

Marine Record

Cite this article: Aluwihare YC, Mateos-Rivera A, Reeve M, Gunasekara SS, Jayasinghe RPPK, Dalpadado P (2025). First genetic and morphological records of Balloon Alfonsin, *Beryx mollis* egg and larvae. *Journal of the Marine Biological Association of the United Kingdom* **105**, e50, 1–7. <https://doi.org/10.1017/S0025315425000177>

Received: 22 January 2024

Revised: 24 August 2024

Accepted: 20 January 2025



Keywords:

breeding grounds; ichthyoplankton; Indian Ocean; molecular approaches

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First genetic and morphological records of Balloon Alfonsin, *Beryx mollis* egg and larvae

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Abstract

Despite the importance of the commercially harvested benthopelagic fish *Beryx mollis*, little information is available on their adult phase and reproduction. This is likely due to the low abundance of this species compared to *Beryx splendens* and *Beryx decadactylus* as well as misidentification of *Beryx* spp. In this study, early life stages of *B. mollis* were found in the southwest region off Sri Lanka during a survey with research vessel Dr Fridtjof Nansen in 2018, coinciding with the southwest monsoon period. As morphological characteristics of eggs and larval stages of the three *Beryx* spp. are very similar, visual identification to differentiate to species level has always been challenging. Therefore, in this study, DNA barcoding was carried out targeting the mitochondrial COI gene. Molecular analysis confirmed that the collected egg and larvae belonged to the *B. mollis* species due to their high identity (>99%) with reference to previously submitted adult *B. mollis* sequences in the GenBank. Phylogenetic analysis showed a closer evolutionary relationship among *B. mollis* and *B. splendens* than with *B. decadactylus*. To the best of our knowledge this is the first genetic and morphological confirmation of *B. mollis* egg and larvae worldwide and suggests the southwest coastal area in Sri Lanka, in the north central Indian Ocean, as a potential spawning ground for this species.

Introduction

The family Berycidae consists of ten species divided into two genera, *Beryx* and *Centroberyx* (Nelson, 2006). The adult fishes of *Beryx* spp. are generally found in the Atlantic, Indian and Pacific oceans (Busakhin, 1982; Vinnichenko, 1997a; Kakora, 2005; Moore, 2016). These fishes are known to have a life span of 8–69 years (Yoshino *et al.*, 1999; Friess and Sedberry, 2011a). The adult length also varied among the three species, *B. decadactylus* reach up to 270–630 mm (Friess and Sedberry, 2011a; Santos *et al.*, 2019), while *B. splendens* to 200–520 mm (Adachi *et al.*, 2000; Rico *et al.*, 2001) and *B. mollis* to 97–330 mm (Yoshino *et al.*, 1999; Borsia *et al.*, 2011; Bineesh *et al.*, 2018).

Beryx spp. can be commonly found in waters above continental shelves and slopes, rocky grounds, seamounts and oceanic ridges (Busakhin, 1982; Clark and O'Driscoll, 2003), and are known as batch spawners with spawning aggregations (Isidro, 1996). They occupy different water masses/layers during their life cycle. The adults live in the benthopelagic zone while juveniles are generally restricted to the mesopelagic zone. Previous studies from different regions show that spawning of *Beryx* spp. generally occurs at 600–900 m depths while eggs and larvae develop in the productive surface waters (Mundy, 1990; Isidro, 1996; Lehodey *et al.*, 1997; Akimoto *et al.*, 2002; Santos *et al.*, 2019). Volcanically originated habitats of ocean seamounts are known as popular spawning grounds for *Beryx* spp. (Rogers, 1994; Kuboshima, 1995; Lehodey *et al.*, 1997).

