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Seamount egg-laying grounds of the deep-water skate *Bathyraja richardsoni*

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Highly localized concentrations of elasmobranch egg capsules of the deep-water skate *Bathyraja richardsoni* were discovered during the first remotely operated vehicle (ROV) survey of the Hebrides Terrace Seamount in the Rockall Trough, north-east Atlantic Ocean. Conductivity–temperature–depth profiling indicated that the eggs were bathed in a specific environmental niche of well-oxygenated waters between 4.20 and 4.55° C, and salinity 34.95–35.06, on a coarse to fine-grained sandy seabed on the seamount's eastern flank, whereas a second type of egg capsule (possibly belonging to the skate *Dipturus* sp.) was recorded exclusively amongst the reef-building stony coral *Solenosmilia variabilis*. The depths of both egg-laying habitats (1489–1580 m) provide a *de facto* refuge from fisheries mortality for younger life stages of these skates.

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Global conservation of sharks, skates and rays is hampered by the stark lack of knowledge of deep-sea elasmobranchs in waters beyond the continental shelf (Kyne & Simpfendorfer, 2010), with 57.6% of deep-sea chondrichthyans listed by the IUCN as Data Deficient (Dulvy *et al.*, 2014).

Seamounts in the deep sea are often thought of as megafaunal hotspots, attracting animals such as sharks, tuna and cetaceans that forage, refuge and mate in the area (Morato *et al.*, 2010). As technology such as baited photo-landers, remotely operated vehicles (ROV) and autonomous underwater vehicles (AUV) become standard tools, seamount exploration offers new opportunities for observing deep-sea elasmobranch behaviours *in situ* that can deepen understanding of habitat associations.

There are three seamounts in the Rockall Trough west of the British Isles. The first ROV investigation of the southernmost seamount, the Hebrides Terrace Seamount

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(HTS), was conducted in 2012 (Roberts *et al.*, 2013). The HTS rises from depths of *c.* 2300 m to its summit at *c.* 1000 m. Exploration of the seamount's summit to its deep flanks revealed a transition in the physical and chemical oceanography (Findlay *et al.*, 2014) and in megafaunal communities and habitats (Henry *et al.*, 2014). A number of priority marine features (PMF; JNCC, 2012) of conservation importance to Scotland, U.K., occur on the HTS, including seamount communities and coral gardens and records of deep-sea sponge aggregations and reef framework-building cold-water corals. These studies and U.K. Government assessments provided the evidence to establish most of the HTS as a marine protected area (MPA), the remaining portion being in the Republic of Ireland's exclusive economic zone (EEZ; JNCC, 2014). Consideration of management options is underway to protect the seamount's biological communities from otter trawling and line fishing, activities that occur on the HTS slopes down to around 1400 and 1500 m, respectively (JNCC, 2014).

The ROV investigation also revealed egg-laying grounds for at least two species of oviparous deep-sea elasmobranchs (Henry *et al.*, 2014). Records of deep-water elasmobranch egg-laying ground occurrences are extremely rare, yet these observations are vital to underpin the spatial management of deep-sea features like seamounts, where human activities, such as bottom trawling, affect species and their habitats. The subjects of the present study were the taxonomic identity of the egg capsules, their stages of embryonic development and the environmental setting of the egg-laying habitats.

The ROV surveys were conducted during the 2012 R.R.S. *James Cook* Changing Oceans Expedition cruise 073 in May to June (Roberts *et al.*, 2013; Fig. 1). Three dive transects (numbers 035, 036, 037) were conducted using the Irish Marine Institute's Holland-I, a work class Quasar ROV manufactured by Soil Machine Dynamics Ltd (www.smd.co.uk). Holland-I was equipped with two manipulator arms, an Insite Mini Zeus video camera (Insite Trittech Inc.; www.insitetrittech.com) with direct high-definition serial digital interface (HDSDI) fibre output, a Kongsberg 14-208 digital stills camera (Kongsberg Maritime; www.km.kongsberg.com), two 400 W SeaArc2 HMI lights (Deep-sea Power & Light; www.deepsea.com), two 25 000 lument APHOS LED lights (Cathx Ocean; www.cathxocean.com) and two lasers indicating a distance of 10 cm apart (Deep-sea Power & Light).

