MPA or mortality. Nevertheless,  
331 despite an absence of detections during this study, CR<sub>A</sub> records show that four of the undetected  
332 individuals have been caught multiple times in the area over extended periods.

333 For acoustically detected individuals ( $n = 33/42$ , 78.57 %), movement time series reveal  
334 heterogeneous patterns (Figure 2; S3–7). Among immature females ( $n = 11$ ), six individuals  
335 were identified as short-term ( $n = 4$ ) or long-term ( $n = 2$ ) residents during the acoustic study  
336 (Figure 2A; Figure S3; Table 1; Table S3) and five had CR<sub>A</sub> records over multiple years  
337 demonstrating site affinity over a longer timescale (Figure S7). During the acoustic study, three  
338 individuals, including the two long-term residents (540 and 249) and one short-term resident  
339 (560), were detected around the southern receiver curtain for  $\geq 150$  days, with only one  
340 substantial gap in detections during a temporary drop in receiver coverage. Concurrent depth  
341 time series for these individuals show repeated movements around a central depth (Figure S3).  
342 For these three individuals, CR<sub>A</sub> data suggest that residency probably continued beyond the  
343 study (Figure S7). Short-term residency was apparent from detections on 24–70 days in three  
344 other immature females (532, 247 and 242) but was not accompanied by clearly repeating  
345 patterns of depth use. One of these individuals (242) was caught outside of the MPA near  
346 Mallaig in 2017, a shortest swimming distance of  $\sim 100$  km from its tagging location. The five



347 immature females that were not identified as residents were detected less often. Nonetheless,  
348 CR<sub>A</sub> records demonstrate that one of these individuals (564) made repeated use of the area over  
349 multiple years (Figure S7).

350         Of the nine mature females detected by receivers, six were identified as short-term (*n*  
351 = 5) or long-term (*n* = 1) residents and eight had CR<sub>A</sub> records over multiple years (Figure 2B;  
352 Figure S4; Figure S7; Table 1; Table S3). The long-term resident (555) was tagged off Kerrera  
353 and detected on more (*n* = 256) days than any other individual. The depth time series shows  
354 extensive use of near-surface depths to c. 220 m. Five short-term residents were identified from  
355 acoustic detections. For two of these individuals (250 and 543), periods of short-term residency  
356 were punctuated by long gaps that are consistent with seasonal site fidelity. For individual 250,  
357 after a prolonged gap in detections over the summer and autumn of 2016, detections in winter  
358 2016–spring 2017 occurred almost continuously at a single receiver (43). However, for the  
359 other three short-term residents (41264, 547 and 558), seasonality was not apparent. Three  
360 individuals were not identified as residents. These individuals were frequently detected during  
361 the first few months of the study but then appeared to move away from receivers. However, all  
362 non-residents have CR<sub>A</sub> records spanning multiple years (Figure S7).

363         Detections of males were less frequent (Figure 2C–D; Figure S5–6). Among immature  
364 males (*n* = 6), only one short-term resident (41269) was identified (Figure 2C) and only two  
365 have CR<sub>A</sub> records in multiple years (Figure S7). During the acoustic study, the five non-  
366 residents were detected less often. For two individuals (41297 and 41262), an initial bout of  
367 detections was repeated after a gap of approximately three months, demonstrating repeated use  
368 of the array, but the remaining three individuals (41261, 41265 and 559) were only detected  
369 for a short period of time around the southernmost receivers following tagging, suggesting  
370 movement to the south. However, one of these individuals (41261) has since been recaptured

371 three times at Kerrera, demonstrating repeated use of the area over a longer timescale (Figure  
372 S7).

373 For mature males ( $n = 7$ ), movement time series suggest periods of short-term  
374 residency, movement beyond the MPA and multi-annual site fidelity (Figure 2D; Figure S6–  
375 7; Table 1; Table S3). Short-term residency was apparent for three individuals (563, 549 and  
376 545). For the two short-term residents (549 and 545) that were at liberty for more than two  
377 seasons, there was some evidence for seasonality, with long gaps between detections following  
378 tagging in March 2016 and subsequent detections in late summer or thereafter. For individual  
379 549, this seasonal absence was associated with a period of prolonged, limited depth use. There  
380 were four non-residents. For individual 542, detections resembled short-term residency but  
381 were constrained by a short period at liberty. Another non-resident (244) exhibited seasonality  
382 in the timing of detections, with an absence of detections over spring–summer associated with  
383 extensive use of deep (up to 311 m) water, suggesting movement beyond the MPA. The  
384 remaining two non-residents (241 and 539) were only detected briefly following tagging.  
385 However, as for individual 244, substantial use of waters deeper than 200 m by individual 539  
386 suggests movement beyond the MPA. Nevertheless, while detections were relatively  
387 infrequent for mature males, in five cases  $CR_A$  records demonstrate site fidelity to the MPA  
388 over multiple years (Figure S7).

