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RESEARCH ARTICLE

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First report of an egg nursery for the Critically Endangered flapper skate *Dipturus intermedius* (Rajiformes: Rajidae)

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Abstract

1. This study provides the first report of an egg nursery for the Critically Endangered flapper skate *Dipturus intermedius* and a description of the habitat, thus contributing towards our understanding of essential habitats for the species.
2. In total, 1,395 flapper skate egg cases were recorded (accounting for overlapping surveys) in two egg case collection dives ($n = 67$ egg cases), one photogrammetry dive ($n = 10$ egg cases), 509 drop-down video (DDV) camera drifts ($n = 510$ egg cases) and 18 remote operated vehicle (ROV) flights ($n = 1,031$ egg cases), carried out in the Inner Sound on the west coast of Scotland from 2018 to 2021. All of the egg cases were found on a shallow bedrock plateau between the Isle of Scalpay and a deep (>100 m) water channel between the Isle of Longay and the Crowlin Islands. Egg cases were observed on a cobble/boulder reef between 25 and 58 m depth, with a modelled annual temperature range of 9–12 °C, modelled current speeds up to 0.2 m^{-1}, a rugosity index of 1.7 and low levels of sedimentation.
3. Flapper skate egg cases are large and the incubation period is protracted (18 months), making them potentially vulnerable to anthropogenic disturbance. A description of the habitat where egg cases were observed in this study will help inform the search for egg nurseries for this Critically Endangered species elsewhere. Targeted DDV, ROV and scuba diving surveys will support this search in areas where suitable bathymetric and hydrodynamic conditions are identified.
4. Safeguarding egg nurseries is essential for successful conservation. Protection should involve the designation of egg nurseries as Marine Protected Areas where activities that are likely to damage or alter seabed habitats are managed.

KEYWORDS
cobble/boulder habitat, egg case, egg nursery, elasmobranch, flapper skate, oviparous

1 | INTRODUCTION

The common skate complex comprises two species (Iglésias, Toulhoat & Sellos, 2010), namely flapper skate *Dipturus intermedius* and common blue skate *Dipturus batis* (Last, Weigmann & Yang, 2016). The common skate complex effectively disappeared from much of the North Sea between the mid-1950s and early 1980s (Walker & Hislop, 1998), and it was extirpated from the Irish Sea in the late 1970s (Brander, 1981). Owing to the severe reduction in range and abundance, the species complex was listed on the International Union for Conservation of Nature Red List as Critically Endangered (Dulvy et al., 2006) and is included on the Oslo/Paris Convention for the Protection of the Marine Environment of the North-East Atlantic List of Threatened and/or Declining Species. More recently, flapper skate specifically was categorized as Critically Endangered (Ellis et al., 2021). However, an increasing trend in relative abundance for the common skate complex was recently reported, suggesting the species complex is beginning to recover (ICES, 2020; Rindorf et al., 2020). Flapper skate occur in the North-East Atlantic, from Scandinavia to the south west of the British Isles, and possibly to Iberian waters (Frost et al., 2020; Bache-Jeffreys et al., 2021), with the species showing localized abundance in Scottish waters (Neat et al., 2015; Frost et al., 2020).

In Scotland, current conservation measures relating to flapper skate include fisheries management, via a prohibition on landings in UK waters, the listing on Sharks, Skates and Rays (Prohibition of Fishing, Trans-shipment and Landing) (Scotland) Order 2012, providing additional protection during recreational angling, the listing on the Priority Marine Features List for Scotland (a list of habitats and species highlighted for protection; Wilding et al., 2016), and the Marine Protected Areas (MPAs) search features list (a list of features for which MPAs should be designated in Scotland; Wilding et al., 2016). The Loch Sunart to the Sound of Jura Nature Conservation Nature Conservation MPA (NCMPA), covering an area of 741 km^2, was designated for the protection of the common skate complex in 2016 based on the high level of site attachment documented in adult flapper skate in the area from mark–recapture records and telemetry (Neat et al., 2015). Flapper skate demonstrated high occupancy of the deep water (100–150 m) within the NCMPA (Lavender et al., 2021a) in the summer months with more movement into shallower areas during the winter (Thorburn et al., 2021; Lavender et al., 2021b). A second, smaller (6.05 km^2) urgent NCMPA was designated in March 2021 (Red Rocks and Longay urgent NCMPA, Figure 1) 70+ km to the north of Loch Sunart to the Sound of Jura NCMPA following initial reports from scallop divers and

