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A holistic and comprehensive data approach validates the distribution of the critically endangered flapper skate (*Dipturus intermedius*)

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Abstract

Morphological similarities between skates of the genus *Dipturus* in the north-eastern Atlantic and Mediterranean have resulted in longstanding confusion, misidentification and misreporting. Current evidence indicates that the common skate is best explained as two species, the flapper skate (*Dipturus intermedius*) and the common blue skate (*D. batis*). However, some management and conservation initiatives developed prior

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to the separation continue to refer to common skate (as '*D. batis*'). This taxonomic uncertainty can lead to errors in estimating population viability, distribution range, and impact on fisheries management and conservation status. Here, we demonstrate how a concerted taxonomic approach, using molecular data and a combination of survey, angler and fisheries data, in addition to expert witness statements, can be used to build a higher resolution picture of the current distribution of *D. intermedius*. Collated data indicate that flapper skate has a more constrained distribution compared to the perceived distribution of the 'common skate', with most observations recorded from Norway and the western and northern seaboards of Ireland and Scotland, with occasional specimens from Portugal and the Azores. Overall, the revised spatial distribution of *D. intermedius* has significantly reduced the extant range of the species, indicating a possibly fragmented distribution range.

KEYWORDS
critically endangered, *Dipturus* cf. intermedia, elasmobranchs, genetics, IUCN, range

1 | INTRODUCTION

Within the North Atlantic, the skate genus *Dipturus* is currently considered to include five recognized species (Ebert & Stehmann, 2013; Froese & Pauly, 2020; Costello *et al*., 2013), namely, *Dipturus batis* (Linnaeus, 1758) and *Dipturus intermedius* (Parnell 1837) (previously both classified as *Dipturus batis* and so referred to as the 'common skate' complex; IUCN Red list Critically Endangered), *Dipturus laevis* (Mitchill, 1818) (Endangered), and *Dipturus oxyrinchus* (Linnaeus, 1758)and *Dipturus nidarosiensis* (both Near Threatened), with the possibility of a further, as yet undescribed, species in the north-eastern Atlantic (Ebert & Stehmann, 2013). All North Atlantic *Dipturus* species share strong K-strategist life-history characteristics, a common feature among elasmobranchs, that make them especially vulnerable to overexploitation (*e.g*., Codling *et al*., 2005; Dulvy *et al*., 2006). Historical data on skate and rays have often been reported at the family level, with taxonomic confusion compromising some of the species-specific data (Ellis *et al*., 2010; ICES, 2020a).

From as early as the 4th century BC, giving similar morphological features, early taxonomists such as Aristotle grouped skate under collective terms such as βάτος (Hoffman & Jordan, 1892). This trend in grouping skate continued in Europe up until 2009, with skate landings by commercial fisheries reported as 'skates and rays' (Ordinyana, 2005; Silva *et al*., 2012). Since 2008 (North Sea) and 2009 (Celtic Seas, Biscay and Iberian waters), it has been mandatory under EU fisheries legislation for the main skate species to be reported at species-specific level (Ellis *et al*., 2010). Notwithstanding improvements in the species-specific reporting of skates (*e.g*., ICES, 2020a; Silva *et al*., 2012), some landings are still reported at the family level and there is some concern over the accuracy of those data relating to the genus *Dipturus* (ICES, 2020a; Iglésias *et al*., 2010). These issues have affected data quality (*e.g*., data relating to catches, species distribution, population structure and abundance) and thus hampered both the assessments of relevant species and stocks, and effective management.

Misreporting of the *Dipturus* species is linked to the superficial physical similarities between species, with some landings being labelled as 'skate' or 'common skate' [or the equivalent local name (*e.g*., ICES, 2020a; Griffiths *et al*., 2010, Barreau, pers. comm., 2021)]. Although current fishing regulations prohibit the retention and landing of *D. batis* and *D. intermedius* from EU waters, poor taxonomic resolution means that prohibited species can be misidentified, misreported or mislabelled (Simpson & Sims, 2016, Hannon, pers. comm., 2021; Griffiths, pers. comm., 2021), as has been reported for other prohibited species (*e.g*., Pazartzi *et al*., 2019). Misreporting, particularly of rare and endangered species, and subsequent impacts on data quality can compromise the effective conservation management of these species.

The issues linked to what exactly constitutes a 'common skate' have followed a long history of taxonomic revision and uncertainty (Figure 1). The first use of *Raja batis* was by Linnaeus (1758), although his description appears to relate more to *Raja undulata*, with a second, less broadly used synonym, *Raja macrorynchus* raised by Rafinesque (1810). Risso (1810) used the name 'floussado' in relation to *R. batis* and subsequently named the 'blue skate' as *Raia flossada* (Risso, 1826). A decade later, Parnell (1837) noted two small skate specimens in a Scottish fish market with characteristics intermediate between *R. batis* and *R. oxyrhynchus* [which, based on Parnell's subsequent account (Parnell 1838), related to white skate *Rostroraja alba*, as opposed to long-nosed skate *Dipturus oxyrinchus*]. Parnell's (1838) original paper described these specimens and named them flapper skate *Raia intermedia*. The line drawings and descriptions provided by Parnell (1837, 1838) match juveniles of what are now considered *Dipturus intermedius* (Supporting Information Figure S1). Later, Gaimardi (Valenciennes, 1851) raised another synonym, *Raia gaimardi*, although this did not receive widespread acceptance. Clark (1926) subsequently synonymised *R. intermedia* with *R. batis*, referring to 'common skate' under the scientific name *Raia batis*, despite commenting on the large variation in clasper length of similar-sized male 'common skate'.