The present study focussed mostly on ROV Dive 037 on the eastern flank of the HTS (Fig. 1). Dive 037 completed a transect 3283 m in length, in waters 1005–1648 m deep. Besides ROV video imagery [Fig. 1(d)], the ROV collected five egg capsules. These were stored in 10% buffered formalin. Three of these capsules were still intact and not hatched (Table I). All capsules were transferred to 70% industrial methylated spirit 1 month later in the laboratory for long-term storage, with two of the intact capsules studied in detail and dissected for analyses of their contents (Table I). These two capsules were deposited and catalogued at the Zoological Museum, Hamburg University, under the Ichthyology Department collection number ZMH 26156.

ROV video was analysed using QuickTime Pro 7 (Apple Inc.; www.apple.com). Dive 037 had a time of 8 h 55 min. The lasers with 10 cm spacing were used to estimate seabed area. The seabed bottom type was constant throughout Dive 037 in areas with eggs, consisting mostly of coarse to fine-grained sands with occasional cobbles.

Conductivity–temperature–depth (CTD) profiling and Niskin bottle rosette deployments (Findlay *et al.*, 2014) were conducted to characterize the environmental settings of the egg-laying habitat. Additional data were collected from a microCAT CTD (Sea-Bird Scientific; www.seabird.com) attached to the Holland-I, processed using the