Pelagic early life stages are known to aid widespread dispersal via oceanic currents (Isidro, 1996). *Beryx* spp. show an aggregating behaviour during the day and scatter during the night, most notably with vertical migrations into shallower waters for feeding (Lehodey *et al.*, 1997; Vinnichenko, 1997b). Common prey of these fishes are small crustaceans, mesopelagic fish, cephalopods, polychaetes and salps (Dürr and González, 2002; Di Blasi *et al.*, 2018).

The genus *Beryx* (Beryciformes (Sawbellies); Berycidae (Alfonsinos)) contains three species: Red Bream *Beryx decadactylus* (Cuvier, 1829), Splendid Alfonsino *Beryx splendens* (Lowe, 1834) and Balloon Alfonsin *Beryx mollis* (Abe, 1959). Among the three species, *B. splendens* and *B. decadactylus* are commonly recorded (Masuzawa *et al.*, 1975; Busakhin, 1982) in the Pacific Ocean (Akimoto *et al.*, 2002, 2006), Mediterranean Sea (Psomadakis *et al.*, 2012; Di Blasi *et al.*, 2018), North Atlantic Ocean (Friess and Sedberry, 2011b) and in the Indian Ocean (Shotton, 2016).

Compared to the other two species, *B. mollis* has fewer observations, likely due to their low abundance (Abe, 1959; Yoshino *et al.*, 1999). Most records of *B. mollis* are in the Indo-West Pacific region, mainly in Japanese waters (Yanagimoto and Chow, 2020, Figure 1A). Recent records in the south eastern Pacific and south west coast of India have further extended have extended its known geographical distribution (Bineesh *et al.*, 2018; Kimura, 2023).

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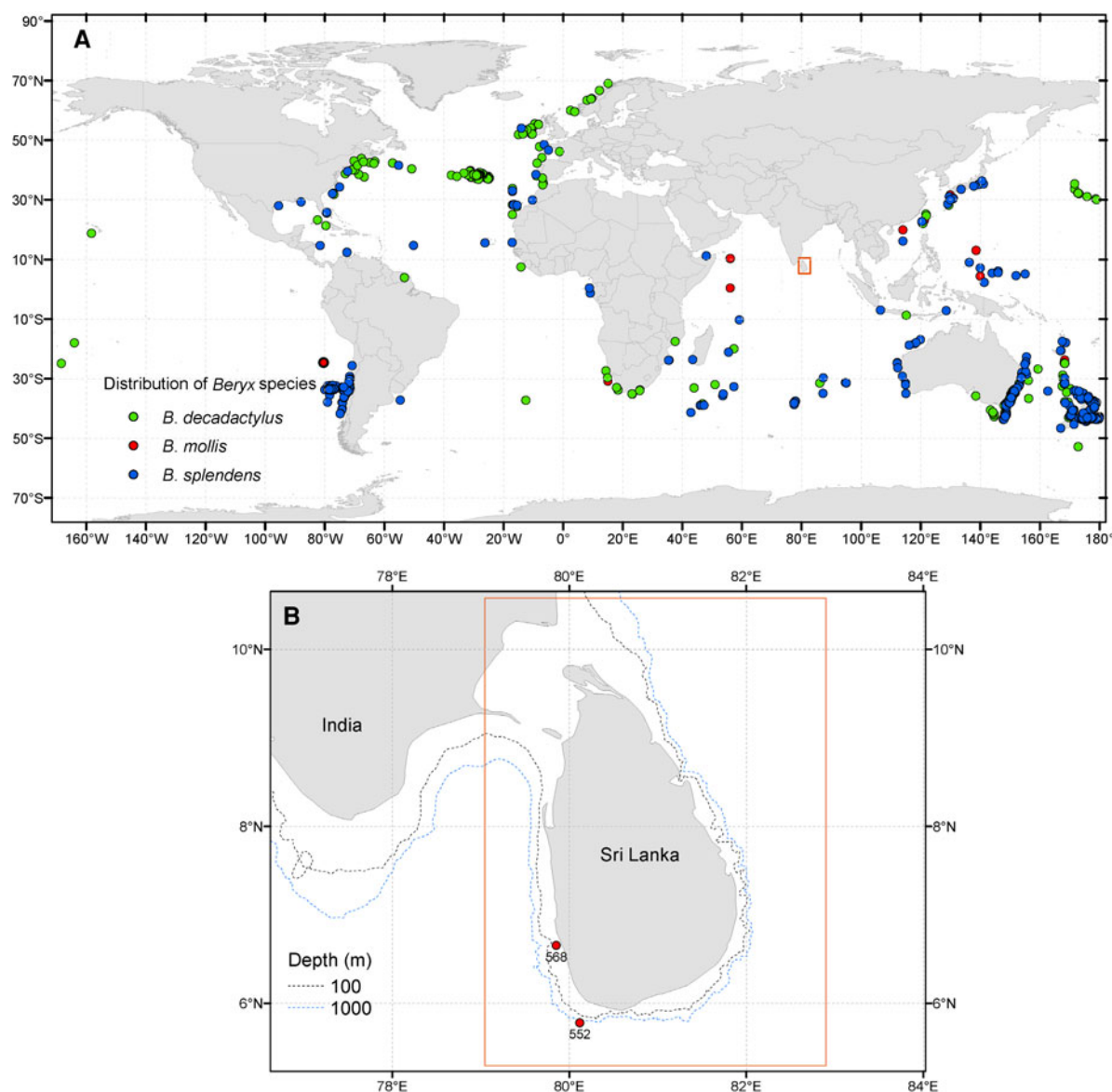