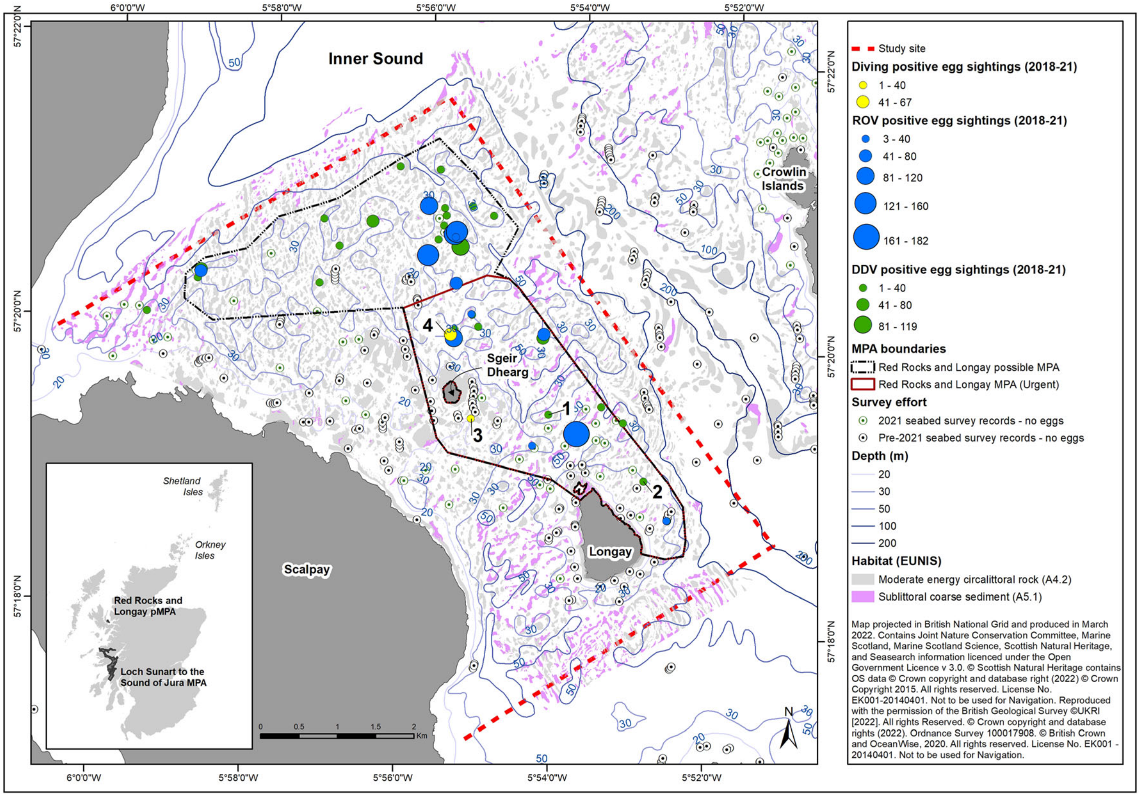

FIGURE 1 The Inner Sound showing the boundary of Red Rocks and Longay urgent MPA and Red Rocks and Longay pMPA and flapper skate egg case locations. (1) Drop-down video (DDV) survey location (latitude 57.322537, longitude −5.898492) where eight flapper skate egg cases were observed in images recorded on 19 July 2018. (2) DDV survey location (latitude 57.312872, longitude −5.872370) where four egg cases were observed in images recorded on 20 March 2019. (3) Location (latitude 57.323533, longitude −5.921833) from where 'widely spread' flapper skate egg cases were reported by scallop divers on 28 October 2019. (4) Shot line location (latitude 57.33325, longitude −5.927183) for dive site known as 'Red Rocks' where flapper skate egg cases were collected on 4 March 2020 and flapper skate egg cases were collected and a photogrammetry dive was carried out on 5 March 2020. DDV and remote operated vehicle (ROV) surveys also carried out here, site known as X2 BSR 3.

recreational divers of high densities of flapper skate egg cases, and subsequent additional dive surveys and a review of drop-down video (DDV) camera footage collected during previous surveys of the area. Subsequently, following further targeted DDV camera and remote operated vehicle (ROV) surveys across a larger area, the boundary of the Red Rocks and Longay urgent MPA was extended across an area of 12.55 km^2 and became the Red Rocks and Longay possible MPA (pMPA) which went to consultation in February 2022.

The split of the species complex into flapper and common blue skate (Iglésias, Toulhoat & Sellos, 2010) has resulted in difficulty in interpreting earlier literature regarding the reproductive biology of the species. Often it is not possible to know whether authors prior to 2010 are referring to flapper or common blue skate, leading to confusion over the biology of each species. For example, Little (1995) noted egg incubation for the common skate complex as taking 2–5 months, yet in 2021 direct observation of a flapper skate egg case in water ranging from 8 to 13 °C recorded an incubation time of 18 months (Benjamins et al., 2021).

Furthermore, the conditions required for egg development may not necessarily be the same as for the juveniles' continued growth. Skates (family Rajidae) often select habitat that is optimal for developing eggs, with neonates moving to juvenile nurseries shortly after hatching, as shown for Alaska skate, *Bathyraja parmifera* (Hoff, 2008) and longnose skate, *Raja rhina* (Love et al., 2008). Various terms have been used to describe the areas where oviparous elasmobranchs deposit their eggs, including spawning grounds and nurseries (Martins et al., 2018). We follow Hoff (2016) and use the terms 'egg nursery' and 'juvenile nursery' to distinguish between the areas where eggs and juveniles develop, respectively (Hoff, 2008).

Sites used as egg nurseries should provide a suitable habitat for egg development: a relatively stable temperature regime that remains within favourable limits (Hoff, 2010) with sufficient current to oxygenate the embryo as it develops (Leonard, Summers & Koob, 1999) and keep the eggs clear of silt, but not so strong as to move them away from the optimal conditions (Hoff, 2010). These are likely to be areas of low egg predation mortality and high biological productivity to meet the energy requirements of adults (Hoff, 2008; Martin et al., 2012).

Flapper skate have been estimated to lay 40 eggs per year (Brander, 1981). The egg cases consist of a roughly rectangular capsule 100–144 mm wide and 130–235 mm long with four short horns, one at each corner. A keel runs down each of the long sides of the capsule and a thin filament of tissue or 'apron' extends between the two horns at each of the thin ends of the capsule; the apron is wider at the anterior end of the egg case from which the embryo emerges during hatching. Flapper skate egg cases are initially smooth and golden in colour, although the exterior condition deteriorates and the golden layer begins to peel from the surface in 'bark-like' strips running parallel to the keels over time (Ebert & Stehmann, 2013; Gordon, Hood & Ellis, 2019; Benjamins et al., 2021). In the Shetland Isles flapper skate egg cases have been reported in a group of 40 and in Argyll in a group of 20. Around the Orkney islands flapper skate egg cases have been reported on boulder or rocky substrate, at greater than 20 m depth with 'high [surface] current flow' (0.58–5.44 m/s on spring tides) from multiple locations in groups of 1–40 (Orkney Skate Trust, Phillips et al., 2021). However, until now, an egg nursery had not been identified for flapper skate in Scotland.

The static nature of flapper skate egg cases, coupled with their long development time, potentially puts them at risk from activities which disturb the sea bed, such as bottom contact, mobile gear fishing. Therefore, the identification and protection of egg nurseries is required to ensure egg survival and subsequent recruitment (Hoff, 2016). Conservation policy makers have recognized that a lack of knowledge on the early life-history stages of flapper skate (especially the location and habitat characteristics of egg and juvenile nurseries) has thus far prevented spatial protection incorporating all life-history stages of the species (Garbett et al., 2020). To address this knowledge gap, this study investigated reports from commercial scallop and recreational divers of flapper skate egg cases near Sgeir Dhearg in the Inner Sound on the west coast of Scotland. To determine if the site is used as an egg nursery, it was assessed against the criteria for the identification of egg nurseries for oviparous elasmobranchs proposed by Hoff (2016). These criteria recognize an 'egg nursery' as a geographic location where: (1) egg cases are deposited at high densities; (2) egg cases are in contact with the sea bed and are non-mobile; (3) use occurs over more than 1 year; and (4) post-hatching juveniles identify with habitats other than egg nursery habitat.

2 | MATERIALS AND METHODS

2.1 | Study site

The study site is located at the southern end of the Inner Sound, the strait separating the Inner Hebridean Islands of Skye, Raasay and Rona from mainland west Scotland (Figure 1). The bathymetry and distribution of cobble/boulder habitats within the study site were mapped using ArcGIS. The European Nature Information System (EUNIS; Davies, Moss & Hill, 2004) substrate data layers 'moderate energy circalittoral rock' and 'subtidal coarse sediment' were used as a proxy for cobble/boulder habitat. The West Scotland Coastal Ocean Modelling system (WeStCOMS) (Aleynik et al., 2016) was used to investigate spatio-temporal variation in modelled current velocities and bottom temperatures across the Red Rocks and Longay pMPA (see Supporting Information).