389 Overall, detection histories provide evidence for short- or long-term residency in 48.48  
390 % of detected individuals and multi-annual site fidelity in 63.64 % of detected individuals.  
391 While the sample size of acoustically tagged individuals was small, the estimates for the  
392 proportion of detected (0.79) and resident ( $\hat{p} = 0.49$  [0.30,0.66]) individuals (Table S3)  
393 suggest that approximately 0.38 [0.24–0.52] of individuals in the study area, or 337 [237–460]  
394 of the 884 individuals recorded in the raw  $CR_A$  database, may have exhibited short-term or  
395 long-term residency since the onset of PIT tagging.

396

### 397 **3.3 Collective spatio-temporal patterns**

398

399         Across all detected individuals, the number of days with detections ranged between 1–  
400 271 (median = 34) days. Detection days were associated with time at liberty, tagging location  
401 and sex. In the model with a three-way interaction (termed Model DD2: see Supporting  
402 Information §2), all terms were strongly significant (Figure 3; Table S4). For females, overall,  
403 detection days were positively related to time at liberty for individuals tagged at Kerrera but  
404 not individuals tagged at Insh, as expected under a pattern of localized residency. However,  
405 there was substantial variability, with high and low detection days indicating both residency  
406 and transiency. For males, detection days were consistently lower. For males tagged at Kerrera,  
407 detection days were negatively related to time at liberty, suggesting transiency among the males  
408 with the longest times at liberty. The detection days of males tagged at Insh were positively  
409 related to time at liberty, but there were fewest observations for this category and the range in  
410 time at liberty was smallest. Hence, this result is not directly interpreted. For all life-history  
411 categories, the model was limited by the number of detected individuals and a simpler model  
412 without any interactions (Model DD3) was weakly preferred by AIC ( $\Delta AIC = 2.68$ ). These  
413 mixed results clearly point towards a mixture of residency and transiency (during the acoustic  
414 study) in all life-history categories that is difficult explain from time at liberty, sex and tagging  
415 location alone.

416         Over time, the proportion of individuals detected fluctuated significantly for all life-  
417 history categories (Figure 4; Table S5). For females, the proportion of individuals detected was  
418 highest following tagging in spring/summer before declining in winter and partially increasing  
419 thereafter (Figure 4A–B). For mature females, the trend was more strongly seasonal. There was  
420 a significantly positive effect of receiver coverage on these trends (estimate =  $0.21 \pm 0.03$

421 standard error), but they remained apparent even after accounting for this effect. Across the  
422 time series, the proportion of detected males was lower (Figure 4C–D). This model explained  
423 49.20 % of the deviance. The model of CR<sub>A</sub> records similarly identified stronger seasonal  
424 patterns for females relative to males, particularly mature females for which the number of  
425 CR<sub>A</sub> records at their peak in late May was approximately double that of immature females  
426 (Figure S8; Table S6). This model explained 65.66 % of the deviance. In both cases, standard  
427 diagnostics were reasonable.

428 Over space, detections and CR<sub>A</sub> records concentrated in specific areas (Figure 5; Figure  
429 S9–S11). All receivers that recorded detections on more than half of their deployment days  
430 were located in the southern receiver array. More northerly receivers also recorded detections,  
431 though these were attributable to only four individuals (560, 555, 558 and 535). The two  
432 receivers furthest east along the Sound of Mull, two receivers on the southern tip of Lismore  
433 and both receivers at the northern tip of Lismore and east of Kerrera never recorded detections.  
434 CR<sub>A</sub> records for all life-history categories were concentrated in a similar area off Kerrera and  
435 Insh where the two favoured fishing marks are found (Figure S11). Fewer CR<sub>A</sub> events were  
436 recorded further south in the Sound of Jura. To the north of the southern receiver curtain, only  
437 13 CR<sub>A</sub> events were recorded.