Figure 1. Worldwide distribution of *Beryx* spp., modified after Source GBIF.org (25th July 2023) GBIF occurrence download; https://www.gbif.org/occurrence/search?taxon_key=2356611 and Kimura (2023). (A) The green, blue and red coloured circles indicate the distribution of *B. decadactylus*, *B. splendens* and *B. mollis*, respectively. The orange squares in Figure 1A, B (zoomed) indicate the location of the sampling area off Sri Lanka. (B) The red filled circles show the collected locations of *B. mollis* in the present study – a single egg and an early larva were collected from station 568 and one post larva from station 552 during the present survey.

Extensive commercial fisheries for *Beryx* spp. can be seen in the Pacific Ocean, with catches up to 15,000 tons in the year 2003 (Shotton, 2016). Moderate fishing occurs in the Atlantic Ocean (2500 tons), often as a by-catch in mixed species fishery (Langley and Walker, 2002; Large *et al.*, 2003). Fishing methods used are deep-sea trawls and longlines (Clarke and Moore, 2002). The Japanese coastal area is a successful spawning and breeding ground for *Beryx* spp. These are a common food fish in Japanese markets (Shotton, 2016). Akimoto *et al.* (2006) emphasizes the fact that even though a wide distribution of *B. mollis* in Indo-West Pacific is presumed, very little data on their abundance are available. Despite *B. mollis* being less prevalent in most regions, it has been found to be most abundant (73%) in catches from some areas of the New Caledonia (Akimoto *et al.*, 2006).

Although there are numerous records and literature available on *B. splendens*, and to a moderate extent, on *B. decadactylus*, very little information is available on *B. mollis*. Until early 1990s, *B. mollis* had only been recorded in Japanese waters

(Kotlyar, 1993; Yoshino *et al.*, 1999; Akimoto *et al.*, 2002). This is likely due to similarities in appearance between *B. mollis* and *B. splendens*. In fact, previously *B. mollis* was considered as a juvenile of *B. splendens*. The historical misidentification of *B. mollis* as *B. splendens* could be a plausible explanation for the late documentation of *B. mollis* in these waters.

