Received: 3 July 2022 | Accepted: 30 October 2022

DOI: 10.1111/jfb.15267

REGULAR PAPER

JOURNAL OF FISH BIOLOGY fsbi

Larval stages of the Antarctic dragonfish *Akarotaxis nudiceps* (Waite, 1916), with comments on the larvae of the morphologically similar species *Prionodraco evansii* Regan 1914 (Notothenioidei: Bathydraconidae)

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Funding information
Explorers Club, Grant/Award Number: OceanX Fellowship; National Science Foundation Antarctic Organisms and Ecosystems Program, Grant/Award Number: PLR-1440435; National Science Foundation Division of Biological Infrastructure, Grant/Award Number: DBI-1349327; Virginia Institute of Marine Science, Grant/Award Number: John Olney Fellowship

Abstract

The notothenioid family Bathydraconidae is a poorly understood family of fishes endemic to the Southern Ocean. There is especially little information on *Akarotaxis nudiceps*, one of the deepest-dwelling and least fecund bathydraconid species. Using genetic and morphological data, we document and describe the larval stages of this unique species, offer a novel characteristic to distinguish it from the morphologically similar bathydraconid *Prionodraco evansii* and use the sampling locations to infer a possible spawning area of *A. nudiceps* along the western Antarctic Peninsula. These results provide important baseline information for locating, identifying and studying the biology of *A. nudiceps*, an important component of the Southern Ocean ecosystem.

KEYWORDS
Akarotaxis, Bathydraconidae, early life history, Notothenioidei, *Prionodraco*, Southern Ocean

1 | INTRODUCTION

Bathydraconidae, the Antarctic dragonfishes, are one of five families of Notothenioidei endemic to the Southern Ocean. The family currently includes 16 species in 11 genera (Eastman & Eakin, 2021). All bathydraconids have an elongate and slender appearance at maturity (Gon & Heemstra, 1990). Morphological analysis suggests that bathydraconids are monophyletic, primarily based on the synapomorphic loss of the first spinous dorsal fin (Derome *et al*., 2002). Although genetic analyses based on sequencing the mitochondrial 16S and 12S regions have suggested that the family is paraphyletic (Bargelloni *et al*., 2000; Bista *et al*., 2022; Daane *et al*., 2019; Near *et al*., 2004, 2012), a recent analysis of *c*. 100,000 nuclear single nuclear polymorphism (SNP) loci recovered a monophyletic Bathydraconidae as a sister lineage of the Channichthyidae (Near *et al*., 2018).

As adults, most bathydraconids are found on the continental shelf and upper slope (de Broyer & Koubbi, 2014) at depths ranging from 500 to 1000 m, although they have been collected from the surface to a maximum depth of 3000 m (Eastman, 2017). Most bathydraconid species likely spawn during austral autumn and early winter (Evans *et al*., 2005; Kock & Kellermann, 1991; Kuhn *et al*., 2011; Loeb *et al*., 1993). Nonetheless, analysis of oogenesis and observations by scuba divers indicate several species also spawn during the summer in the southern Scotia Arc (Barrera-Oro & Lagger, 2010; La Mesa *et al*., 2012), Ross Sea (La Mesa *et al*., 2007) and the Weddell Sea (La Mesa, Calì, *et al*., 2018, La Mesa, Riginella, *et al*., 2018, Van der Molen & Matallanas, 2003). Egg guarding has been reported for several species of bathydraconids; adults generally deposit 200 to 20,000 eggs measuring 1–4 mm in diameter onto rocks (Barrera-Oro & Lagger, 2010; Evans *et al*., 2005; Kock & Kellermann, 1991;

Kuhn *et al*., 2011; La Mesa *et al*., 2021). Eggs will develop for 5–10 months (Evans *et al*., 2005; Kock & Kellermann, 1991), with most larvae hatching in late spring during October and November (Kellermann, 1990).

With just 200 to 300 oocytes, *Akarotaxis nudiceps* (Waite, 1916) has one of the lowest absolute fecundities of all Antarctic notothenioids (Kock & Kellermann, 1991; La Mesa *et al*., 2007). Adults have been recorded in the Weddell, Ross, Bellingshausen and Davis Seas; the species likely has a circumpolar distribution on the Antarctic shelf (Ekau, 1990; Gon & Heemstra, 1990; La Mesa *et al*., 2019). With a depth range of 371–1191 m, *A. nudiceps* is also among the deepest-living bathydraconids (Eastman, 2017). In deep coastal areas of the Weddell Sea, *A. nudiceps* has been reported as one of the most dominant fish species, although very little is known about its biology (Ekau, 1990; La Mesa *et al*., 2019). It has been suggested that *A. nudiceps* exhibits nest guarding due to its low fecundity (La Mesa *et al*., 2007), although this behaviour has not yet been observed. Given the limited number of eggs per female and the inherent challenges of sampling in the Southern Ocean, it is not surprising that the earliest life-history stages of *A. nudiceps* are largely unknown.