438 The predominance of detections around the southern receiver curtain was associated  
439 with tagging location and depth and/or salinity. The model with all covariates and global  
440 smoothers (SP1) was the best supported model according to AIC (Table S7). This model  
441 received substantially more support than the model (SP2) with group-level smoothers ( $\Delta$ AIC  
442 = 211.14). The biological interpretation of this result is that the relationships between detection  
443 counts, tagging location and environmental variables were similar among individuals. Across  
444 all individuals, the effect of distance on detection counts was clearly negative (Figure 6A;  
445 Table S8). In models including either depth or salinity (SP3 and SP4), both variables were

446 identified as significant, with detections occurring on more days at receivers in relatively  
447 deeper, saltier water. However, in the best-supported model with both predictors (SP1), the  
448 effect of depth appeared to explain detection patterns less successfully than salinity (Figure 6B  
449 versus 6C). While the range in median salinities was small, this result reflects the fact that  
450 receivers without detections were predominately located in near-shore areas adjacent to sources  
451 of freshwater input (Figure 5) that can experience more substantial fluctuations in salinity. This  
452 result was also supported by a comparison of Model SP3 versus SP4 in terms of AIC (Table  
453 S7). In contrast to the effects of depth/salinity, according to the best-supported model (SP1),  
454 bottom roughness and current speed were not clearly related to detections, after conditioning  
455 on the effects of other variables (Figure 6D–E). However, concavity estimates from Model  
456 SP1 for all smooth terms (except individual) ranged between 0.69 and 0.91, suggesting these  
457 effects were difficult to distinguish (Table S9). This model explained 74.48 % of the deviance  
458 but did not fully explain the longest residency times.

459  $CR_A$  records and detection time series also shed light on the prevalence of social  
460 interactions and their possible role as a driver of the spatial distribution of detections. In  $CR_A$   
461 records, 79 cases (comprising 66 individuals) were identified in which the same pair of  
462 individuals was re-caught together on two separate occasions. Repeated  $CR_A$  records of pairs  
463 of males were least common and only documented for 15 pairs. More common were repeated  
464  $CR_A$  records of pairs of males and females (30 pairs) and pairs of females (34 pairs). Three  
465 pairs of individuals were caught as pairs on three separate occasions. Nearly all of these  
466 repeated  $CR_A$  records occurred off Kerrera from March–October.

467 Detection time series suggest that these associations were probably largely  
468 coincidental. Across all pairs of individuals, 0.00–29.68 (median = 0.00) % of detections were  
469 shared (Figure 7). Most individuals shared few detections with other individuals, but at least  
470 one individual in each of two pairs shared 15.00–20.00 % of detections with the other

471 individual and there was one pair of individuals in which an individual shared 29.68 % of its  
472 detections with the other. All shared detections occurred around the southern receiver array  
473 and were most prevalent in spring/summer 2016 when most individuals were at liberty. In  
474 terms of life-history category, while the percentage of shared detections was generally low,  
475 both immature and mature females shared more detections than either category shared with  
476 immature or mature males, while detections of males coincided with detections of females  
477 more often than with other males (Figure 7).

478         Among the individuals who shared a high proportion of detections, further examination  
479 of overlapping acoustic and depth time series did not suggest that individuals that shared  
480 detections were intimately associated in space for prolonged periods. Instead, most acoustic  
481 associations appear coincidental, prevailing among individuals occupying similar but distinct  
482 areas. In the few cases in which both acoustic and depth time series were similar, there were  
483 no consistent patterns in their nature or timing that could be attributed to particular types of  
484 interactions, such as mating.

485

#### 486 **4 DISCUSSION**

487

488         This is one of the first studies to examine the movements of a skate species at fine  
489 spatial scales over prolonged periods. For flapper skate,  $CR_A$  records and acoustic telemetry  
490 have previously demonstrated site affinity, especially among mature females, to the LStSJ  
491 MPA, but the prevalence, scale and drivers of this pattern remained unclear (Little, 1995; Little,  
492 1997; Wearmouth & Sims, 2009; Neat et al., 2015). This study provides the first evidence that  
493 residency within the LStSJ acoustic array is relatively common among all life-history  
494 categories (at least for individuals >107 cm in length) and extends for periods of three months  
495 (short-term residency) to at least 15 months (long-term residency). This result strengthens the

496 evidence that spatial management approaches such as the LStSJ MPA should benefit flapper  
497 skate over monthly and seasonal timescales and suggests that studies on similar, large-bodied  
498 rajids in relation to MPAs would be worthwhile. At the same time, this study corroborates  
499 evidence for site fidelity and transiency for some individuals in the area (Neat et al., 2015).  
500 There is stronger evidence that movement patterns may differ among demographic groups, but  
501 the hypothesis that individuals associate closely in pairs or groups is refuted.

502         The dominant movement pattern in detection time series was short-term residency. This  
503 was documented in approximately 50 % of tagged individuals and all life-history categories.  
504 In theory, an individual only had to swim into the array once a month for three months to be  
505 identified as a ‘short-term resident’, but detection histories demonstrated that short-term  
506 residents typically spent weeks or months around receivers, particularly in the southern  
507 receiver curtain. In the most extreme case, detections of one female concentrated around a  
508 single receiver for five months, though there is a possibility that this individual shed its tag or  
509 died in this area. Long-term residency was documented in a further 10–20 % of immature and  
510 mature females, respectively, but may have been more common given that 38 % of short-term  
511 residents were only at liberty for relatively short periods. Taken together with previous  $CR_A$   
512 and acoustic analyses (Neat et al., 2015; Pinto, 2015), these results suggest that residential  
513 behaviour, especially short-term residency, is common among skate in the LStSJ MPA.