Although meristic traits such as number of dorsal-fin rays are generally considered to be a distinctive character in segregating *Beryx* spp., this does not apply for *B. mollis* and *B. splendens*, as the numbers to a large extent overlap in these two species (Yoshino *et al.*, 1999; Yoshino and Kotlyar, 2001; Akimoto *et al.*, 2006; Nishida *et al.*, 2022). Furthermore, length/body depth ratio and body colour traits are also very similar (Nishida *et al.*, 2022), making the segregation of these two species even more difficult.

Conversely, *B. decadactylus* is easily distinguishable due to its unique morphological features. It has a greater body depth and number of soft rays in the dorsal fin (Yoshino *et al.*, 1999; Yoshino and Kotlyar, 2001). Yoshino *et al.* (1999) confirmed *B.*

mollis as a valid species by examination of morphological and morphometric characteristics. Later, the species is verified by observations of adult fishes from both the Indian and Pacific oceans (Yoshino and Kotlyar, 2001; Akimoto *et al.*, 2006; Bineesh *et al.*, 2018).

With the development of molecular techniques, identification of *B. mollis* and *B. splendens* became both easier and reliable. Recent studies using restriction enzymes or species-specific PCR primers have successfully distinguished the three species (Akimoto *et al.*, 2002, 2006; Nishida *et al.*, 2022). Using molecular approaches on adults, Akimoto *et al.* (2002) showed that *B. splendens* is more closely related to *B. mollis* than to *B. decadactylus*.

Species identification of early life stages of *Beryx* spp. is even more difficult than in adults. Even though there are records of early life stages of *B. splendens*, this is not the case for egg, larval and juvenile stages of *B. mollis* (Akimoto *et al.*, 2006).

The survey area around Sri Lanka, an island in the Indian Ocean, has a unique coastal geographic structure, with a narrow border with shallower depths, and steeper incline continental shelf (De Vos *et al.*, 2014). The ocean around the southern tip of Sri Lanka experiences the exchange of contrasting water masses between the low-saline Bay of Bengal and the high-saline Arabian Sea. Seasonal circulation patterns are influenced by the monsoons. During the highly productive summer (the southwest monsoon, May–September), the monsoon current flows eastward, from the Arabian Sea towards western waters off Sri Lanka (De Vos *et al.*, 2014; Hood *et al.*, 2017) and in the winter (the northeast monsoon, November–February), the East Indian Coastal Current flows westward (Shankar *et al.*, 2002; Lee *et al.*, 2016; Hood *et al.*, 2017). The south western coast of Sri Lanka is the focused area in this study (Figure 1B). Spatial patterns of zooplankton and Chlorophyll-*a* concentrations are closely associated with the monsoons, and a coastal upwelling off the south coast of Sri Lanka is distinctly evident during the peak southwest monsoon period (Yapa, 2000; Dalpadado *et al.*, 2021, 2023; Wimalasiri *et al.*, 2021) providing good feeding opportunities for planktonic organisms.

DNA barcoding techniques have greatly aided the identification of early life stages of fish, expanding existing knowledge on organisms in the Ocean (Leyva-Cruz *et al.*, 2016; Rathnasuriya *et al.*, 2019, 2021; Kerr *et al.*, 2020; Lima *et al.*, 2020). Precise identifications are essential for the conservation and management of these ecologically and economically important fish stocks such as *B. mollis*. Molecular methods combined with morphological measures have proven to be the best method for an accurate and reliable identification of earlier life stages of fish. Therefore, in this study, the morphological characteristics of early life stages of *B. mollis* (egg and larval stages) have been evaluated and species identification confirmed by using molecular approaches targeting the mitochondrial COI gene.

Materials and methods

Sampling

An ecosystem survey was conducted from 24 June to 16 July 2018 in Sri Lankan waters during the southwest monsoon period (Figure 1A, B) using the research vessel Dr. Fridtjof Nansen. The survey was conducted under the framework of the EAF-Nansen Programme (2017–2021) with the objects of encompassing marine resources, pollution and climate (Krakstad *et al.*, 2018). Ichthyoplankton samples were collected using a Manta net (0.1159 m² opening and 335 µm net mesh size). The Manta net was towed horizontally at a speed of ~1.5 ms⁻¹ for 15 min. Although Manta nets were primarily designed for collecting microplastic samples from the surface waters (Pasquier *et al.*,

2022), these gears have later been recognized also as an efficient method for ichthyoplankton sampling (Jonathan, 1988; Kang *et al.*, 2015).