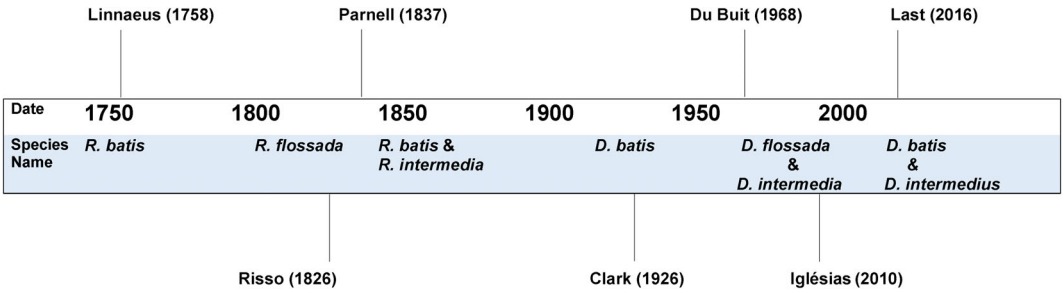

FIGURE 1 Historical timeline of flapper skate (*Dipturus intermedius*) taxonomic names. Key dates are indicated, including the name and date of the authoritative author. D, *Dipturus*; R, *Raja*. The blue area denotes the names associated with flapper and blue skate, including lumping and splitting events

Based on the different sizes at first sexual maturity, Du Buit (1968) also remarked on the potential for two 'races' of 'common skate'. Clark's (1926) revision of European skates was widely accepted and so data for the 'common skate' complex became confounded over much of the 20th century, including the period when the subgenus *Dipturus* was elevated to a distinct genus (McEachran & Dunn, 1998), and until the work of Iglésias *et al.* (2010).

Based on distinct morphology, genetics and ecology, Iglésias *et al.* (2010) confirmed that the two types of 'common skate' were in fact two discrete species and this remains the currently held view. Iglésias *et al.* (2010) referred to these two species as *Dipturus* cf. *flossada* (blue skate) and *Dipturus* cf. *intermedia* (flapper skate). A subsequent study by Griffiths *et al.* (2010) also independently supported the taxonomic status of these two cryptic species, noting that they were apparently represented by northern and southern distributions. Whilst subsequent taxonomic studies (*e.g.* Ebert & Stehmann, 2013; Weigmann, 2016) accepted that these were distinct species, the nomenclature was finalized by Last *et al.* (2016), with the common blue skate retaining the Linnean name *D. batis* (Linnaeus, 1758) and the flapper skate designated as *D. intermedius* (Parnell, 1837).

A decade after the work of Iglésias *et al.* (2010), *D. batis* and *D. intermedius* continue to be primarily managed under the 'common skate' complex umbrella. Since 2009, EU fishing regulations have listed the 'common skate' complex as prohibited species that cannot be retained or landed from EU waters, meaning that individuals of both species should be promptly released by fishers if caught in EU waters. Regulation (EU) 2015/812 requires that all discards of 'common skate' complex in EU waters are recorded by commercial fishers. Some earlier conservation actions relate to 'common skate' (as '*D. batis*'), including their listing as a Threatened and Declining Species under Annex V of OSPAR, and as a priority species under the UK Biodiversity Action Plan (UK Biodiversity Group, 1999). A recent assessment (ICES, 2020b) and subsequent advice to OSPAR (ICES, 2020c) was provided for both species in the complex, where it was also recommended that the two species should have separate listings (ICES, 2020c). Northern Ireland listed 'common skate' (as *D. batis*) under the Wildlife (Northern Ireland) Order [1985 (as amended) through the Wildlife and Natural Environment Act (Northern Ireland) 2011]. The complex is also listed as a high priority species on the Helsinki Commission Priority List in 2007 (HELCOM, 2006). HELCOM refers to those species in the Baltic Sea, within which *D. batis* (complex) are reported as extremely rare (Zidowitz *et al.*, 2008). Only Ireland's Red List of Threatened Species (Clarke *et al.*, 2016) and this year's updated IUCN assessment give specific listings for both species in the complex (Ellis *et al.*, 2021).

Beyond these measures, spatial management of both species is limited. A marine protected area (MPA) was designated for the complex in Scottish waters, from Loch Sunart to the Sound of Jura (Scottish Natural Heritage, 2013), although it essentially protects the local community of *D. intermedius*. In March 2021, after a large number of *D. intermedius* egg cases were discovered in the Sound of Skye, an emergency MPA known as the Red Rocks and Longay Urgent MPA was established to protect the potential egg laying ground from damage by fishing activities (Scottish Government, 2021). The specifications of more permanent measures will be determined on review.

The earlier IUCN assessment estimated the distribution of the 'common skate' complex (as '*D. batis*') as ranging from Iceland and the Barents Sea in the north to as far south as Senegal and the Azores, including the Mediterranean Sea, with this based on published literature (Dulvy *et al.*, 2006). The relatively recent splitting of the 'common skate' complex (Iglésias *et al.*, 2010), as well as wider taxonomic confusion across the genus, has raised the question of delineating the species-specific distributions (both current and historic) of *D. batis* and *D. intermedius* within the previously considered distribution area of the 'common skate' complex. Recently, both *D. intermedius* and *D. batis* received species-specific IUCN assessments (Ellis *et al.*, 2021), with both species in the complex still listed as Critically Endangered. This most recent assessment estimated the extant distribution of *D. intermedius* to include the Faroe Islands, Ireland, Norway and the United Kingdom (Ellis *et al.*, 2021). As such, the 2021 IUCN assessment noted the unverified presence of *D. intermedius* in Belgium, Denmark, France, Germany, Iceland, the Netherlands, Portugal, the Russian Federation (European Russia) and Spain (Ellis *et al.*, 2021). Further afield, a recent genetic study by Bache-Jeffreys *et al.* (2021a) confirmed the presence of *D. intermedius* as far south as Portugal and the Azores.