2.2 | Egg case collection dives

Two 20 min dives were undertaken at a site north of Sgeir Dhearg known as 'Red Rocks' from MV Skua on 4–5 March 2020 to verify reports of flapper skate egg cases received from scallop divers and recreational divers and to collect egg cases. Both dives began from a shot line placed at 57.33325, longitude −5.92718 in 28.5 m (Figure 1). Divers descended to the sea bed, identified areas where egg cases were present, and collected as many as possible during the bottom time allowed. During dive 1, a pair of divers moving in an approximately south-westerly direction followed a 17 × 4 m transect, covering 68 m^2, collecting all the egg cases they could see within the transect, before surfacing at latitude 57.33313, longitude −5.92737 (Figure 2). During dive 2 the divers moved in an approximately southerly direction from the shot line (Figure 2), collecting all the egg cases they could see. the Dive end position was not recorded for dive 2 for technical reasons. Water depth was between 28 and 39 m for both dives. The divers brought the egg cases to the surface in string bags, which were submerged in holding tanks on the vessel's dive lift before being raised onto the vessel. Egg case density was estimated for dive 1 (as the number of egg cases collected in the estimated area surveyed). Egg case density was classified according to the Marine Nature Conservation Review (MNCR) Super-abundant, Abundant, Common, Frequent, Occasional, Rare (SACFOR) scales (Hiscock, 1996).

2.3 | Egg case characterization

For this study the term 'full egg case' is used for an intact egg containing a viable yolk or embryo and 'empty egg case' for a hatched egg. The term 'egg case' refers to full eggs and empty egg cases collectively. Eggs cases were initially checked to see if they had already hatched by squeezing the keels together at the anterior end to see if they opened. Those that opened were categorized as empty egg cases, those which did not were assumed to be viable and were categorized as full egg cases. The full egg cases were then individually placed in a small plastic aquarium where they were photographed, and their external appearance categorized as undamaged or degraded. The aquarium was placed on a lightbox to examine the internal contents of each full egg case. If the light from the lightbox was inadequate to penetrate the membrane and illuminate the yolk and/or embryo, a brighter light (a dive torch) was used to provide extra backlighting. A photograph and/or short video clip was taken of any visual contents using a Canon IXUS 70. The length of the embryo was estimated by laying a ruler next to the aquarium and the development stage described by comparing the length of the embryo with the length of the capsule (i.e. the length of the egg case minus the horns) of the egg case (approximately 14 cm); larger embryos were curled inside the capsule as they were too long to lie straight. Full egg cases were categorized as either transparent (contents visible with backlight) or opaque (contents not visible using backlight). Transparent full egg cases were further categorized as 'yolk only' if no embryo was visible; 'developing' if a small (≤14 cm length) embryo was observed; and 'well developed' if a large embryo (>14 cm length) was observed. Finally, 0.5 cm^2 of the anterior apron of the egg case was removed and stored in 100% ethanol for future genetic analysis and comparison with reference samples at the University of Aberdeen. Following investigation, full egg cases were returned to the holding tank. When all the full egg cases had been examined (after approximately 5 hours) they were returned to the sea bed by the divers, replacing them into crevices between cobbles and boulders. The empty egg cases were individually bagged, labelled and frozen so that samples can be collected in the future for genetic relatedness analysis.

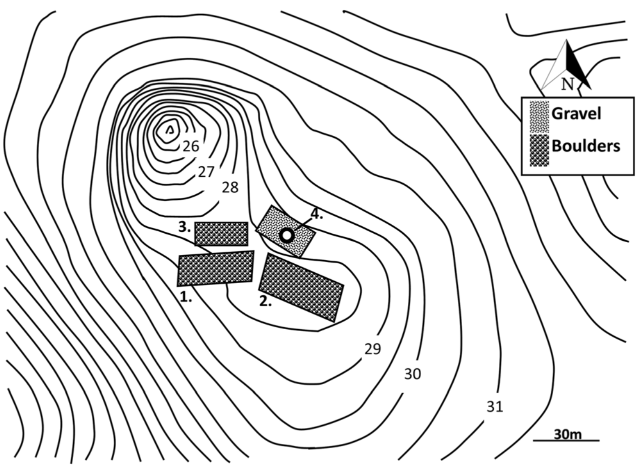

FIGURE 2 Detail of the dive site known as 'Red Rocks' showing collection and photogrammetry survey dive locations; note estimate of dive area is approximate. (1) Collection dive 1, 4 March 2020. (2) Collection dive 2, 5 March 2020. (3) Photogrammetry survey dive 3, 5 March 2020. (4) Shot line on coarse sand/gravel.

2.4 | Photogrammetry

During a dive on 5 March 2020 an area of sea bed measuring 55 m^2 to the west of the shot line where egg cases had not previously been disturbed was photographed for photogrammetry using a Sony RX100 MkV and paired Weefine 3600 lumen video lights (Figure 2). This area was selected because it was adjacent to where the egg cases were collected and it was visually determined by the divers as having the same characteristics and as having egg cases present.

The imagery collected was processed using Agisoft Metashape V1.6.2 to produce a high-resolution point cloud, mesh and digital elevation model for orthomosaic generation and complexity analyses (rock size/crevice-volume distribution) using Gwyddion (http://gwyddion.net/). Cobbles and boulders were characterized using grain size analysis and classified using the MNCR methodology (Hiscock, 1996), which follows the Wentworth scale (cobble, >64–256 mm; boulder, >256–4,069 mm). Rugosity of the entire 55 m^2 was calculated using the arc–chord ratio rugosity index (Du Preez, 2015) from the surface area measurements within Metashape. The volumes of skate egg cases observed within the survey site were calculated within Metashape using the 'measure area and volume' mesh analysis tool and compared with the crevice volume distribution calculated by Gwyddion.

2.5 | Remote surveys

Drop-down video images ($n = 267$) collected during a previous survey searching for Priority Marine Features in the Inner Sound in 2018–19

(O'Dell et al., 2020; Pasco et al., 2021; Shucksmith, Shelmerdine & Shucksmith, 2021) were reviewed to check for the presence of skate egg cases. Following this review, the egg case collection and photogrammetry dives in March 2020 ($n = 3$) and examination of the bathymetry and substrate type in the area, the Red Rocks and Longay urgent MPA was designated in March 2021. In July–September 2021 further DDV ($n = 242$, July–August 2021) and ROV surveys ($n = 18$, September 2021) were used to search for egg cases more comprehensively within the urgent MPA (6.06 km^2), on the shallow bedrock plateau around the urgent MPA (22 km^2) and in the area north of the Crowlin Islands (1.5 km^2; Figure 1). Based on the observations from the egg case collection dives and reports of flapper skate egg cases elsewhere in Scotland (Phillips et al., 2021), the DDV surveys were preferentially targeted on cobble/boulder habitat in depths of 20–50 m (Figure 1). However owing to the patchy nature of the seabed substrata, DDV drifts encompassed a variety of benthic substrates (including cobble/boulder, shell gravel, mixed sediments and maerl) in depths of 23–65 m. Following O'Dell et al. (2020), at each station a high-definition video camera in a waterproof housing and steel frame with lights and a stabilizing fin attached was deployed by winch from a vessel. The camera was lowered until the sea bed was visible on a surface viewer and the start position recorded. The vessel was allowed to drift, and its position was recorded every 30 s for 5 min (over 5.5–299 m) at which point the end position was recorded and the camera was winched back onto the boat. A total distance of 2,675 m was surveyed in this way. The video footage was viewed to count the number of egg cases, calculate a metric of egg case density (the number of egg cases per unit distance) and categorize the substrate visually as cobble/boulder, maerl, shell gravel and mixed sediments. It was not possible to estimate egg case density in terms of the number of egg cases per unit area from the video collected during the DDV drifts since the camera was not equipped with lasers to define the width of the video swathe and it was impossible to estimate the width of the swathe owing to the different heights above the sea bed at which the camera had to be deployed to avoid snags and collisions.