Fish egg and larvae preserved in 96% ethanol were examined under a stereo microscope for morphological features and meristic measurements. Thereafter, a single egg and larvae were assigned specific sample numbers and were placed individually into 1.5 ml micro-centrifuge tubes with 96% ethanol and stored at 4 °C prior to molecular analyses.

DNA isolation, PCR amplification and sequencing

DNA was extracted using a solution containing 75 µl of 5% Chelex 100 Resin (BioRad, CA, USA) and 15 µl of Proteinase K (Qiagen, Germany). Samples were then incubated at 56° C for 1 h and 10 min at 96° C. PCR amplification targeting the mitochondrial COI gene was performed following the protocol described by Mateos-Rivera *et al.* (2020). The resulting sequences were manually curated and uploaded to the GenBank with the accession numbers OR234865, OR234866 and OR234867.

Phylogenetic tree

To make the phylogenetic tree, downloaded COI sequences from the GenBank were retrieved and aligned together with the sequences from this study using MUSCLE in MEGA V11 (Tamura *et al.*, 2021). We applied Neighbour-joining analysis (Saitou and Nei, 1987) and Kimura's two-parameter method (1980) with the percentage replicates in which the associated taxa clustered together in the bootstrap test with 1000 replicates.

An adult *Gephyroberyx darwinii* collected in the same Nansen survey as the current study (accession number OR378763), together with two other sequences of the same species downloaded from the GenBank were used to root the phylogenetic tree. *Gephyroberyx darwinii*, (Johnson, 1866) belonging to the same family Berycidae as *B. mollis* was caught in two bottom trawl stations (6°01'N 81°30'E, 8°45'N 79°31'E) at ~270 m depth during the Nansen survey in 2018. This reef-associated benthopelagic species is widespread in the Indo-West Pacific, Atlantic and Mediterranean subtropical waters (Andrade *et al.*, 2004; Moore, 2016). They occupy depths up to 1200 m (Bertoncini *et al.*, 2004).

Results and discussion

Manta trawl, a reliable method for sampling fish eggs

The manta trawl, resembling the shape of a manta ray, is effectively used to collect ichthyoplankton in surface waters (Brown and Cheng, 1981). This trawl is recognized as a more effective gear in the collection of ichthyoplankton (<15 mm) compared with other Neuston nets (Jonathan, 1988; Kang *et al.*, 2015). Even though the primary objective of the manta trawl in the Nansen ecosystem survey in 2018 was to collect microplastics in the surface water layer, recent studies confirm the effectiveness of this gear in catching pelagic fish eggs in the Indian Ocean.

Molecular and morphology analyses

Based on morphological approaches and DNA sequencing, a single egg and two larval developmental stages of *B. mollis* were identified in the southwestern region (stations 568 and 552, Figure 1B). The egg recorded in this study was 0.98 mm in diameter and contained a single oil droplet of 0.17 mm diameter (Figure 2A, Table 1). The pre-larva and post-larva had standard lengths of 1.6 and 2.8 mm, respectively (Figure 2B, C). To our knowledge, this is the first