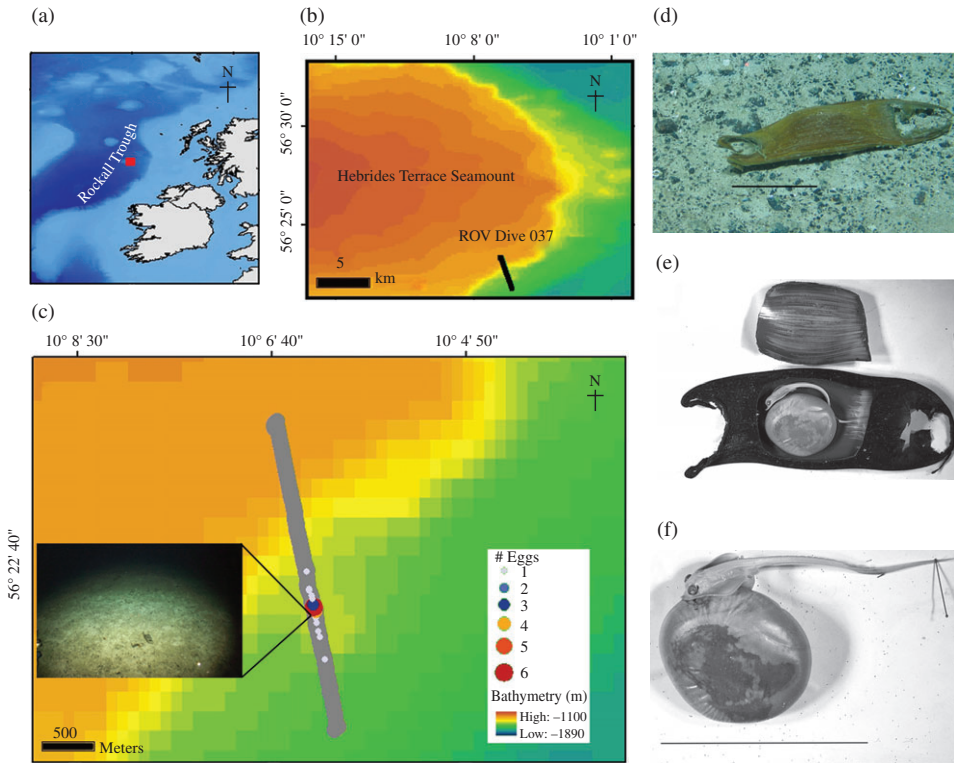


FIG. 1. Regional setting of (a) the Hebrides Terrace Seamount, (b) ROV dive 037, (c) *Bathyraja richardsoni* egg-laying habitat, (d) ROV close-up of *B. richardsoni* egg (scale bar = 10 cm), (e) dissected egg case (scale bar = 30 cm) showing (f) developing embryo (scale bar = 10 cm). Multi-beam data supplied by Ifremer collected from the Ifremer-CARTOPEP campaign 1995 (Enet *et al.*, 1998): no warranty granted from Ifremer for any use of the results, any rights reserved.

SBE 7.21 g data processing (Sea-Bird Scientific) and time-matched to the ROV's latitudinal and longitudinal positional logs to measure depth, salinity, temperature and oxygen saturation (%). Owing to the inconsistency of sampling frequency between the CTD and the ROV GPS log, the four nearest temperature, salinity and oxygen saturation measurements (using latitudinal and longitudinal distance to create a surrounding box) were averaged (mean) for each egg case location (Tables SI and SII, Supporting Information).

A quadrant method was used to count egg capsules along Dive 037, from the steep flank up to the summit. Egg capsules of one type were observed in a discrete region 895 m in length (27% of the total transect length). This region was divided into equal-length quadrants by calculating the surface area of each quadrant using the image analysing software Image J (U.S. National Institutes of Health; www.imagej.nih.gov). Using the Holland-I 10 cm laser scale as the reference, average quadrant width was 3.7 m. Thus, in order to have equal area quadrants of 100 m², the 895 m egg-laying region was subsequently divided into 33 equal length quadrants (each 27 m long, 3.7 m wide). Numbers of egg capsules were enumerated in each quadrant [*e.g.* two eggs counted in Fig. 1(c)], categorized into Marine Nature Conservation Review (MNCR)

TABLE I. Skate egg capsule collection stations and capsule state on 10 June 2012 at the Hebridean Terrace Seamount positions provided by the remotely operated vehicle Holland-I ultra short baseline (USBL)

| Station | Time (UTC) | Latitude (N) | Longitude (W) | Depth (m) | Capsule condition |
|------------------------|---------------|----------------|---------------|--------------|----------------------|
| JC073_161_ROV37/BIOB05 | 18:54:41 | 56° 22.397952' | 10° 6.260112' | 1532 | Intact |
| JC073_161_ROV37/BIOB06 | 18:58:16 | 56° 22.39692' | 10° 6.257358' | 1532 | Intact |
| JC073_161_ROV37/BIOB06 | 19:00:02 | 56° 22.395012' | 10° 6.252888' | 1532 | Intact |
| JC073_161_ROV37/BIOB06 | 19:01:20 | 56° 22.403418' | 10° 6.256032' | 1533 | Empty |
| JC073_161_ROV37/BIOB07 | 19:52:10 | 56° 22.60203' | 10° 6.342912' | 1510 | Empty |

SACFOR (superabundant, abundant, common, frequent, occasional, rare) abundance scales (JNCC; <http://jncc.defra.gov.uk/page-2684>) and mapped over multi-beam acoustic bathymetry (Eneet *et al.*, 1998; Fig. 1).

Two of the intact egg capsules collected by the ROV were compared to published accounts (Stehmann & Merrett, 2001) of five embryos (BMNH.1999.2.2.1–5) and four egg capsules (BMNH.1999.2.2.6–9). These samples had been obtained from the Goban Spur on the north-west European continental margin (RRS *Challenger* cruise 134, station 21/1997, 16 August 1997; 49° 32.5' N; 12° 48.5' W; 1541 m depth) using an semi-balloon otter trawl towed along the seafloor by a single warp. The third intact capsule from the HTS was kept for future studies and museum accession.