On 1 and 2 September 2021 an ROV was deployed at 18 locations, including one station where egg cases had been observed previously by diving and DDV, seven locations where skate egg cases had been observed previously in DDV images, four locations that had been surveyed by DDV drifts but egg cases had not been observed and six locations that had not been surveyed previously. In each survey, the ROV was flown at depths of 23–40 m approximately 1 m from the sea bed (±0.3 m), with the camera facing forwards viewing a distance of approximately 5 m. The width of the field of view was approximately 2 m. The number of egg cases present in the video images collected by the ROV were counted and the substrate described as above. Care was taken during the video analysis not to recount egg cases if the ROV was flown over the same area twice. The time at which egg cases were observed and the time at which egg cases ceased to be observed during each flight were recorded, which allowed the track distance between egg cases being observed and eggs ceasing to be observed to be calculated (i.e. the distance travelled over patches of egg cases). Egg case density was estimated from video footage collected by ROV flights as the number of egg cases observed over the area surveyed (track length × estimated field of view). The total area surveyed by ROV was 12,104 m^2. In order to examine within-transect (i.e. small-scale) variability in egg case densities, densities for sections of the ROV flight during which the most egg cases were observed (010921bROV) were estimated by counting the number of egg cases in sections of the flight (e.g. egg cases were first observed at time code 2 min 45 sec and ceased to be observed at 9 min 20 sec, started to be observed again at 12 min 30 s and stopped at 17 min 47 s etc.) over the area surveyed during that time period. Linear modelling was used to examine the relationship between egg case counts and surveyed area (see Supporting Information §2). A bootstrapping approach was used to estimate the area within which different numbers of egg cases would be found; we specifically estimated the area expected to contain 80 egg cases because this is the minmum number of egg cases required in an area to indicate use by multiple females and/or over multiple years, assuming a fecundity of 40 eggs (Brander, 1981; see Supporting Information Section 2).

2.6 | Egg case site characteristics

Bathymetry, sediment type and hydrodynamic conditions were characterized across all sites where egg cases were observed ($n = 31$), as for the study site at large (see Section 2.1), to examine the conditions in the sites in which egg cases were located relative to background variation (see Supporting Information Section 1).

3 | RESULTS

3.1 | Study site characteristics

The study site is a roughly rectangular, shallow (20–86 m) bedrock plateau of around 22 km^2 which extends from the north-east coast of the Isle of Scalpay (Figure 1). GIS mapping of substrates associated with cobble and boulder habitat in the area revealed a patchy distribution of these substrates covering approximately 30% of the shallow bedrock plateau (Figure 1). Across the pMPA, the modelled bottom temperature ranged from a minimum of 9 °C in April to a maximum of 12 °C in September (annual mean = 10.5 °C; Figure S1). Modelled near-bottom current speeds varied between 0.00 and 0.40 (mean = 0.04 ± 0.03 interquartile range) m^{-1} without any pronounced seasonality.

3.2 | Egg case counts and densities

Egg case counts and densities were generated from egg case collection dives (Figure 1, yellow dots), a photogrammetry dive and remote (DDV (Figure 1, green dots) and ROV (Figure 1, blue dots)) surveys. During the two egg case collection dives, a total of 45 full egg cases and 22 empty egg cases were collected: 27 full egg cases and 12 empty egg cases during dive 1; and 18 full egg cases and 10 empty egg cases during dive 2. Egg case density for dive 1 was estimated as 0.57 eggs cases m^{-2} (39 egg cases/68 m^2 searched area) which equates to Common on the MNCR SACFOR abundance scales (Hiscock, 1996). Ten egg cases were counted in the 55 m^2 area of sea bed analysed using photogrammetry images, resulting in an estimated egg case density of 0.18 eggs cases m^{-2} (Common). The distribution of eggs cases observed using photogrammetry was consistent with the divers' *in situ* observations that egg cases were not evenly distributed but located between the cobbles and boulders in clusters at all developmental stages from newly laid to empty and deteriorating (Figure 4).

In the remote surveys carried out in the Inner Sound in 2018 and 2019, only two clusters of egg cases were observed in 267 (0.75%) locations sampled by DDV (O'Dell et al., 2020; Pasco et al., 2021; Shucksmith, Shelmerdine & Shucksmith, 2021). One cluster of eight egg cases was observed at latitude 57.32254, longitude −5.89849 (Marine Scotland, Loch Alsh and Inner Sound benthic camera survey, 2018, Station 48) and one cluster of four egg cases at latitude 57.31287, longitude −5.87237 (Marine Scotland Inner Sound benthic camera survey, 2019, Station 140).

In the 2021 survey of the 22 km^2 shallow bedrock plateau, eggs cases were observed in 33 of the 260 (12.69%) locations sampled by DDV. The number of egg cases per single DDV drift varied from 0 to 119 and totalled 498 egg cases (Table S1). In the subsequent ROV survey egg cases were observed in 12 of the 18 (66.67%) ROV flights (Figure 1, Table 2). Egg case numbers ranged from 0 to 182: 0–40 egg cases were observed in three flights; 41–80 egg cases were observed in three flights; 81–120 egg cases were observed in two flights; and 120+ egg cases were observed in four flights (Figure 1). Linear modelling of the relationship between egg counts and surveyed areas for the ROV data resulted in an estimated gradient parameter of $\beta =$ 0.10 [0.07–0.13] egg cases m^{-2} (Figure S3). The estimated area containing the threshold number of egg cases (80) was 818 (598–1,140) m^2. The total number of egg cases observed in the ROV flights was 1,031 (Table S2). In total 22 stations, 674.80 m on the shallow bedrock plateau, were surveyed by DDV and 12 stations, 104 m^2 (0.00055%), were surveyed by ROV.

In the locations that were surveyed using multiple techniques, there were clear differences in the number of egg cases identified by the different techniques. At station 'X2, BSR, 3', the divers collected 67 egg cases during two 20 min dives, while 24 egg cases were counted in a DDV drift (distance = 188.5 m) and 115 egg cases were counted via ROV survey (distance = 1,009 m, area surveyed 2,018 m^2). In the eight locations surveyed using both DDV and the ROV, 50% of the DDV surveys underestimated the number of egg cases counted using the ROV when the shorter track length of the DDV surveys was accounted for (Table S3).