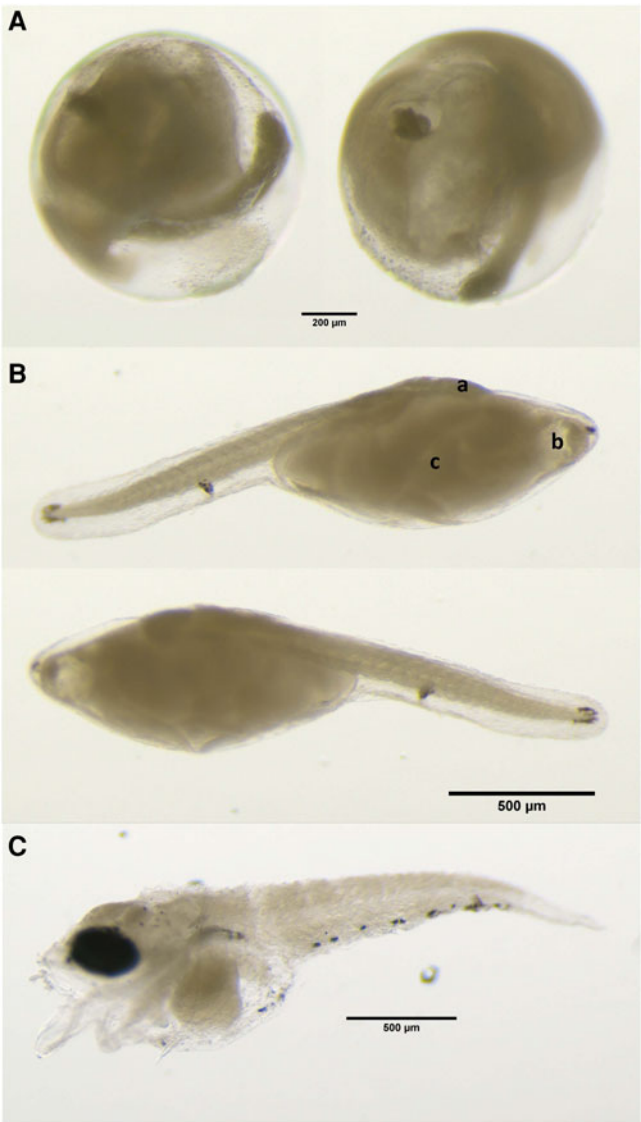


Figure 2. Microscopic images of the early development stages of *Beryx mollis* (A) egg; (B) pre-yolk sac absorption larva (collected in station 552); (C) post-larva (collected in the station 568). Placement of head (a), yolk sac (b) and oil globule (c) in larvae. See Figure 1B for locations. All images were taken from 96% ethanol preserved samples.

morphological description and genetic confirmation of *B. mollis* early developmental stages documented so far.

Phylogenetic analysis

The phylogenetic tree constructed with the sequences from the samples collected in this study together with sequences from the GenBank database showed how the three different *Beryx* species are clustered. The *B. mollis* from this study are clustered together with individuals reported in other regions, e.g. off Japan and India. The *B. mollis* cluster is more closely related to the *B. splendens* than the *B. decadactylus* cluster (Figure 3). Comparison of morphological characteristics exhibited close similarities among *B. mollis* and *B. splendens* than with *B. decadactylus* (Akimoto et al., 2002), as can also be related to their close phylogenetic and evolutionary relationship (Figure 3).

Occurrences of early life stages of Beryx mollis

Fish eggs and larvae of the three *Beryx* spp. share very similar morphological appearances (Akimoto et al., 2002). The morphological descriptions provided by Mundy (1990) and Akimoto et al. (2002), for *Beryx* spp. were used for comparison with our findings (Table 1). These studies have described *Beryx* spp. fish eggs of size 1.08–1.22 mm and having an orange oil globule ranging 0.16–0.31 mm in diameter (Akimoto et al., 2002, Table 1), which agrees with the egg characteristics recorded in our study. Most studies on measurements of fish eggs are on preserved samples. In previous studies on early life stages of *Beryx* spp., samples were collected first in formalin (5–10%) and thereafter transferred to ethanol (ca. 96%) for sorting of species (Mundy, 1990; Akimoto et al., 2002). In our study, the eggs were preserved only in 96% ethanol. The smaller egg diameter (0.98 mm, see Table 1) can most likely be explained by a slight shrinkage due to storage in ethanol (Fowler and Smith, 1983). Combined morphological and molecular approaches from our study confirm the presence of early life stages of *B. mollis* in the north central Indian Ocean.