514         However, the prevalence and spatial-temporal scale of residency remain partially  
515 unclear, given the number of tagged individuals and limited receiver coverage. In the gaps  
516 between detections, individuals could have moved into other parts of the MPA or beyond MPA  
517 boundaries (Williamson et al., 2021). In some settings, alternative array designs, such as paired  
518 gated arrays, provide additional (directional) information that can help to distinguish these  
519 possibilities (Heupel, Semmens & Hobday, 2006). Gated designs are particularly common in  
520 riverine systems for studies of salmonid movements (e.g., Rechisky et al., 2020) but logistically

521 challenging in non-linear, open systems. Hence, new analytical methods that integrate acoustic  
522 detections with ancillary data to reconstruct movements in the gaps between detections would  
523 also benefit analyses of the prevalence and scale of residency.

524         Residency is emerging as a relatively common movement pattern for many mobile  
525 marine species (Abecasis et al., 2015; Chapman et al., 2015; Hartman et al., 2015). Yet much  
526 of this research has focused on the movements of reef-associated teleosts (Abecasis et al., 2015;  
527 Garcia, Mourier & Lenfant, 2015; Afonso et al., 2016; Rojo, Sánchez-Meca & García-Charton,  
528 2019). Among elasmobranchs, research has also tended to focus on reef-associated species,  
529 especially sharks (Flowers et al., 2016). For instance, blacktip (*Carcharhinus melanopterus*),  
530 whitetip (*Triaenodon obesus*) and Caribbean (*Carcharhinus perezii*) reef sharks all show strong  
531 patterns of residency (Randall, 1997; Papastamatiou et al., 2010; Bond et al., 2012; Heupel,  
532 Lédée & Simpfendorfer, 2018). Some wide-ranging species, such as basking sharks  
533 (*Cetorhinus maximus*) (Doherty et al., 2017, 2019) and spurdog (*Squalus acanthias*) (Thorburn  
534 et al., 2015) also exhibit residency at certain times of year or in specific locations. Among  
535 rajids, only a handful of studies have examined residency (Hunter et al., 2005a; Morel et al.,  
536 2013; Neat et al., 2015; Sousa et al., 2019). However, a study in the southern North Sea  
537 suggested that many thornback rays remain in the Thames estuary year-round (Hunter et al.,  
538 2005a). Similarly, an acoustic study of three white skate (*Rostroraja alba*) revealed short-term  
539 residency within a marine park for two individuals and long-term residency lasting over 20  
540 months in a mature female (Sousa et al., 2019). During this time, core activity areas were  
541 around 0.4 km<sup>2</sup>, within a home range of approximately 3.2 km<sup>2</sup>. For flapper skate, detection  
542 patterns suggest a similar scale of residency. While evidence is limited, the emerging picture  
543 from these studies is that residency may be an important aspect of the biology of rajids.

544         The drivers of residency remain unclear. Short-term residency may reflect natal,  
545 nursery, aggregation or mating philopatry (Chapman et al., 2015). These behaviours are poorly



546 understood in flapper skate, but the use of nursery habitats by immature individuals may  
547 contribute towards residency in this group (Kinney & Simpfendorfer, 2009; Speed et al., 2010).  
548 Over seasonal and annual timescales, depth time series for three resident immature skate tagged  
549 in this study exhibit a pattern of repeated movements around particular depths, which points  
550 towards central foraging or refuging behaviour (Humphries, Simpson & Sims, 2017;  
551 Papastamatiou et al., 2018). Amongst other elasmobranchs, long-term residency appears to  
552 predominate among tropical or subtropical species (Chapman et al., 2015) but has been  
553 documented in a few deep-water, benthic species in higher latitudes, including the bluntnose  
554 sixgill (*Hexanchus griseus*) (Andrews et al., 2009), the prickly shark (*Echinorhinus cookei*)  
555 (Dawson and Star, 2009) and white skate (Sousa et al., 2019). These patterns suggest that  
556 environmental stability, if coupled with a consistent food supply, may promote residency  
557 (Chapman et al., 2015).