Estimated flapper skate egg case density ranged from 0.01 egg cases m^{-2} (Frequent) to 0.25 egg cases m^{-2} (Common) in the ROV flights where egg cases were recorded (Table 1 and Table S2). It was

TABLE 1 Summary of egg case numbers and density recorded using each survey method: scuba diving, drop-down video (DDV) and remote operated vehicle (ROV)

Survey	Number of locations surveyed	Surveyed distance (m) or area (m^2)	Number of locations with egg cases	Minimum number of egg cases observed	Maximum number of egg cases observed per survey	Total number of egg cases observed across all surveys	Egg case density (m^{-2})	MNCR SACFOR scales description
Egg case collection dives	2	68 m^2 (dive 1) unknown (dive 2)	2	28	39	67	0.57	Common
Photogrammetry dive	1	55 m^2	1	–	–	10	0.18	Common
DDV camera footage (2018–2019)	267	–	2	0	8	12	–	–
DDV camera footage (2021)	242	22,675 m	33	0	119	498	–	–
ROV footage (2021)	18	9,966 m^2	12	0	182	1,031	0.10	Common
Total						1,618		
Corrected (highest count used where two methods were used to survey the same site)						1,395		

TABLE 2 Change in egg case counts and densities during ROV flight 010921bROV

Time code for skate egg cases	Flight track distance	Estimated area surveyed (m^2)	Number of egg cases observed	Egg case density (m^{-2})	MNCR SACFOR scales description
02:45–9.20	89.50	179	100	0.56	Common
12:30–17:47	88.00	176	13	0.07	Frequent
26:43–30:12	48.00	96	55	0.57	Common
32:10–33:20	16.00	32	10	0.31	Common
35:00–35:45	23.00	46	4	0.09	Frequent

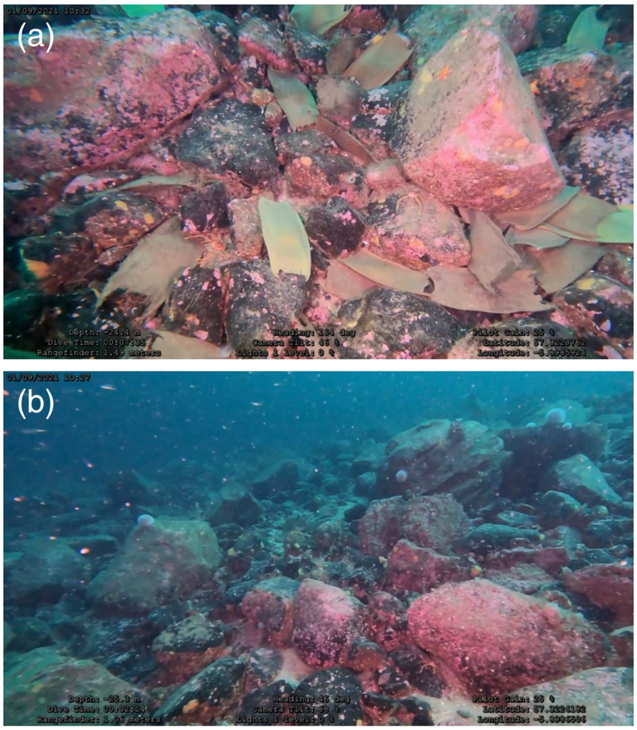

FIGURE 3 Two images from ROV flight 010921bROV at different time codes showing (a) high density of egg cases (19 in an estimated area of 2 × 5 m; therefore 10 m^2 = 1.9 egg cases m^{-2}, Abundant) and (b) no egg cases present.

not possible to tell from the images whether the observations were of full or empty egg cases. Visual examination of the videos collected during ROV flights showed that egg case density varied within ROV flights when cobble/boulder habitat was continuous. For example, during the ROV flight 010921bROV in which the most egg cases were observed (182 in total), egg case density varied from 0.00 to 0.57 m^{-2} (Table 2 and Table S2). At instances during this ROV flight egg case density was higher (e.g. at 7 min 35 s, 1.9 egg cases m^{-2} (Abundant), 19 egg cases in the estimated field of view (2 × 5 m = 10 m^2), Figure 3a) and at some instances no egg cases were observed (e.g. 2 min 14 s, Figure 3b) despite the habitat being cobble/boulder throughout this ROV flight. Egg case densities were highest on the tops and flanks of raised areas of boulders – geological features known as boulder moraine belts.

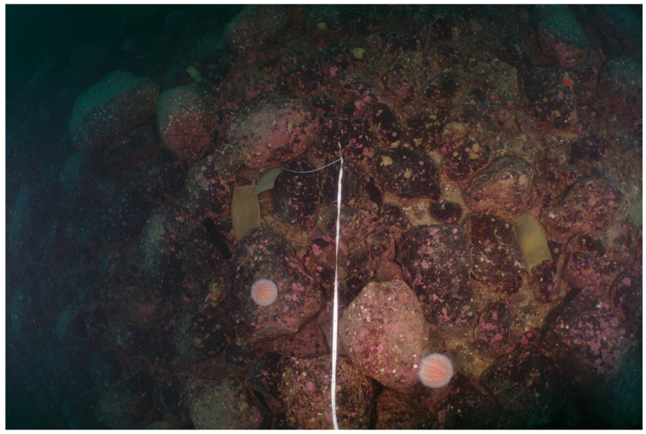

FIGURE 4 Photograph of the flapper skate egg nursery habitat in the Inner Sound, Scotland, taken for the photogrammetry survey with egg cases visible *in situ*.

3.3 | Egg case habitat characteristics

During the egg case collection dives, all egg cases were observed at a depth of 28–39 m on cobble/boulder habitat with low sedimentation (Figure 4). The photogrammetry revealed a rugosity index (Du Preez, 2015) of 1.7 within the 55 m^2 sampled area, with 6,200 crevices in excess of 10 cm^3, predominantly between 100 and 500 cm^3, mean volume = 256 ± 150 cm^3 standard deviation (Figure 5). Similarly, in the DDV surveys in 2018/2019, egg cases were observed on cobble/boulder habitat at depths of 25 and 27.5 m. In the DDV surveys in 2021, egg cases were exclusively identified on boulder/cobble substrate at depths of 29–58 m. In the ROV surveys, egg cases were identified at depths between 17 and 40 m in 12 (67%) of the flights that passed over cobble/boulder habitat but none of the flights (n = 3) that passed over other habitat types (i.e. maerl bed, flame shell bed, mixed coarse sediments). Across all locations at which egg cases were located, bottom temperature and current velocity predictions were similar to those predicted across the pMPA at large (Figure S2).