Low global records of Beryx mollis

Adults of *B. mollis* have been observed in the northwest Arabian Sea (off Somalian waters) and near the coast of Indonesia (Figure 1A). These observations imply that (i) *B. mollis* adults have migrated towards the north central Indian Ocean from the Arabian sea; or

Table 1. Morphological and morphometric characteristic comparisons between *Beryx mollis* egg and larvae from this study and *Beryx* spp. from previous literature.

Sample type		Features	Other studies (<i>Beryx</i> spp.)	This study (<i>Beryx mollis</i>)
Egg	Egg diameter		1.08–1.22 mm	0.98 mm
	Oil globule diameter		0.16–0.31 mm	0.17 mm
Pre-yolk sac absorption larva	Myomeres no.		23	23–25 (poor condition)
	Oil drop diameter		0.15 mm	0.16 mm
	Oil drop located at anterior end of an ovoid yolk		Yes	Yes
	Pigmentation on anterior edge of oil droplet		Yes	Yes
	Pigmentation end of intestine and notochord tip		Yes	Yes
Post larva	Early forming long pelvic fin		Yes	Yes (damaged)
	Pigmentation at gas bladder and posterior intestine		Yes	Yes
	Snout becomes pointed with characteristic concave profile		Yes	Yes
	Early forming and prominent teeth on the premaxilla		Yes	Yes

Egg (Akimoto et al., 2002) and larvae (Mundy, 1990).

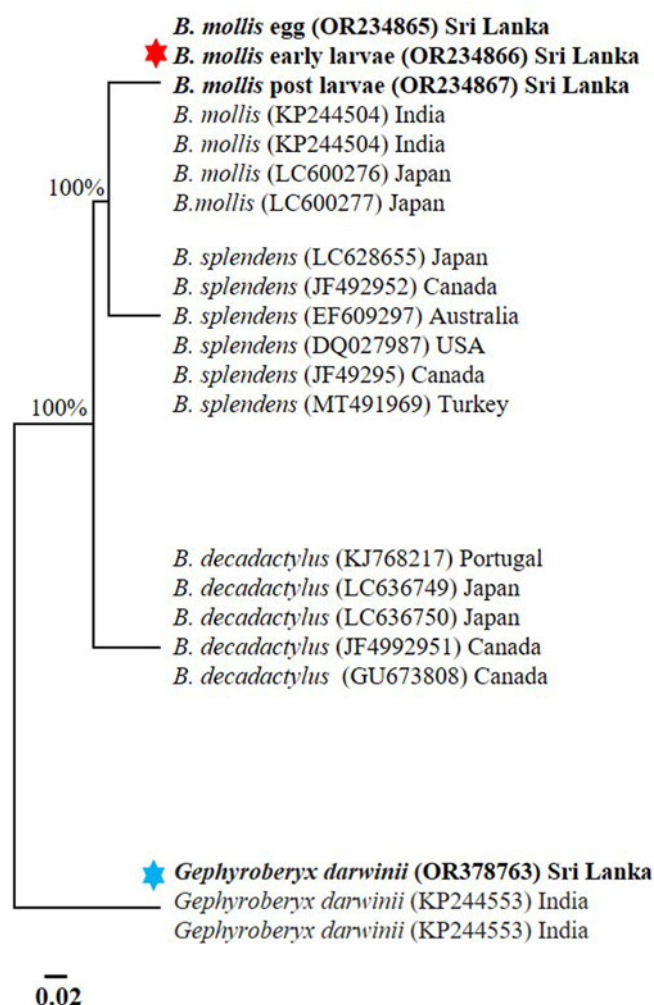


Figure 3. Neighbour-joining phylogenetic tree. COI gene sequences of *B. mollis* from the present study are shown in bold and marked with a red star. The *Gephyroberyx darwinii* collected from the Nansen survey is shown in bold and marked with a blue star. Accession numbers are provided within parenthesis. Evolutionary distance showed in each branch with the scale of 0.02.