558         Another movement pattern apparent from detection time series is one of repeated  
559 detections in an area punctuated by gaps. This pattern is difficult to interpret because detections  
560 and the gaps between detections varied in duration and the locations of undetected individuals  
561 were generally unknown. Nevertheless, there is evidence of seasonal site fidelity that might be  
562 attributable to mating. In March/April, when mating is believed to occur (Day, 1884), 8/11  
563 mature females tagged near to the array and all mature males that were at liberty were detected.  
564 Thereafter, a clear, seasonal gap in the detections of at least two females (250 and 543) and  
565 three males (549, 244 and 545) followed over the summer/autumn, which may be associated  
566 with movement offshore (Little, 1997). Seasonal site fidelity has been reported in other  
567 elasmobranchs, such as short-tailed (*Dasyatis brevicaudata*) and round (*Urobatis halleri*)  
568 stingrays (Vaudo & Lowe, 2006; Le Port, Sippel & Montgomery, 2008) but, for flapper skate,  
569 further evidence is needed to understand fully these patterns given the density and scale of the  
570 acoustic array used in this study.

571           There was evidence of transiency in all life-history categories. Previous CR<sub>A</sub> analyses  
572 from the LStSJ MPA have indicated the presence of transient individuals (Neat et al., 2015).  
573 In the present study, the biological interpretation of transiency hinges on the interpretation of  
574 the lack of detections, which could have been caused by one or more of a number of factors:  
575 limited to moderate movements outside of receiver detection ranges within the MPA; more  
576 extensive movements to areas beyond MPA boundaries, possibly as part of a longer-term  
577 pattern of site fidelity; tag shedding, malfunction or removal; or mortality. CR<sub>A</sub> and depth time  
578 series data shed light on these options. One mature female (546) that was tagged in the Sound  
579 of Jura and appeared ‘transient’ from the perspective of acoustic detections probably continued  
580 to reside in this region, where she was re-caught by anglers during the study. At least three  
581 individuals moved away from the MPA, including two mature males (244 and 539) which  
582 moved into deeper waters, and one immature female (242) which moved north to Mallaig.  
583 Other individuals could also have moved beyond MPA boundaries during their time at liberty,  
584 given historical evidence for long (> 100 km) northwards journeys (Ritchie, 1923; Wheeler,  
585 1969; Little, 1995). One individual also shed its acoustic tag, though the true extent of tag loss  
586 remains unclear (Neat et al., 2015).

587           There is evidence that movements differed between life-history categories. Across the  
588 board, detections were lower for males, reflecting a difference between the sexes in terms of  
589 the time they spent around receivers and perhaps more widely. In other elasmobranchs, sex-  
590 biased dispersal is relatively common and typically involves wider ranging movements in  
591 males (Pardini et al., 2001; Daly-Engel et al., 2012; Chin et al., 2013; Portnoy et al., 2015;  
592 Roycroft, Le Port & Lavery, 2019). A number of hypotheses might explain this behaviour  
593 (Wearmouth & Sims, 2010), such as differing habitat requirements in relation to divergent  
594 reproductive strategies (Economakis & Lobel, 1998) and the competitive exclusion of males  
595 by larger females (Corcoran et al., 2013). For flapper skate, while the prevalence of male-

596 biased dispersal is unclear, this study strengthens the evidence that male and female movements  
597 differ and points towards other approaches, such as archival tags, as the means to clarify the  
598 movements of males.

599         Despite variation in movement patterns, over space almost all detections occurred  
600 around the southern receiver array. Only four tagged skate (560, 555, 558 and 535) were  
601 detected at receivers elsewhere and only one of these individuals (555) was detected in most  
602 areas of the array. However, the implications of this pattern depend on the relative influences  
603 of habitat preferences, detection probability, social interactions and sampling location.

604         In terms of habitat preferences, detections were more numerous away from shallow,  
605 inshore habitats close to sources of freshwater input. While skate certainly use shallow-water  
606 habitats (Wearmouth & Sims, 2009; Neat et al., 2015; Pinto & Spezia, 2016; Pinto et al., 2016;  
607 NatureScot, 2021; Thorburn et al., 2021), this pattern may reflect a preference for deeper water.  
608 This hypothesis is consistent with the location of CR<sub>A</sub> sites over deep troughs, a species  
609 distribution model (Pinto et al., 2016) and observed depth time series (Thorburn et al., 2021),  
610 and may be related to prey distribution (e.g., the presence of *Nephrops* in deep water channels)  
611 or refuging behaviour, away from storms, water currents or previous mobile fishing activity.  
612 Alternatively, this apparent depth preference may have been driven by the complete absence  
613 of detections at receivers in shallow, near-shore habitats proximate to sea lochs, a pattern which  
614 appeared to be captured more effectively by salinity. In elasmobranchs, salinity variation often  
615 correlates with movement (Schlaff, Heupel & Simpfendorfer, 2014). While the causal links  
616 between these variables vary among systems (Heupel & Simpfendorfer, 2008; Knip et al.,  
617 2011; Simpfendorfer et al., 2011), most elasmobranchs are stenohaline (Froeschke, Stunz &  
618 Wildhaber, 2010; Martin et al., 2012), so it is plausible that flapper skate avoid areas around  
619 sea lochs which experience greater salinity variation. Space use may be affected by

620 anthropogenic influences, such as aquaculture (Wearmouth & Sims, 2009), but further research  
621 is required to investigate their effects.