3.4 | Egg case characterization

Based on the egg case samples collected from the two egg case collection dives, examination using backlighting of the 45 full egg

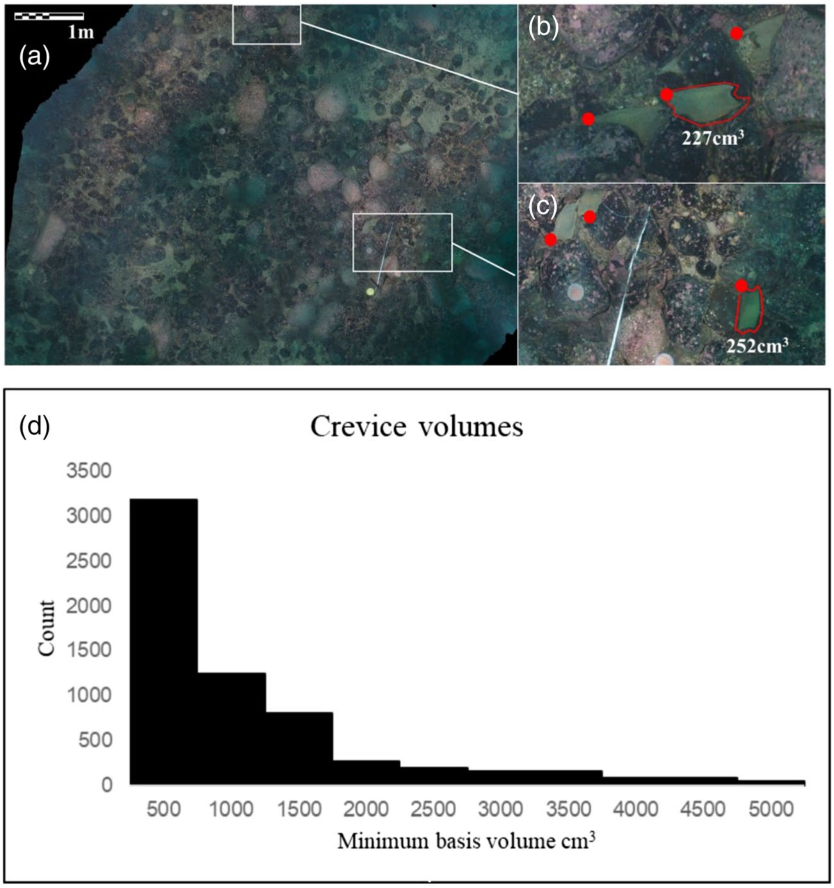

FIGURE 5 (a) Orthomosaic of a representative section of the egg nursery, derived from photogrammetry. (b) Egg case cluster lodged in crevices, featuring smallest measured egg case. (c) Egg case cluster featuring the largest measured egg case. (d) Crevice volumes between 100 and 5,000 cm^3 in a 25 m^2 subsample, derived from inverse grain-size analysis via Gwyddion.

TABLE 3 Summary description of 45 full flapper skate egg cases collected at the dive site known as 'Red Rocks' on 4 and 5 March 2020.The full egg cases were categorized as follows: transparent/opaque depending on how easy it was to observe the contents on the light box; undamaged/degraded depending on the external appearance and yolk only; developing or well developed depending on what could be observed internally by placing the egg on a light box or shining a bright diving torch through it

	Description of egg case contents			
Description of egg case	Empty	Yolk only	Developing	Well-developed
Transparent, undamaged	0	23	1	0
Transparent, damaged	0	2	0	0
Opaque undamaged	0	1	0	0
Opaque degraded	0	0	3	15

cases showed that 27 contained yolk only, four had developing embryos (≤14 cm) and 14 had well-developed embryos (>14 cm, Table 3). The mean volume of the egg cases observed during the photogrammetry dive was 235 ± 19 cm^3 standard deviation.

The external appearance of the full egg cases varied. Some were smooth, golden and curled at the horns. These were also transparent (it was easy to observe the contents on the lightbox) and contained only yolk (Figure 6a, b). In the dark coloured, opaque, full egg cases, developing embryos (≤14 cm) were observed, and some of their features could be identified, including moving tails (Figure 6c, d) or wing tips.

The exterior fibrous material had begun to split or peel on some full egg cases. Embryos >14 cm which were curled up in the capsule with moving tails (Figure 6f), pelvic fins (Figure 6g, h) and the tip of the rostrum visible (Figure 6i, j) could be observed in the full egg cases with more degraded exteriors. Two out of the 45 full egg cases collected at Red Rocks had potential predators attached (spiny starfish *Marthasterias glacialis*). None of the full egg cases or empty egg cases were excessively fouled; only one full egg case (EGL10) had fouling visible to the naked eye—a worm tube (Figure 6j). The empty egg cases were in a much more degraded state; some had lost all their external bark and were almost entirely black and others had begun to break up into pieces.

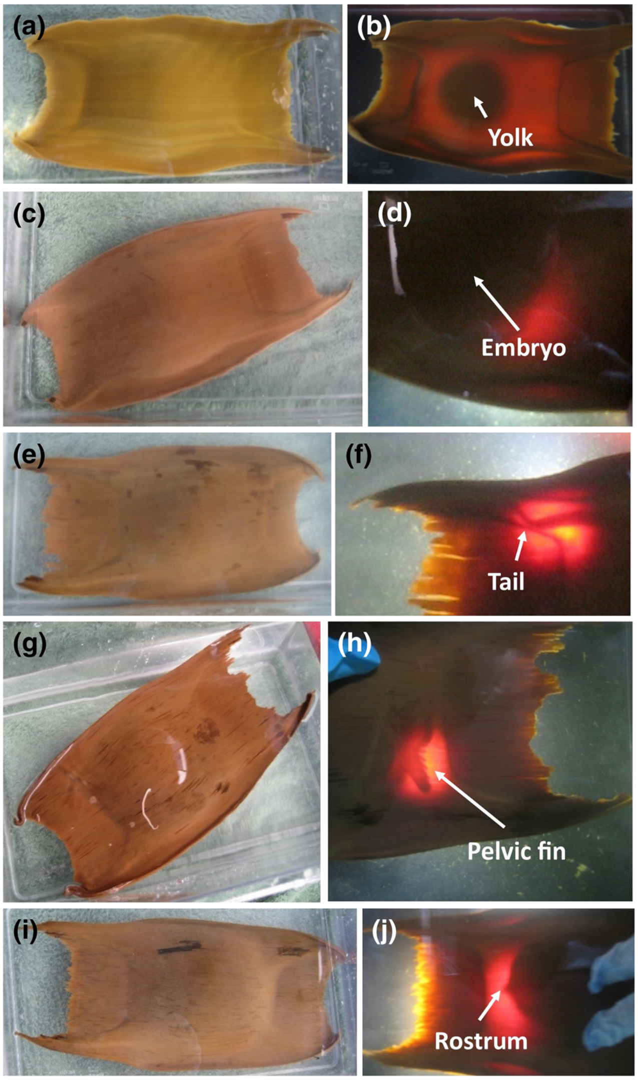

FIGURE 6 Photos of full egg cases at different stages of development. (a, b) Development stage category 1, yolk only. (c, d) Development stage category 2, developing embryo visible. (e, f) Development stage category 3, well-developed embryo visible, tail visible. (g, h) Development stage category 3, well-developed embryo visible, pelvic fin visible. (i, j) Development stage category 3, well-developed embryo visible, rostrum visible.