Within the UK and Ireland, Griffiths *et al.* (2010) noted a strong degree of latitudinal separation between *D. intermedius*

TABLE 1 Occurrence data for *Dipturus intermedius* obtained from researchers, fisheries, survey and angler databases

Source	Data	*n*	Survey period	Area	Format latitude/longitude data
Cefas	Fisheries-independent survey data	8	2011–2019	North Sea and Celtic Sea	Haul latitude Haul longitude
Cefas	Fisheries-independent GOVL survey (ELASMOS series)	29	2014–2017	Celtic Sea	Haul latitude Haul longitude
DATRAS	Fisheries-independent survey data	64	2012–2021	North-east Atlantic	Haul latitude Haul longitude
IFI	Angler records	870	1990–2013	South and west coasts of Ireland, Northern Ireland coast	Latitude Longitude
IMR	Survey data (fisheries-independent)	2	2013, 2019	North Sea, Norwegian Sea	Latitude Longitude
IMR	Reference fleet data (fisheries-dependent)	10	2013–2029	North Sea, Norwegian Sea	Latitude Longitude
SSACN	Angler records	1381	1990–2014	West coast of Scotland	Latitude Longitude
Barreau & Iglésias, pers. comm., 2021	Verified occurrences	109	2005–2018	Western coasts of Ireland and Scotland, Celtic Sea and Bay of Biscay	Haul average latitude Haul average Longitude
Lynghammar pers. comm., 2021	Verified occurrences	9	2009–2021	Southern Norway and Skagerrak	Latitude Longitude

Abbreviation: Cefas, Centre for Environment, Fisheries and Aquaculture Science; DATRAS, Database of Trawl Surveys; ICES, International Council for the Exploration of the Sea; IFI, Inland Fisheries Ireland; IMR, Institute of Marine Research; SSACN, Scottish Sea Angling Conservation Network.

(more northerly and easterly) and *D. batis* (more southerly and westerly). A subsequent study found that both species had a much more widespread, overlapping distribution than previously thought (Frost *et al*., 2020). This study found that *D. intermedius* and *D. batis* appeared to inhabit many of the same habitats within the region, with the former covering relatively more inshore areas (of sufficient depth).

One of the key requirements for the IUCN assessments is an accurate delineation of both the historical and contemporary distributions of these species to better allow for a more quantitative evaluation of any reduction in geographic range. Furthermore, the depleted status of the 'common skate' complex in North Atlantic waters requires improved taxonomic resolution for effective management (*e.g*., Jansen *et al*., 2018). Traditionally, the lowest taxonomic unit used is the species (or, in terms of fisheries management, any discrete biological stocks of a species) as this provides the most appropriate information for biodiversity conservation and conducting stock assessments. Continued poor taxonomic resolution can lead to errors in estimating population viability and range, fisheries management and conservation status. Species-specific ecological data, therefore, are paramount to the successful conservation of *D. intermedius*.

Here, we will demonstrate how a concerted taxonomic approach, using molecular data and a combination of survey, angler and fisheries data, in addition to expert witness statements, can be used to build a more granular and higher resolution distribution map of *D. intermedius*. These novel revised georeferenced data were used to establish a distribution map to better reflect current distribution patterns. We argue that this new information can be used to support future decision-making processes by informing spatially explicit conservation and fisheries management as well as IUCN conservation designation.

2 | MATERIALS AND METHODS

2.1 | Distribution

Georeferenced data points for *D. intermedius* occurrences were obtained from fisheries survey databases and angler records. Records collected from 1990 onwards were extracted for *D. intermedius*, *D. batis* and the 'common skate' complex from available datasets to provide a contemporary distribution for the species (Table 1).

ICES DATRAS [hereafter as 'DATRAS', the Database of Trawl Surveys managed by International Council for the Exploration of the Sea (ICES)] occurrence records for '*D. intermedia*', '*D. batis*' and '*D. flossada*' (note the outdated nomenclature) were extracted using the icesDatras package (version 1.2-0; Millar *et al*., 2019) from all available surveys. Relevant metadata including species length and associated geographical locations for each data point were combined into a single database. For the additional sources, including the Centre for Environment, Fisheries and Aquaculture Science (Cefas), the Institute of Marine Research (IMR), Inland Fisheries Ireland and The Scottish Sea Angling Conservation Network, equivalent information was

TABLE 2 Presence of *Dipturus intermedius* or *D. batis*(complex) in regional species checklists and catalogues within the current IUCN distribution of *D. batis* (complex)

Region	Listed species	Listed common names	Presence	Source	Reference
Azores	Not listed	na	na	Marine fishes of the Azores: annotated checklist and bibliography	Santos *et al.* (1997)
Azores	*D. batis* complex	Blue skate	Present	Sharks and Rays from the Azores; an illustrated catalogue	Barreiros & Gadig (2011)
British Isles	*D. intermedius*	Flapper skate, grey skate	Present	Shark and ray ID cards, flapper skate ID guide	Shark Trust (2020)
Irish waters	*D. intermedius*	Flapper skate	Present	An inventory of elasmobranch databases for Irish waters	Varian (2011)
Mediterranean	*D. batis* complex	Common skate, Norwegian skate, grey skate	Present	The Conservation Status of Sharks, Rays and Chimaeras in the Mediterranean Sea	Dulvy *et al.* (2016)
Mediterranean and Black Sea	*D. batis* complex	Grey skate	Present	Elasmobranchs of the Mediterranean and Black Sea	Bradai *et al.* (2012)
Mediterranean and Black Sea	Not listed	na	na	The Mediterranean Large Elasmobranchs Monitoring (MEDLEM) database	Mancusi *et al.* (2020)
Mediterranean and Black Sea	Not listed	na	Questionable	Species diversity, taxonomy and distribution of Chondrichthyes in the Mediterranean and Black Sea	Serena *et al.* (2020)
North Sea	*D. batis* complex	Common skate	Present	Sharks, skates and rays of the southern North Sea and the (eastern) English Channel	Brevé *et al.* (2015)
North Sea	*D. batis* complex	Common skate, blue skate	Present	An annotated checklist of North Sea cartilagenous fish	George (2009)
Western Baltic Sea	*D. batis* complex	Common skate, blue ray	Extremely rare	Sharks in the Baltic	Zidowitz *et al.* (2008)
Western Baltic Sea	*D. batis* complex	Skate	Temporary occurrence	Checklist of Baltic Sea macro-species	HELCOM (2012)

Abbreviation: na = not applicable.

obtained by direct email request (SSACN; Supporting Information Table S1).