A total of 62 egg capsules were observed in Dive 037 (Table SII). Preliminary taxonomic evaluation from the ROV images and collected egg capsules suggested they were deposited by the deep-water skate *Bathyraja richardsoni* (Garrick 1961). Although uncommonly reported (Neat *et al.*, 2015), this oviparous species is widely distributed in the North Atlantic Ocean, the northern mid-Atlantic ridge and the south-west Pacific Ocean (Ebert & Stehmann, 2013) and has a bathy demersal habitat (501–3055 m) (Orlov *et al.*, 2004). It reaches a maximum total length of *c.* 174 cm (Templeman, 1973), making it one of the larger skates within the British 200 mile waters.

Taxonomic identity of the capsules was confirmed as *B. richardsoni* in every regard when compared with capsules reported by Stehmann & Merrett (2001). The outer surfaces of both capsules were densely covered by rough spiny fibres arranged in close-set parallel rows and thus appeared striated, as has been described earlier (Stehmann & Merrett, 2001). One capsule was dark brown in colour, with both aprons fused along the entire length of the anterior and posterior horns.

The darker, older capsule contained an embryo [Fig. 1(e),(f)] that appeared to be male: the inner edges of the embryo's posterior pelvic lobes had thickened and were not transparent as in the remainder of this lobe, but the claspers had not yet separated. Embryonic morphometrics were obtained (Table SIII). External gill filaments protruded from gill apertures. Caudal thorns and oral teeth were not yet sufficiently formed to be counted. Lateral tail folds were well developed beginning from a little behind the pelvic axils to beyond the origin of the first dorsal fin (D1). Interestingly, several measurements were close to those for embryos in more advanced developmental stages (Table SIII): this was particularly noted for horizontal eye–orbit diameter–length. This observation indicates that the eyes are developed early on before the final pre-hatching size, without much further growth from then onwards.

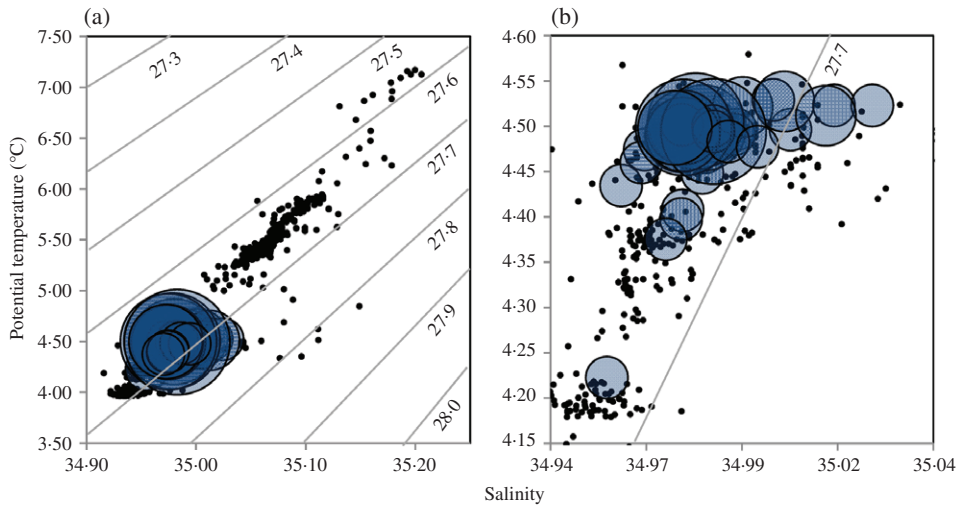


FIG. 2. Potential temperature-salinity plots for dive 037 showing CTD data (●) and corresponding T-S values for the location of the egg capsules (●). The circle size represents the number of egg capsules found in each quadrant. Also shown are the isopycnals (grey lines and numbers). (a) Shows the entire dive data, while (b) shows a close-up of the data in the location of the egg-laying ground. Note the different scales between (a) and (b).