4 | DISCUSSION

This study describes the first known egg nursery for the flapper skate *Dipturus intermedius* anywhere and its characteristics: a cobble/boulder habitat in water 25–58 m deep with an annual temperature range of 9–12 °C, current speeds of up to 0.2 m^{-1}, a rugosity index of 1.7 and low sedimentation. In total, 1,618 egg cases were counted in 267 DDV drifts (2018/2019, $n = 12$ egg cases) two egg case collection dives ($n = 67$), one photogrammetry dive ($n = 10$), 242 DDV drifts (2021, $n = 498$ egg cases) and 18 ROV flights ($n = 1,031$ egg cases). Accounting for overlapping surveys, 1,395 egg cases were identified at 31 of the 513 locations surveyed across the study area. Although the pMPA and the wider region have been extensively surveyed in the last 5 years, it is likely that a number of egg cases were missed owing to the extent of cobble/boulder habitat, its patchy distribution and spacing of the camera drops. Taken together, these results point towards the use of the Red Rocks and Longay pMPA as an egg nursery for flapper skate that requires the highest possible level of protection from potentially damaging activities through strict control measures.

Red Rocks fulfils three of the four criteria for the identification of an elasmobranch egg nursery as defined by Hoff (2016). The first of these criteria is a 'geographic location where eggs are deposited at high densities'. A SACFOR density of Common or above has been suggested to characterize skate egg nurseries (Henry et al., 2016; Phillips et al., 2021). In this study, egg cases were described on cobble/boulder habitat at estimated densities of 0.57 egg cases m^{-2} (Common) during dive 1, 0.18 egg cases m^{-2} (Common) in the photogrammetry dive and from 0.01 (Frequent) to 0.25 (Common) egg cases m^{-2} in the ROV flights. These results suggest that Hoff's (2016) 'high density' criterion should be qualified by the number of egg cases identified in a survey and the area over which they are distributed. For example, while egg cases were classified as Common on the first survey dive, the relatively small number of egg cases ($n = 39$) and the small area (68 m^2) surveyed suggest that an assessment of Common alone is insufficient to define an egg nursery. Hence, it would be useful to refine Hoff's (2016) 'high-density' criterion on a species-specific basis that recognizes female fecundity and the habitats used for egg laying. For the common skate complex, fecundity has been estimated as 40 eggs per year (Brander, 1981). It is possible that female skate return to the same site year on year to lay eggs in a similar way to lemon sharks (*Negaprion brevirostris*) returning to their natal nursery area (Feldheim et al., 2014). Therefore the presence of ≥80 eggs cases suggests the site is likely to have been used by at least two females and/or over multiple years. Linear modelling of the ROV results shows that the expected area of suitable habitat required to contain ≥80 egg cases is 818 m^2. Thus, for flapper skate the results suggest that at a minimum candidate egg nurseries for flapper skate should contain ≥80 egg cases and span ≥818 m^2 (density category Common). However, further research on flapper skate fecundity and philopatry, genetic relatedness analysis, the efficacy of different sampling techniques and the frequency with which a site is actively visited for egg laying would support refinement of this suggestion. For example, the relatively low efficacy of DDV surveys compared with diver and ROV surveys, the apparent rarity of flapper skate egg nurseries in Scotland and their importance for flapper skate conservation suggest that smaller numbers of egg cases in a single DDV drift may be sufficient to warrant further investigation of an area.

Furthermore, elsewhere, larger areas may need to be surveyed in order to identify flapper skate egg nurseries (given the patchiness in the distribution of egg cases and uncertainty over the wider applicability of these results) and quantify their relative importance (with egg nurseries sites containing thousands of egg cases, as identified here, likely to be more important for flapper skate than sites with fewer egg cases). Patchy distributions of egg cases within a defined egg nursery have been documented in other skate species. For example, in the longnose skate (*Beringraja rhina*), 'clumps' of egg cases (1,740 egg cases in all) were identified across an area of

2,552 m^2 (Love et al., 2008). Similarly, in a study on the deep-water skate (*Bathyraja richardsoni*) highly localized concentrations of egg cases (peak density 0.21 m^{-2}) were identified across a 3,283 m^2 area surveyed (Henry et al., 2016). In this study, there was notable patchiness in the distribution of egg cases, with a complete absence of egg cases in some locations and up to 182 egg cases in others. For spatial management, this means that protection of relatively small areas (spanning hundreds of square metres) is likely to deliver the preservation of a portion of the egg cases found in an area, but protection over larger areas (spanning tens of kilometres) are likely to be required to safeguard an egg nursery in its entirety.

In other locations in Scotland, discrete clusters of flapper skate egg cases have been documented in specific locations but egg case densities have not been estimated. For example, in Shetland egg cases have been reported in a group of 40 and in Argyll in a group of 20. In Orkney egg cases were reported in six discrete groups of ≥10 (including one group of 40 egg cases) between 2006 and 2022 on cobble/boulder habitat a minimum of 3 km apart (Orkney Skate Trust; Phillips et al., 2021). Whilst the groups of egg cases reported in Orkney have not been fully assessed against Hoff's (2016) criteria (Phillips et al., 2021), the high numbers of flapper skate egg cases washed ashore in Orkney suggest that egg cases may be deposited in high numbers but in a more dispersed way or that an egg nursery is alluringly close. Further seabed surveys of the intensity presented here and investigation of the habits of adult skate in the area are required to confirm or eliminate the presence of a flapper skate egg nursery.

The second of Hoff's (2016) criteria, 'the habitat is benthic and eggs are contacting benthic or stationary materials (i.e. non-mobile on a large scale)', is met at Red Rocks since the egg cases were observed lying between cobbles and boulders. Skate species are known to actively select habitats to optimize embryo development (Hoff, 2008). It is possible that cobble/boulder habitats are chosen for the deposition of egg cases by female flapper skate because the high surface rugosity of these habitats (1.7 in this study, which is similar to highly structurally complex coral reefs; Holmes, 2008) helps to retain the egg cases in suitable conditions, with the egg cases catching in crevices if exposed to currents or wave action. While predicted maximum near-bottom current speeds suggest that this consideration may be limited in the Red Rocks and Longay pMPA, micro-topographic features that are not captured by WeStCOMS may have a significant influence on currents near the sea bed and therefore the conditions experienced by skate egg cases warrant further investigation. Indeed, in other sites, including those observed in Orkney, where much higher surface current speeds reported by admiralty charts suggest elevated near-bottom speeds (Phillips et al., 2021), the selection of high-rugosity sites may be more important. At Red Rocks, the presence of skate egg cases in rock crevices only slightly larger in volume to egg cases could reduce exposure to predation, in a similar way to longnose skate (*R. rhina*) depositing their egg cases on sponges (Love et al., 2008).