To ensure only records of *D. intermedius* were retained, data points from the combined resulting database were filtered to include only specimens ≥160 cm, as *D. batis* (the smaller of the 'common skate' complex) has a maximum length of *ca.* 150 cm (ICES, 2020b; Iglésias *et al.*, 2010). Where length information was missing, weight data were converted into length, using formulae given by McCully *et al.* (2012), for the 'common skate' complex. Following the size-based selection, a total of 83 records was retained from the DATRAS dataset, out of a total of 3529 records. in some of the surveys carried out by Cefas (FV Govenek of Ladram (GOVL) survey, 2014–2017; Bendall *et al.*, 2018), including surveys on a commercial fishing vessel which specifically targeted both species, *D. intermedius* were identified according to the morphological features described by Iglésias *et al.* (2010). These features include the colour of the iris, the wing blotches, the direction of the lateral tail thorns, the interspace between dorsal fins and the shape of the teeth (see Iglésias *et al.*, 2010). These latter records were considered to be verified and included in the final data set regardless of size. To further validate species ID, each record obtained from IMR was confirmed by contracted fishermen, who were responsible for data collection. Datasets were collated in R, version 4.0.2 (Rstudio Team, 2020) and visualized using ArcGIS Pro® GIS software (ArcGIS Pro, 2020). ICES reference layers used to classify point locations were downloaded online (ICES Spatial Facility, 2005).

Additional data on the distribution of *D. intermedius* were obtained through email correspondence with relevant personnel from several museums, universities and research institutions within the purported range of the 'common skate' complex. For these data, where possible, records were verified using the key morphological traits detailed in Iglésias *et al.* (2010) or by using length information. Available literature and catalogues on skates and rays in these regions were consulted to investigate for the presence of *D. intermedius* (Table 2).

2.2 | Molecular analysis

Cytochrome c oxidase I (CO1) sequences of North Atlantic *Dipturus* species were downloaded from GenBank (see Supporting

Information Table S2 for a full list of species and sequence accession numbers). This gene region has previously been shown to be useful to uncover cryptic diversity in North Atlantic *Dipturus* (Bache-Jeffreys, 2019; Carugati *et al*., 2021; Iglésias *et al*., 2010) and other species complexes (Cariani *et al*., 2017). In each case, species names were checked against WoRMS (Costello *et al*., 2013). Multiple sequence alignments were carried out using both CLUSTALV (Higgins *et al*., 1992) and MUSCLE (Edgar, 2004), checked manually in Aliview (Larsson, 2014), and conservatively trimmed to ensure consistency among samples (equal sequence length of 459 bp). The final alignment consisted of 94 sequences, which had been reported across a range of valid and invalid scientific names: '*D. flossada* ($n = 3$), *D. intermedia* ($n = 3$), *D. batis* ($n = 5$), *D. intermedius* ($n = 1$), *D. nidarosiensis* ($n = 37$), *D. oxyrinchus* ($n = 37$), *D. laevis* ($n = 7$) and *R. clavata* ($n = 1$) (Figure 3b and Supporting Information Table S2).

Prior to phylogenetic analyses, jModeltest v2. 1 (Darriba *et al*., 2012) was used to determine the most appropriate nucleotide substitution model for the alignment data. Hasegawa-Kishino-Yano was the best fit model chosen by jModeltest with the best Bayesian information criterion score. Sequences were aligned alongside the outgroup *Raja clavata*, rooted using a single fragment for *R. clavata*. Phylogenetic analysis was completed in MrBayes 3.2.6. The final analysis used two simultaneous runs of 10 million generations sampled