622         Apparent habitat preferences may have been affected by detection probability (Kéry &  
623 Schmidt, 2008). For example, receivers in shallow water on the mainland sides of Kerrera and  
624 Lismore may be exposed to higher levels of disturbance, which could decrease detection  
625 probability (Kessel et al., 2014). However, these factors are likely to influence the daily  
626 detection count more than the detection days metric used in this study. Moreover, a complete  
627 lack of detections in a few areas probably reflects a genuine absence of tagged skate in these  
628 areas over the study. Specifically, given the position of the coastline, it is likely that no tagged  
629 skate travelled all of the way along the eastern sides of Lismore or Kerrera, despite using the  
630 western sides of both of these islands.

631         Social interactions may have further influenced spatial patterns of detections (Jacoby,  
632 Croft & Sims, 2012). Yet despite circumstantial evidence for single sex groups in flapper skate  
633 (Little, 1997) and for grouping behaviour in other elasmobranchs (Jacoby, Croft & Sims,  
634 2012), the hypothesis that individuals closely associate in pairs or groups for substantial periods  
635 was unsupported. Even individuals from the same life-history category located in a similar area  
636 at the same time generally exhibited distinct depth time series. However, looser associations,  
637 for instance with many immature females remaining in similar areas through time, perhaps due  
638 to shared feeding grounds or overlapping territories, may be important and probably explain  
639 patterns in CR<sub>A</sub> records.

640         Sampling location also affected the spatial distribution of detections. Specifically,  
641 given the prevalence of localized movement patterns, capture at a few favoured angling sites  
642 appeared to contribute towards the appearance of detection hotspots around capture sites.  
643 Beyond these areas, localized movement suggests that skate probably remain undersampled by  
644 recent PIT tagging efforts (2011–present). The implication is population-level inferences from

645 a handful of sites may be unrepresentative and a wider, more representative spatial distribution  
646 of CR<sub>A</sub> effort would benefit analyses of habitat preferences and the estimation of population  
647 trends (Sollmann, Gardner & Belant, 2012; Sun, Fuller & Royle, 2014; Hays, Rattray &  
648 Esteban, 2020). More sampling is also required in the winter months to clarify seasonal  
649 movement patterns, especially for males with sparser detection time series, and for the smallest  
650 size classes, which remain understudied.

651 This research has implications for skate conservation. Taken together with historical  
652 CR<sub>A</sub> records that demonstrate skate occur throughout the MPA (Little, 1995; Little, 1997;  
653 Scottish Natural Heritage, 2014; Neat et al., 2015), the strength of site affinity revealed by  
654 recent PIT tagging CR<sub>A</sub> data and the acoustic time series analysed here suggests that removing  
655 pressures such as fishing from areas the size of the MPA has the potential to benefit multiple  
656 life-history categories, especially females, over monthly and seasonal timescales. In fact,  
657 prolonged residency within particular areas of the acoustic array suggests that smaller protected  
658 areas could be beneficial to some individuals over these timescales. At the same time, the  
659 spatial scale of residency implies that skate may be particularly vulnerable to localized  
660 pressures, especially in areas that are disproportionately important for their life history (Kinney  
661 & Simpfendorfer, 2009; Flowers et al., 2016). These results add to the accumulating evidence  
662 in support of the use of MPAs for skate (Hunter et al., 2006; Wiegand, Hunter & Dulvy, 2011;  
663 Sousa et al., 2018, 2019) and in elasmobranch conservation more broadly (Ferretti et al., 2018;  
664 MacKeracher, Diedrich & Simpfendorfer, 2019; Dwyer et al., 2020). However, an open  
665 question remains regarding the extent to which protection from fisheries over monthly and  
666 seasonal timescales supports population recovery.

667 Within the MPA, the results further confirm the importance of the deep-water basins  
668 around angling sites for skate, as found in other parts of the MPA (Neat et al., 2015; Thorburn  
669 et al., 2021). In contrast, there were a few specific locations in which tagged skate were not

670 detected. However, further research is required to evaluate the suitability of MPA boundaries  
671 given the small sample size, the influence of tagging location on detection patterns and other  
672 considerations that affect the benefits of management measures, such as habitat suitability  
673 (Lauria et al., 2015; Pinto et al., 2016) and potential fishing pressure (Langton et al., 2020).