In temperatures comparable with those in the study area, flapper skate egg cases take 18 months to develop to hatching ($n = 1$, Benjamins et al., 2021), therefore the egg cases with well-developed embryos ($n = 15$) probably have been on the sea bed for between 12 and 18 months and the empty egg cases ($n = 22$) a minimum of 18 months and some much longer given the state of their degradation. In addition, egg cases at different development stages (yolk only, developing, well developed and hatched) were observed at the time of the egg case collection dives in March 2019, confirming that the site was used for egg laying at that time and that multiple cohorts of flapper skates were developing simultaneously. This satisfies Hoff's third criterion, 'sites are used over multiple years'. Hoff's (2016) fourth criterion 'post-hatching juveniles identify with habitats other than egg nursery habitat' is possible since no juvenile or adult skate were observed during the dives, the DDV surveys or ROV surveys conducted or reported by commercial or recreational divers to the authors. In the Loch Sunart to the Sound of Jura MPA, juvenile skate have been recorded outside of any known egg nursery, demonstrating that Hoff's (2016) fourth criterion is met in other locations. Little is known about the habitat preference of neonate flapper skate, but limited evidence from the west coast of Scotland has recorded neonatal skate on mud habitats in 50–100 m of water (MEFS project, unpublished data). This suggests that juvenile skate may move away from the cobble/boulder habitat favoured for egg laying after hatching. Nevertheless, in this study it also is possible that juvenile (and adult) skate were disturbed by divers, DDV cameras and ROVs, and further surveys, including stationary remote underwater video deployments, are required to evaluate the extent to which juveniles remain in the egg nursery habitat or move elsewhere.

The depth distribution of egg cases documented in this study is consistent with previous studies of vertical movement in adult flapper skate. The water depths of the egg nursery are towards the shallower limit of the depth range of adult flapper skate studied on the west coast of Scotland (Neat et al., 2015; Thorburn et al., 2021; Lavender et al., 2021b). Mature female flapper skate spend more of their time in water shallower than 50 m during the winter (November–April) and it is possible that this is linked to egg laying (Thorburn et al., 2021; Lavender et al., 2021b). Water temperature has been shown to affect the incubation time of elasmobranch eggs (Hume, 2019) and it is possible that females deposit their egg cases in shallower water to benefit from warmer summer water temperatures, which may decrease the overall incubation period (Benjamins et al., 2021). Further investigation into the timing of egg laying in flapper skate is required to evaluate this hypothesis. A similar, although more extreme, example of skate selecting thermally optimal habitats is the Pacific white skate, *Bathyraja spinosissima*, which uses the warmer waters around active hydrothermal vent fields to accelerate the incubation periods for its eggs (Salinas-de-León et al., 2018). However, the distribution of egg cases documented within the study site may also have been influenced by the depth of surveys, which occurred between 22.7 and 65 m.

Adult skate have been shown to use depths of 100–150 m (Neat et al., 2015; Thorburn et al., 2021). Therefore the close proximity of the egg nursery at Red Rocks and Longay pMPA to the deep (150+ m) channel, running roughly north west to south east between the Isle of Longay and the Crowlin Islands may be advantageous to sexually mature female flapper skate as they would expend little energy travelling to the egg nursery from their preferred habitat in order to lay eggs.

The flapper skate egg nursery identified at Red Rocks shares similar physical characteristics to those described for deepwater skates (Hitz, 1964; Etnoyer & Warrenchuk, 2007; Hoff, 2008; Love et al., 2008; Quattrini, Partyka & Ross, 2009; Hoff, 2010; Hunt, Dhugal & Raushan, 2011; Treude et al., 2011; Serra-Pereira et al., 2014; Henry et al., 2016; Hoff, 2016), which are located on seamounts and shelf breaks close to deeper water. It has been suggested that these characteristics provide favourable conditions of egg case ventilation for successful incubation (Treude et al., 2011). The flapper skate egg nursery at Red Rocks shares a further similarity to the egg nursery of the longnose skate (*R. rhina)* described by Love et al. (2008) as having 'significantly more eggs over the highest relief [shallower] areas'. Stewart, Cooper & Lewis (2022) described boulder moraine belts 'commonly 2–5 m in height, 10–20 m wide and 80–380 m in length' on the sea bed in the Red Rocks and Longay pMPA and egg case density was observed to be highest on the tops and flanks of these structures in ROV flights. These localized elevated areas may be selected to help deliver optimal current conditions for ventilation of egg cases for successful incubation in a similar way to oviparous deep-water sharks which are reported to preferentially deposit their egg cases on elevated colonies of octocorals and gorgonians (Etnoyer & Warrenchuk, 2007).

The protection of egg nurseries can support the conservation of oviparous elasmobranchs, particularly as egg nurseries often cover a much smaller area than that required for the protection of the adult life stage of large mobile species (Kinney & Simpfendorfer, 2009). The description of the first flapper skate egg nursery in this study through the deployment of multiple survey methods will inform the search for other egg laying sites and the classification of further egg nurseries. Continued research on the conditions at Red Rocks and Longay pMPA will support this search by refining our understanding of the characteristics of the only known egg nursery. In particular, the collection of *in situ* environmental data (e.g. using current velocity meters), the development of a nested (fine-scale) hydrodynamic model for the study area and further surveys at Red Rocks and Longay pMPA would support the development of habitat preference models and the identification of other egg nurseries. For future surveys, drop cameras provide a means to survey areas relatively quickly but are likely to underestimate the number of egg cases present compared with divers and ROV flights. In this study, the ROV was the most effective method for recording egg cases perhaps because the locations for ROV surveys were selected following previous DDV surveys and the ROV can be directed over areas where highest egg case density is observed rather than drifting with currents or wave or wind action. In addition, the ROV footage was very high resolution and ROV flights are suited to producing egg case density estimates.

However, a successful conservation strategy requires protection across all life history stages of a species (Kinney & Simpfendorfer, 2009), particularly strongly K-selected species such as flapper skate (Ellis et al., 2021). Off the west coast of Scotland, flapper skate show high levels of site affinity to particular areas (Neat et al., 2015; Lavender et al., 2021a); therefore if areas containing habitats important for all life history stages (eggs, juveniles and adults) could be identified and protected, this could deliver important conservation benefits for the species. Thus far, an egg nursery or juvenile nursery have not been identified within the Loch Sunart to the Sound of Jura NCMPA which was designated for the presence of adult skate. While flapper skate are capable of making long-range movements (Little, 1995; Lavender et al., 2021a), very heavily pregnant females have also been observed within the Loch Sunart to the Sound of Jura MPA (Benjamins et al., 2021) suggesting that there is an egg nursery within or close to the site. Analysis of the genetic samples collected at Red Rocks and Longay and comparison with reference samples from around Scotland (held by the University of Aberdeen) would help define the degree of genetic connectivity between eggs laid at Red Rocks and Longay pMPA and adults in Loch Sunart to the Sound of Jura NCMPA. Given the number of MPAs for flapper skate in Scotland ($n = 2$), their spatial separation (70+ km shortest straight-line distance over land and sea between the two sites) and their differences in size and the habitat protected, expanding the coverage of protected areas and improving their connectivity should be a priority for future research and recovery of the species. Building on this study and previous work (Thorburn et al., 2021; Lavender et al., 2021a), a key knowledge gap for future research remains establishing the movements of juveniles and the identification of sites for their protection.

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CONFLICT OF INTEREST

There are no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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