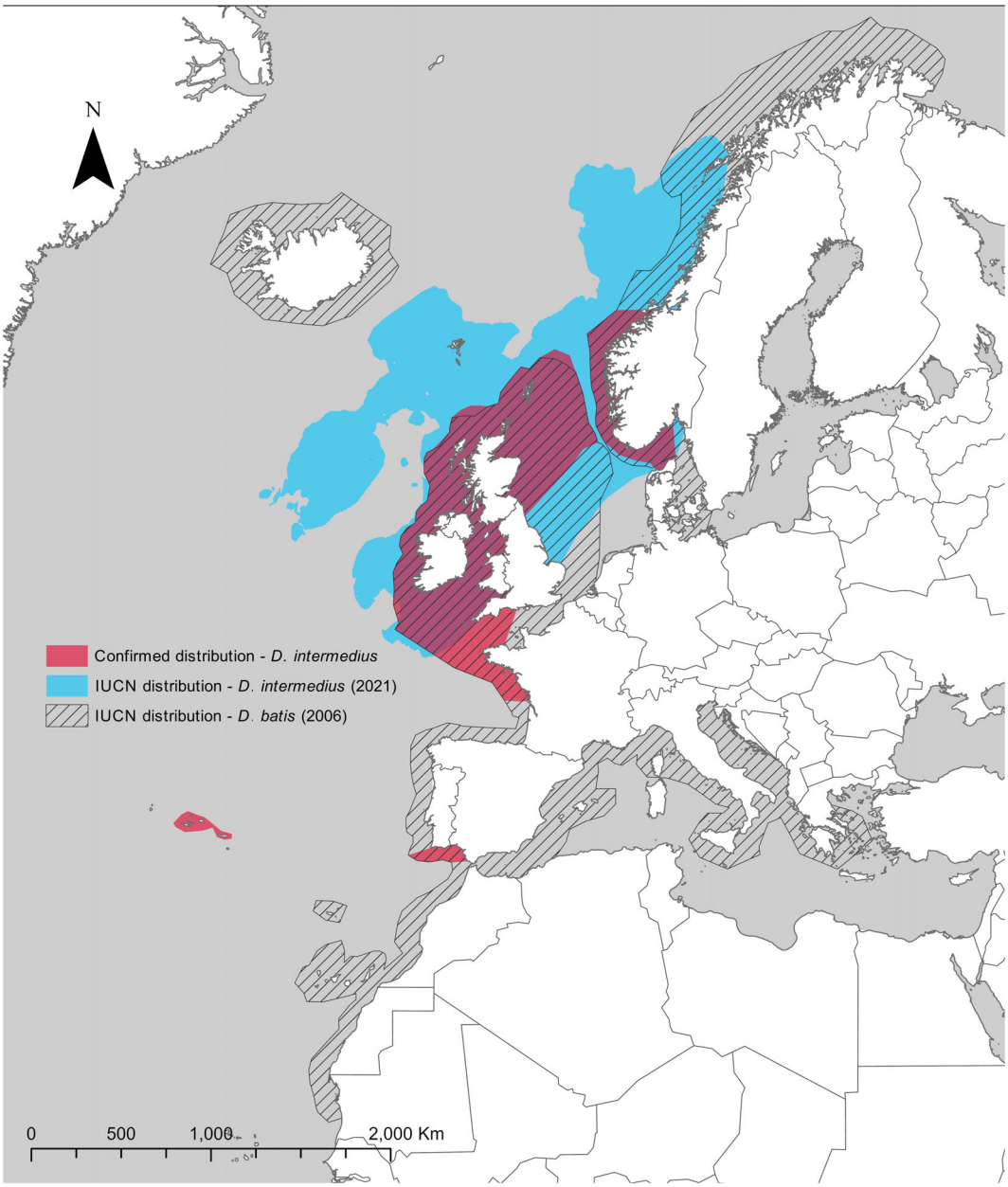

FIGURE 2 Verified distribution of *Dipturus intermedius* compared to the previous IUCN distribution of the 'common skate' complex and the current IUCN distribution for species. *D. intermedius* occurrences obtained from fishery trawling surveys, angling and genetic databases.

every 1000 steps. The retained 12 000 trees were summarized as a 50% majority rule consensus tree.

Haplotype networks of the CO1 gene were constructed in PopART (Leigh & Bryant, 2015) using the TCS method (Clement *et al*., 2002) to infer relationships among the reduced subset of samples. An overall haplotype network was produced to visualize interconnections among all individuals sampled in all species and colour coded based on approximate location of sample collection derived from the original published article (Supporting Information Table S2 and Figure S2).

3 | RESULTS

3.1 | Distribution

Occurrence records, as obtained from fisheries survey databases, angling associations, Genbank and relevant researchers in the field, confirmed a consistent presence of *D. intermedius* in the north-east Atlantic, concentrated in the northern North Sea and the northern and western seaboards of Scotland, Northern Ireland and Ireland, as far south as the Celtic Sea (Figure 2 and see also Supporting Information Figure S3). *D. intermedius* was also recorded as far north as southern and western Norway, with exceptional/rare reports in the French Bay of Biscay, Portugal and the Azores. Data points were concentrated in coastal shelf seas at depths of 50–600 m.

Publicly available species catalogues and checklists within the IUCN distribution of *D. batis* largely listed the 'common skate' complex (see Table 2).

3.2 | Molecular analysis

The North Atlantic species of *Dipturus* were observed to be monophyletic in this phylogenetic analysis, with *R. clavata* as an outgroup (Figure 3b). The majority of species sequences accurately clustered together in their assigned species groups. Within the CO1 tree, *D. oxyrinchus* and *D. intermedius* appeared to be sister species, as were *D. laevis* and *D. batis* (Figure 3b). Sequences of *D. oxyrinchus* were available from the eastern and western Mediterranean and from the north-east Atlantic (Norwegian and Iberian waters; Figure 3), while all samples of *D. intermedius* are linked to the Celtic Seas, Greater North Sea and the Azores, with no evidence of them in the Mediterranean (see Supporting Information Figure S2 for map of ICES ecoregions). *D. nidarosiensis* formed a distinct clade. *D. laevis* and *D. batis* consistently grouped together as a clade in both the phylogenetic tree and in the haplotype network (Figure 3a,b), despite not being reciprocally monophyletic.