(ii) were already present in these areas but never detected. Although in some situations it would be reasonable to suggest one of the hypotheses as to be more likely, this might not be the case for *B. mollis*. As mentioned above there is a misidentification of *B. mollis* as *B. splendens* historically due to their similar morphological features (Yoshino *et al.*, 1999; Akimoto *et al.*, 2006), but also due to that adult *B. mollis* can migrate into several regions across long distances. That would also explain the trans-oceanic migration and distribution of the species (Akimoto *et al.*, 2006). Nonetheless, it was observed that the *B. mollis* sequences in this study showed a high identity (>99%) with two individuals described as *B. cf. splendens* uploaded by Akimoto *et al.* (2006) in the GenBank database (accession numbers GU673458 and GU673459). However, these authors already highlighted the uncertainty of the sequence identity, stating it is likely that these sequences are indeed *B. mollis*. This evidence reinforces not only the high similarity in the morphological characteristics between *B. mollis* and *B. splendens* but also the importance of having a robust and accurate database, especially in poorly researched areas like the north central Indian Ocean.

Although trawling for demersal fish was conducted on our survey, this was only carried out in specific regions to avoid damage to benthic organisms, corals reefs, etc. This could be a contributing factor for not recording adult *Beryx* spp. in the survey catches from this region. The presence of both egg and larvae

in the study region does, however, indicate the likelihood of the presence of adult *B. mollis* in the region.

Future research focus

The present study shows that the productive areas southwest of Sri Lanka are an important spawning ground of *B. mollis*. Future studies should be focused on strengthening combined morphological and molecular approaches to reveal spatial distribution, abundance and species diversity of ichthyoplankton in the region. For such studies to be successful, it is necessary to establish appropriate sampling strategies of fish eggs and larvae using available research vessels and ships of opportunity. Further details of survey, sampling and management strategies in the Indian Ocean ecosystem have been documented in a recent study (Dalpadado *et al.*, 2023).

Acknowledgments. This paper uses samples and data collected through the scientific surveys with the R/V Dr. Fridtjof Nansen as part of the collaboration between the EAF-Nansen Programme of the Food and Agricultural Organization (FAO) and the government of Sri Lanka. The authors thank the scientists and the crew of the survey for their enormous help in sample collection. The support given by the National Aquatic Resources Research and Development Agency (NARA), Sri Lanka, and the Institute of Marine Research (IMR), Norway is highly appreciated.

Author contributions. *In situ data collection and database management:* Sudheera S. Gunasekara, R. P. Prabath K. Jayasinghe, Padmini Dalpadado. *DNA Barcoding:* Alejandro Mateos-Rivera. *Formal analysis:* Yasmin C. Aluwihare, Alejandro Mateos-Rivera, Magnus Reeve, Padmini Dalpadado. *Writing:* All authors contributed to the writing of this manuscript.

Financial support. Financial support for this research work was provided by NARA through counter funds for Sri Lanka-Norway bilateral project (15670 – Technical Assistance to Improve Management of the Fish Resources of Sri Lanka, Phase II LKA-3183, LKA-19/0001).

Competing interest. None.

Ethical standards. These studies were requested and given permission by the Sri Lankan and Norwegian governments under the bilateral research agreement in the Sri Lanka and Norway. Hence, any other specific permission was not required. The animals (ichthyoplankton) used in this work were collected from the sea (their natural environment) in accordance with the national and international regulations compiled by the two countries. No animals were kept in experimental conditions in this study.

Data availability. All data generated in this study are included in the published article.

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