The second egg capsule appeared younger, being lighter golden-brown in colour, which suggests it was more recently laid (Concha *et al.*, 2009). No embryo was observed upon inspection; instead, only a large yolk ovum was visible. Aprons in this capsule were fused to the horns as in the first capsule (Table SIV). The lateral lamellae-keels of both capsules were broad, with thick bone-hard massive outer edges.

There were some similarities and differences between the HTS eggs and others from off western Ireland (Stehmann & Merrett, 2001). Measurements of capsule lengths without horns and maximum capsule width were both generally similar between the two areas. Thus, some of the differences between areas were probably artefacts due to shrinkage in the Irish specimens: previous morphometrics were originally reconstructed from fresh specimens photographed with an underlying ruler (Stehmann & Merrett, 2001). There was a difference in measurements of capsules total length (L_T) that included horns: 340–452 mm (Stehmann & Merrett, 2001) *v.* 290–295 mm in the HTS samples (Table SIV). Differences in L_T with horns, however, also related to the fact that all horns in the Irish specimens were relatively straight whereas those from the HTS were strongly curved inward (Table SIV). In addition, comparison of fresh with dry capsule dimensions demonstrated an assumed shrinkage of 20–30% in the Irish specimens (Stehmann & Merrett, 2001).

Egg-laying grounds on the HTS were in waters 1489–1580 m deep (Table SII). The ROV's CTD from Dive 037 indicated that well-oxygenated waters (69.2–79.9% oxygen saturation) ranging between 4.20 and 4.55 °C and salinity 34.95–35.06 (Tables SI and SII and Fig. 2) bathed the egg-laying grounds. These waters corresponded to a layer of cooler, fresher Wyville Thomson Ridge Overflow Water (WTOW) enriched in oxygen relative to the warmer more saline overlying surface layers (Henry *et al.*, 2014).

All 62 egg cases were deposited on coarse to fine-grained sands with occasional cobbles. Egg density peaked at 21 eggs 100 m^{-2} ($=0.21\text{ eggs m}^{-2}$), corresponding to a SACFOR category of common. Note, the 100 m^2 quadrant was 27 m long x 3.7 m wide, thus, there were very likely to be more eggs on both sides of the dive transect: ROV surveys conducted in a square v. rectangular mission pattern would have probably resulted in even higher densities.

Habitat usage by two other batoid species were also observed, including another instance of egg-laying by a possible *Dipturus* sp. and an observation of what appears to be a *Rajella* sp. (Fig. S1).

There are a growing number of published accounts of deep-water egg-laying grounds of oviparous elasmobranchs (ICES, 2015). The importance of seamounts for elasmobranch biology and ecology is becoming more apparent, with many seamounts acting as hotspots for mating, cleaning stations and foraging (Oliver *et al.*, 2011). There are few accounts of elasmobranch egg-laying grounds on seamounts, although Hunt *et al.* (2011) provides an account of egg-laying on the Shiribeshi Seamount in the Sea of Japan by *Bathyraja smirnovi* (Soldatov & Pavlenko 1915). The lack of other accounts could be an artefact, due to egg cases being overlooked amongst the often dense biologically rich communities (Henry & Roberts, in press) rather than indicating a lack of egg-laying habitat. It is likely that the complex, rugged nature of some of these habitats, *e.g.* cold-water coral reefs (Henry *et al.*, 2013), or in spaces between rocky outcrops (Hunt *et al.*, 2011) could be attractive to oviparous elasmobranchs as optimal egg-laying sites with reduced risk of predation. Therefore, deep-sea ROV and AUV video and images around the globe could be important archives of data on egg-laying grounds for many other oviparous elasmobranchs.