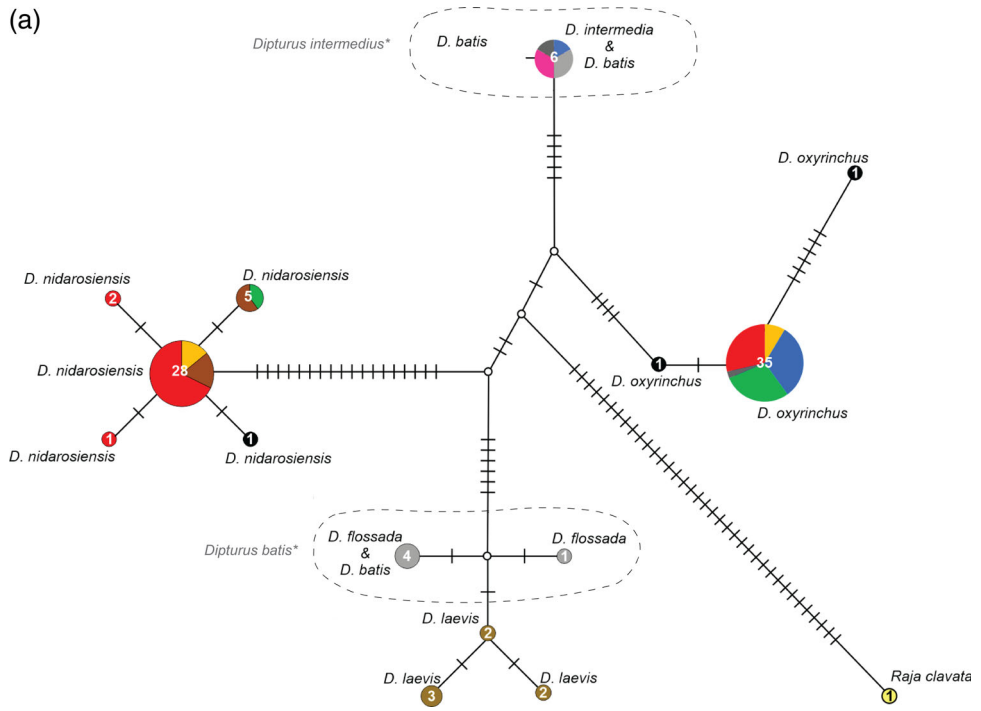

FIGURE 3 Phylogenetic analysis of North Atlantic species of *Dipturus*. (a) Haplotype network of the CO1 marker for north Atlantic species of *Dipturus* constructed with the TCS program, rooted with *Raja clavata*. Each line segment represents an inferred mutation step. Haplotypes are labelled by species groupings and starred labels represent confirmed species ID for 'common skate complex' (*D. batis*) records, coloured by ICES Ecoregions (ICES Spatial Facility, 2005; Supporting Information Figure S2) and scaled proportionately to the number of supporting sequences. (b) CO1 phylogenetic gene tree constructed using Mr. Bayes for north Atlantic species of *Dipturus* (*D. nidarosiensis*, *D. intermedius*, *Dipturus intermedia*, *D. laevis*, *D. flossada*, *D. batis*, and *D. oxyrinchus*) rooted with *Raja clavata*. ■, Azores; ■, Bay of Biscay; ■, Celtic Seas; ■, Central Mediterranean Sea; ■, Eastern Mediterranean Sea; ■, Greater North Sea; ■, Norwegian Sea; ■, Oceanic Northeast Atlantic; ■, Unknown; ■, Western Atlantic; ■, Western Mediterranean Sea

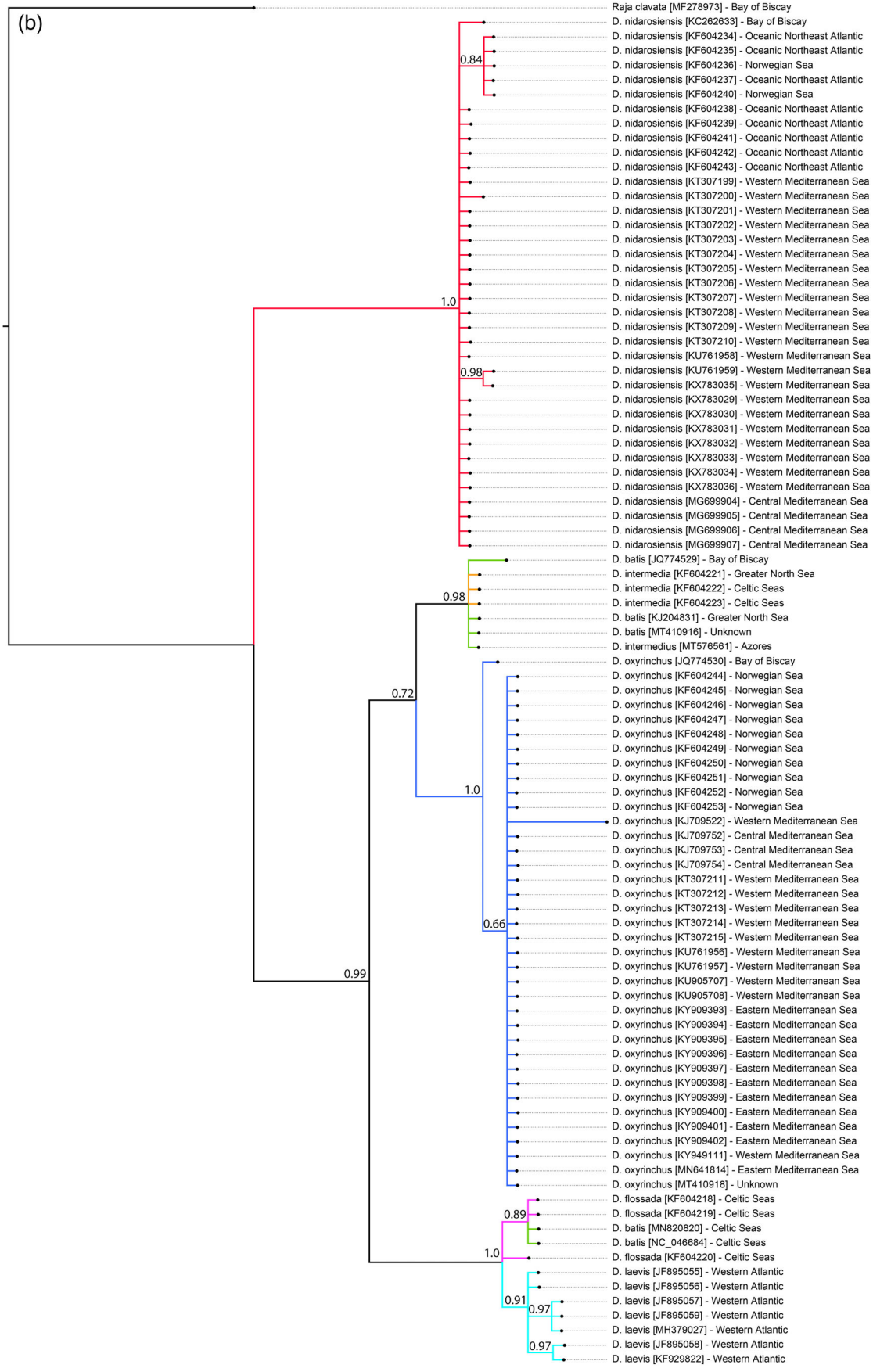

FIGURE 3 (Continued)