674         There are eight areas in the MPA in which seasonal fisheries are permitted from  
675 October–March. Acoustic detections demonstrate that there is the potential for skate–fisheries  
676 interactions during this time, especially for mature females for which seasonal detection  
677 patterns were strongest. Unfortunately, the absence of CR<sub>A</sub> and acoustic data from fished areas  
678 precludes further evaluation in this study of the prevalence of these interactions. However, this  
679 should be a priority for future research.

680         Beyond the LStSJ MPA, evidence for wider movements suggests that the LStSJ MPA  
681 alone is not fully adequate for the protection of flapper skate found in this area. Flapper skate  
682 are no longer commercially targeted, but they are caught as bycatch in bottom-trawl fisheries  
683 (Bendall et al., 2017) and survivorship estimates for related species (Benoît, Hurlbut & Chassé,  
684 2010; Dulvy et al., 2014), along with estimates of vital rates (Régner et al. in press), suggest  
685 that this has the potential to impede population recovery. If short-term residency in  
686 winter/spring typically precedes offshore movement (Wheeler, 1969), flapper skate may be  
687 particularly vulnerable to this source of mortality in summer/autumn. For some individuals,  
688 localized movements are likely to increase the severity, but reduce the area, of overlaps  
689 between skate and fisheries. For other individuals, especially males, longer distance  
690 movements away from protected areas may increase the time over which individuals are  
691 potentially exposed to fisheries, which has the potential to lead to sex-biased exploitation  
692 (Mucientes et al., 2009). However, technical measures, such as the removal of ‘tickler’ chains,  
693 which startle skate resting on the seabed in front of trawls into nets, can substantially reduce

694 the bycatch of skate (Kynoch, Fryer & Neat, 2015) and should be considered as a potential  
695 management tool in areas in which flapper skate occur.

696         Alongside fisheries, in coastal areas flapper skate are potentially exposed to aquaculture  
697 farms (Bell et al., 2016), pollutants (Bezerra, Lacerda & Lai, 2019), electromagnetic cables  
698 (Hutchison et al., 2018) and other anthropogenic stressors (Wheeler et al., 2020). For example,  
699 recent research has reported notable concentrations of plastic (Smith, 2018) and other  
700 pollutants (Gelsleichter & Walker, 2010; Bezerra, Lacerda & Lai, 2019; Tiktak et al., 2020) in  
701 elasmobranchs, which may have physiological and population-level impacts (Wheeler et al.,  
702 2020), as reported in marine mammals such as orcas (*Orcinus orca*) (Desforges et al., 2018).  
703 As a result, MPAs like the LStSJ MPA need to be embedded within an ecosystem-based  
704 management approach that recognises the suite of stressors to which species are exposed in  
705 order to deliver management objectives (McLeod et al., 2005; Thrush & Dayton, 2010;  
706 Wheeler et al., 2020).

707

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1144 **TABLES**

1145

1146 **Table 1. The number of short-term and long-term residents in each life-history category.**

1147 *N* refers to the total number of individuals detected in each life-history category. Within each

1148 category, the number of ‘short-term’ and ‘long-term’ residents (individuals with periods of

1149 detections spaced less than 31 days apart over more than three or 12 months, respectively) is

1150 denoted by  $N_R$ . Note that *N* is greater than the total number of residents ( $N_R$  combined across

1151 residency categories) because only a portion of individuals met the criteria for short- or long-

1152 term residency. *p* is the observed proportion of individuals that were short- or long-term

1153 residents (out of *N*). Statistical estimates and confidence intervals are provided in Table S3.

1154

Sex	Maturation Status	<i>N</i>	Short-term residents		Long-term residents		Total residents	
			$N_R$	<i>p</i>	$N_R$	<i>p</i>	$N_R$	<i>p</i>
Female	Immature	11	4	0.364	2	0.182	6	0.545
	Mature	9	5	0.556	1	0.111	6	0.667
Male	Immature	6	1	0.167	0	0.000	1	0.167
	Mature	7	3	0.429	0	0.000	3	0.429
Totals		33	13	0.394	3	0.091	16	0.484

1155 **FIGURE LEGENDS**

1156

1157 **Figure 1. The study site. A**, The Loch Sunart to the Sound of Jura MPA. The inset shows the  
1158 location of the MPA within Scotland. The main figure outlines the MPA in grey. The coloured  
1159 points mark receivers. The stars mark acoustic tagging sites. Fishing gear is prohibited  
1160 throughout the MPA, with the exception of mechanical dredges and demersal trawls (excluding  
1161 beam trawls) in eight seasonally open areas (shown in blue). These measures extend beyond  
1162 the MPA to the southwest through the Firth of Lorn Special Area of Conservation. **B**, The  
1163 receiver array. Receivers are grouped into eight main sites by which they are coloured  
1164 according to a colour wheel which approximately relates to site location (see key). The  
1165 coordinate reference system is British National Grid. Background Ordnance Survey maps ©  
1166 Crown copyright and database rights [2019] Ordnance Survey (100025252).