The present account is the first to verify egg-laying grounds for two species of elasmobranchs on a seamount in the Rockall Trough. This study also extends the known geographical distribution of egg-laying habitats for *B. richardsoni* from the Goban Spur in the Porcupine Seabight to the southern Rockall Trough. This wider area spans Irish and British EEZs and incurs high fishing pressure (Witt & Godley, 2007), with increasing amounts of frontier exploration by the oil and gas industry. Cross-sectoral use of the region, combined with rapid climate changes (ocean warming and acidification) in the Rockall Trough, could have cumulative effects on development, respiration and survival of early life-history stages of elasmobranchs (Rosa *et al.*, 2014).

In terms of fishing mortality, a major concern is that many deep-water elasmobranchs deposit eggs in waters more shallow than those occupied by the adults (Stehmann & Merrett, 2001; Ebert & Stehmann, 2013). Multinational deep-water fisheries operating in the region typically fish down to 1500 m; however, egg-laying grounds on the HTS were deeper still (1489–1580 m), providing a *de facto* fisheries refuge for the eggs, assuming that sediment plumes from trawling are not transported downslope. This *de facto* depth refuge for both adults and eggs would be further strengthened by the latest evidence-based recommendations to impose a 600–800 m depth limit to bottom fisheries off the west coasts of Scotland and Ireland (Clarke *et al.*, 2015).

With regard to global climate change, the restricted depth range of egg-laying grounds on the HTS overlapped with what appeared to be a relatively oceanographically stable zone centred *c.* 1500–1700 m deep (Henry *et al.*, 2014). Here, capsules were developing in a narrow oceanographic niche of cooler, fresher and very well-oxygenated water, an envelope of conditions that continues to change in the Rockall Trough (McGrath *et al.*, 2012).

New knowledge in the context of the present study could be used to contribute to any future IUCN assessment of *B. richardsoni*, which currently lists this as a species of least concern (Kulka *et al.*, 2015). This assessment may have to be updated as industry and ocean conditions evolve in the greater Goban Spur and Rockall Trough region.

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Supporting Information

Supporting Information may be found in the online version of this paper:

FIG. S1. Two instances of habitat-use by deepwater skates on the Hebrides Terrace Seamount (HTS). (a) Three egg capsules that differed morphologically from *Bathyrāja richardsoni* on living coral framework formed by the reef framework-forming coral *Solenosmilia variabilis* during remotely operated vehicle Dive 035 (scale bar = 10 cm). Their large sizes, subquadrangular shape, and short horns suggest that these capsules were deposited by another skate species, possibly a *Dipturus* sp. (Ebert & Stehmann, 2013). Notably, both egg-laying habitats (for *B. richardsoni* and the possible *Dipturus* sp.) occurred on the deeper flanks of the Hebrides Terrace Seamount whereas none were observed on the seamount summit (Dive 036). (b) An adult skate, probably *Rajella* sp., observed at 1267 m water depth during Dive 035 (scale bar = 10 cm). Dorsal spine morphology observed in this image suggests that it was likely *Rajella kukujevi*, but that it could also have been *Rajella bathyphila*. Notably, at this depth, this *Rajella* spp. are vulnerable to fisheries bycatch on the HTS.

TABLE SI. Conductivity–temperature–depth measurements from the remotely operated vehicle Holland I collected during Dive 037 in the vicinity of skate spawning habitat on the eastern flank of the Hebrides Sea Terrace.

TABLE SII. Counts of skate egg capsules in each ROV video quadrant. Also shown are the means of four surrounding temperature, salinity and oxygen saturation measurements taken closest to the location of each quadrant.

TABLE SIII. Embryonic morphometrics from one of the rajid egg capsules collected on the seamount. These are compared to those reported previously (Stehmann & Merrett, 2001) N/A refers to a measurement that was not applicable.

TABLE SIV. Description and wet measurements of *Bathyrāja richardsoni* egg capsules ($n = 2$).

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