Haplotype networks generated from all available CO1 sequences of North Atlantic *Dipturus* species highlighted the separation between species groups (Figure 3a). The confirmed distribution of *D. intermedius* from DNA data, reported here, limited the species range to the UK, Ireland, the northern North Sea to Norway and the northern Skagerrak, as well as Portuguese and Azorean waters (Bache-Jeffreys *et al.*, 2021a; Costa *et al.*, 2012; Knebelsberger *et al.*, 2014; Lynghammar *et al.*, 2014). There was no obvious geographic separation of haplotypes within species groups (Figure 3a). The results also highlighted a distinct *Dipturus oxyrinchus* sequence (Figure 3) from the Bay of Biscay.

After processing the CO1 gene region for all available North Atlantic *Dipturus* samples, species identity for each sequence was verified and phylogenetic relationships between all sequences inferred (see Supporting Information Table S2). We observed eight potential sequences from the 'common skate' complex that require updating to conform with the currently accepted nomenclature (see Supporting Information Table S2).

4 | DISCUSSION

The result of this investigation, capitalizing on previously published data sets and existing public databases, clearly shows that *D. intermedius* has a more constrained, coastal distribution than previously presumed for the 'common skate' complex (*sensu* Dulvy *et al.*, 2006). Furthermore, this study was able to confirm the presence of *D. intermedius* in Spain, Portugal and the Azores (Figures 2 and 3, and Table 2), which was unverified in the most recent species-specific IUCN assessment (Ellis *et al.*, 2021). Validation to the results presented here is provided by the fact that most observations support the findings of previous research (Frost *et al.*, 2020; Griffiths *et al.*, 2010; Iglésias *et al.*, 2010). The southern limit of the species distribution appears to be the Azores and Portugal (Bache-Jeffreys *et al.*, 2021a; Bache-Jeffreys, 2019; Costa *et al.*, 2012, Iglésias, pers. comm., 2020). There is validated evidence of one specimen (a juvenile of *ca.* 70 cm, no. 2040) from Madeira, although there have been no records in the last century (Biscoito *et al.*, 2018) and so further inferences as to the historical distribution in this area should be viewed with caution. The northern limit of *D. intermedius* appears to be 63°N, which was validated with records from the Norwegian Sea (Lynghammar *et al.*, 2014, Junge, pers. comm., 2021), although they are much less abundant at this latitude. Recent surveys have not recorded any *D. intermedius* from Icelandic waters (Bache-Jeffreys *et al.*, 2021a; Jakobsdóttir, pers. comm., 2021) and it is likely that the large historical specimen was a misidentified *Bathyraja* spp. (see Johannesen *et al.*, 2017). Beyond this distribution, the complex was also listed as having a temporary or rare occurrence in the Western Baltic Sea. These finding are largely supported by existing distribution models for the species that predicted a strong presence of *D. intermedius* in the ICES division 27.6.a (Bache-Jeffreys *et al.*, 2021b; Pinto *et al.*, 2016).

This study was unable to confirm any presence of *D. intermedius* in the Mediterranean Sea. The early, anecdotal records of 'common skate' in the Mediterranean by Risso (1810) described a 'spotted grey backed skate with firm and tasty white flesh', which offers limited evidence. Additionally, no records from the area provide any evidence (*e.g.*, drawings, measurements, DNA, photographs) to confirm their validity. Indeed, there have been no recent reports or genetic identification of either member of the 'common skate' complex in the Mediterranean (Cariani *et al.*, 2017; Minos, pers. comm., 2020), although there have been numerous accounts relating to *D. oxyrinchus* and *D. nidarosiensis* (*e.g.*, Serena *et al.*, 2020). Whilst a recent parasitology-based study has nominally reported '*D. batis*' in the Mediterranean (Benmeslem *et al.*, 2019), the identification material used by the author pre-dated the split in the complex, and no specific morphological information was provided, therefore this record should be considered as questionable without further means of confirmation.

The absence of any recent scientifically verified specimens of either *D. batis* or *D. intermedius* from the Mediterranean, and apparent lack of verifiable historical samples, supports previous reservations about the presence of the 'common skate' complex in the Mediterranean (Clark, 1926; Last *et al.*, 2016; Norman, 1935). Confirmed *Dipturus* records for the Mediterranean are limited to *D. nidarosiensis* and the closely related *D. oxyrinchus* (*e.g.*, Cariani *et al.*, 2017; Landi *et al.*, 2014; Ramírez-Amaro *et al.*, 2017). The high degree of morphological conservatism of these species may explain the probable misidentification in the Mediterranean, especially for smaller specimens. It is therefore likely that any records of 'common skate' in the Mediterranean refer to misidentified *Dipturus* species or other skate genera such as *Raja*. However, this absence of evidence is not necessarily evidence for absence, and more dedicated studies of regional fish collections should be undertaken.