1167

1168 **Figure 2. Detection histories for each life-history category. A**, immature females; **B**, mature  
1169 females; **C**, immature males; and **D**, mature males. Each point (+) defines the time of a  
1170 detection for a particular individual. Filled points (•) mark the date of tagging and tag removal  
1171 (if applicable) respectively. Point colour corresponds to receiver location (see Figure 1), with  
1172 tagging events off Insh (away from receivers) shown in pink and tag removal events in  
1173 unrecorded locations shown in grey. The background colouration highlights the season. Y-axis  
1174 labels define individual IDs, residency categories (N, non-resident; S, short-term resident; L,  
1175 long-term resident) and the total number of days with detections (by which individuals are  
1176 ordered). Short-term and long-term residents are individuals with periods of detections spaced  
1177 less than 31 days apart over more than three or 12 months, respectively.

1178

1179 **Figure 3. Detection days in relation to time at liberty for each sex and tagging location.**

1180 Points, lines and envelopes mark the observations, fitted values and 95 % confidence intervals  
1181 from a robust generalized linear model of detection days in relation to time at liberty (days),  
1182 sex (M, male; F, female) and tagging location (K, Kerrera; I, Insh). These are shaped according  
1183 to sex and coloured according to tagging location. Point size is proportion to the total length  
1184 (cm) of each individual. Numbers in brackets define the number of individuals in each  
1185 category.

1186

1187 **Figure 4. Trends in the proportion of individuals detected in each life-history category.**

1188 **A**, immature females; **B**, mature females; **C**, immature males; and **D**, mature males. In each  
1189 subplot, the grey line is the proportion of individuals detected on each day. Line thickness is  
1190 proportional to the total number of individuals at liberty in each life-history category on each  
1191 day. The black line and surrounding envelope show the trend in the expected proportion of  
1192 detected individuals, surrounded by 95 % pointwise confidence bands, from a binomial  
1193 generalized additive model of the number of detected individuals in each life-history category,  
1194 out of the total number that could have been detected in that category, while holding the  
1195 receiver area constant at its median value (11.05 km<sup>2</sup>).

1196

1197 **Figure 5. The spatial distribution of detections.** Crosses denote receivers and the size of the

1198 surrounding bubbles denotes the proportion of days during which there were detections at each  
1199 receiver over its deployment time, coloured by site (see Figure 1). Proportions are shown rather  
1200 than counts since receivers were deployed for variable time periods (but the latter show a very  
1201 similar picture.) The coordinate reference system is British National Grid. Background map ©  
1202 Crown copyright and database rights [2019] Ordnance Survey (100025252).

1203

1204 **Figure 6. Smooth terms for the effects of tagging location and environmental conditions**  
1205 **on the spatial distribution of detections.** Smooths for the following variables were estimated:  
1206 **A**, the shortest distance between receiver and tagging locations (m); **B**, the median depth (m);  
1207 **C**, the median (bottom) salinity (psu); **D**, the median absolute deviation in depth (m); and **E**,  
1208 the median (bottom) current speed (m/s). In each subplot, the smooth shown by the black line  
1209 represents the change in the expected number of days with detections (the ‘detection count’)  
1210 on the scale of the link function across the range of each explanatory variable. Smooths are  
1211 shown on the scale of the link function so that the 95 % pointwise confidence bands, marked  
1212 in grey, relate solely to the uncertainty in the smooth rather than uncertainty in both the smooth  
1213 and the mean of the response (detection count). Thus, expected detection counts are higher at  
1214 receivers near tagging sites (**A**) and (**C**) saltier water, but are not clearly related to the receiver  
1215 depth (**B**), the metric of bottom roughness (**D**) or current speeds (**E**).

1216

1217 **Figure 7. Co-occurrence patterns in detections.** Each cell ( $i, j$ ) shows the percentage of the  
1218 detections of individual  $i$  (on the x axis) that are ‘shared’ with individual  $j$  (on the y axis). The  
1219 diagonal of the matrix is highlighted in grey. Life-history categories—immature females (I, F),  
1220 mature females (M, F), immature males (I, M) and mature males (M, M)—are labelled. Within  
1221 each category, individuals are ordered by the total number of days over which they were  
1222 detected (i.e., following Figure 2). Note that the percentage of observations shared by pairing  
1223  $i, j$  may not equal the percentage shared by pairing  $j, i$  when individuals have differing numbers  
1224 of detections.

1225