The validated distribution presented here is quite fractured, with no recent observations from the southern North Sea, Irish Sea or Mediterranean (Brander, 1981; Dulvy *et al.*, 2000; this study). These gaps suggest a potential extirpation from parts of the former range. However, it should be noted that fisheries records of flapper skate represent incidences of bycatch, and a sufficiently low presence of the species in some regions may cause it to appear absent entirely. An analysis of catchability effects on flapper skate bycatch records was beyond the scope of this study, and therefore the distribution presented here is considered conservative. Earlier research has already shown the decline and regional extirpation of the 'common skate' complex from the Irish Sea and North Sea over the course of the 20th century (Brander, 1981; Dulvy *et al.*, 2000; Walker & Hislop, 1998). Importantly, recent studies have suggested that *D. intermedius* have limited home ranges and express strong site fidelity (Neat *et al.*, 2015; Thorburn *et al.*, 2018). It could therefore be suggested that the current fragmented distribution presents challenges for genetic connectivity between any discrete populations. It is worthwhile to note that the data in this study are provided for the most part by large, mature *D. intermedius*, and current knowledge of the distribution and ecology of juveniles and subadults is still limited. Further targeted surveys to

account for habitat variability, juveniles and temporal patterns are recommended.

Inspection of available catalogues and species checklists within the IUCN distribution of the 'common skate' complex largely corresponded with this study. Despite being previously listed as present in some Mediterranean checklists (Bradai *et al*., 2012; Dulvy *et al*., 2016), more recent information either neglects to include either species of common skate or states their presence as 'questionable' (Mancusi *et al*., 2020; Serena *et al*., 2020). Surprisingly, some reports from the Baltic Sea indicate a temporary or rare presence of the 'common skate' complex in their waters, just beyond the verified distribution of *D. intermedius* and *D. batis* (HELCOM, 2012; Zidowitz *et al*., 2008). This listing, coupled with their protected status under the Helsinki Commission (HELCOM, 2006), presents a good reason to assume some small historical presence of either species in the Baltic Sea. Whilst these 'records' were not verifiable, they did highlight issues with the nomenclature associated with these species. The 'common skate' complex has many associated common names (grey skate, smooth skate, big skate, blue ray, soft skate etc.) throughout Europe, Scandinavia and the Mediterranean, which further exacerbates misidentification with similar species (Table 2). For example, in Irish waters, blue skate are often logged as black skate by fishermen due to their dark colouration (Hannon, pers. comm., 2021). Likewise, in Norway, the complex is known as 'storskate' (translated as 'big skate'), but such an ambiguous name can cause similar problems with misidentification (Junge, pers. comm., 2021). An important target for regional conservation is to improve education and awareness of the morphology and taxonomic nuances surrounding these species using tools such as species-specific illustrated ID guides (see *e.g*., Trust, 2020).

Recent morphological and genetic evidence has contested traditional systematics by indicating a closer relationship between *D. intermedius* and *D. oxyrinchus* than previously thought. Furthermore, the north-eastern Atlantic *D. batis* grouped with the north-western Atlantic barndoor skate *D. laevis* (Carugati *et al*., 2021; Griffiths *et al*., 2010; Naylor *et al*., 2012; this study), despite these species having nonoverlapping distributions on either side of the Atlantic Ocean (Dulvy *et al*., 2006; Ebert & Stehmann, 2013; Kulka *et al*., 2020). While they do not appear to be reciprocally monophyletic (Figure 3), species delimitation in this clade is consistently challenging, as noted in previous studies (Bache-Jeffreys *et al*., 2021a; Ball *et al*., 2016). Both these species are largely shelf-species, although they are found to depths of *ca*. 600 m [and *D. laevis* can be found to 1000 m depth (Dulvy *et al*., 2006; Kulka *et al*., 2020)]. Whilst geographically separate and with distinguishing morphological features (1), these sister taxa could be the results of allopatric speciation (Carugati *et al*., 2021), given that they are separated by a barrier of cold water from the east Greenland Current, beyond which only deep-water skate species are found (Ebert & Stehmann, 2013; Kulka *et al*., 2020; Lennon *et al*., 2021). Beyond this supposition, these findings have important consequences for the management for these species. Considering the phylogenetic relationships elucidated here and in other studies, it would be reasonable to adjust the management strategies accordingly. For a species such as *D. batis*, about which little is known, it could be useful to draw on the available data collected for *D. laevis*. Likewise, with the data-poor *D. intermedius*, ecological information on the closely related *D. oxyrinchus* could be applied, with caution, until further species-specific data are collected.

A recognized caveat of size-based selection of catch records is that while it precludes the inclusion of common blue skate, it may have allowed inclusion of *D. nidarosiensis*, as this species can reach lengths of up to 230 cm (Stehmann *et al*., 2015). Bycatch records of juvenile flapper skate and smaller mature individuals were also omitted using this approach. Nonetheless, size-based selection remains the most dependable means of validating the bycatch records, which are known to be replete with incidences of misidentification and misreporting (Iglésias *et al*., 2010). Our study highlights that good taxonomic resolution is important to resolve the fundamental biological and ecological requirements for species, otherwise the geographic distribution and population estimates can become inflated. Overall, the revised distribution of *D. intermedius* based on confirmed species-specific records has significantly reduced the species' known extant range, demonstrated the possible existence of isolated populations and has shown that spatial species-specific management may be required to ensure the long-term survival of this vulnerable skate species.

AUTHOR CONTRIBUTIONS

S.L.L. and J.T. were involved in writing and editing the manuscript. J.R.E., T.B., M.B., C.B., J.B., A.M.G., C.J., A.L., N.D.P., P.A.P. and S.P.I. assisted with review and editing. T.B., J.B., M.C., A.M.G., G.H., K.J., C.J., G.M., W.R., A.L. and S.P.I. provided data for the study. A.G., S.L.L., C.B., M.McC. and P.A.P. were involved in data analysis. P.C.C. and A.G. were involved in conceptualization, writing and editing.

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CONFLICTS OF INTEREST

The authors declare that they are not aware of any competing interests.

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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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