In this study, we document and describe the larval stages of *A. nudiceps* caught in the Bellingshausen Sea off the coast of the western Antarctic Peninsula (WAP) based on morphological and genetic data. We also describe characters that differentiate *A. nudiceps* from the morphologically similar, sympatric bathydraconid *Prionodraco evansii* (Regan, 1914). Finally, we map the sampling locations of *A. nudiceps* larvae and discuss possible spawning areas.

2 | MATERIALS AND METHODS

2.1 | Sample collection, measurements and photography

Larval *A. nudiceps* and *P. evansii* were collected using a 2-m^2 frame Metro net (700 μm mesh) towed to *approximately* 120 m depth. The net tows were conducted during austral summer (January–February) as part of the Palmer Antarctica Long-Term Ecological Research (Palmer LTER) programme. Scientists on Palmer LTER cruises collect multidisciplinary data in a fixed-sampling grid (see Smith *et al*., 1995) in the Bellingshausen Sea along the WAP (Ducklow *et al*., 2007). Specimens were preserved in a formaldehyde (1995–2013) or 95% ethanol (2014–present) solution and catalogued in the Nunnally Ichthyology Collection at the Virginia Institute of Marine Science (VIMS), William & Mary (Gloucester Point, VA, USA). The authors used Mitutoyo 500-752-20 digital callipers for all measurements and photographed larvae using a high-resolution AxioCam digital camera mounted on a Zeiss Discovery V20 stereomicroscope, and used Z-stacking to increase the depth of field. Photoshop© was used to adjust colour and contrast of images, clean the background (*e.g*., remove dust from the background; no alteration of the subject was made) and assemble the photographic figures.

2.2 | DNA extraction

We extracted DNA from single eyeballs of larvae following a modified magnetic bead-based protocol. Due to the extended preservation period for several specimens (up to 8 years) and the relatively small size of the eye in these specimens, incubationperi for several steps of the protocol were extended to 24 h periods to ensure successful DNA recovery. Samples were digested in a standard digestion buffer for 24 h at 55°C and vortexed. For each sample, 10 μl of carboxylated magnetic beads (McLab, San Francisco, CA, USA) were cleaned 3× with 100 μl of 0.5 M EDTA, rehydrated in 100 μl of NACL PEG solution and incubated for 24 h at 32°C, followed by three 70% ethanol washes. Finally, DNA was eluted from the magnetic beads in 0.1 TE buffer for 24 h at 32°C prior to amplification.

2.3 | Amplification and sequencing

The full-length mitochondrial-encoded nicotinamide adenine dinucleotide (NADH) dehydrogenase subunit 2 gene

(ND2; *mt-nd2*) and a fragment of the cytochrome oxidase I (COI; *mt-co1*) mitochondrial gene were amplified in a portion of specimens that were suspected to be *A. nudiceps*. We selected these gene regions because they have been demonstrated to distinguish closely related notothenioid fishes (Near & Cheng, 2008) and because of the availability of vouchered reference sequences on GenBank. The COI region was amplified with the COI-3 primer set (Ivanova *et al*., 2007) and the *mt-nd2* region using primers GLN and ASN (Kocher *et al*., 1995). The PCR products were purified using the QIAquick PCR Purification Kit (Qiagen, Hilden, Germany). The purified PCR products were Sanger sequenced in the forward and reverse directions with an ABI BigDye Terminator v3.1 Cycle Sequencing Kit (Thermo Fisher Scientific, Waltham, MA, USA). The resulting fragments were electrophoresed on an ABI 3500 capillary sequencer, and bases were called using the integrated Data Collection Software. The resulting sequences for each sample and locus were edited and assembled into contigs using Sequencher 5.3.6 (Gene Codes Corp., Ann Arbor, MI, USA). NCBI-BLASTN searches (Altschul *et al*., 1990) were conducted with the edited sequences to identify sequences with the highest similarity within the database using MegaBLAST. Sequences without specimen vouchers were excluded from the analysis.

2.4 | Ethical statement

All *A. nudiceps* and *P. evansii* specimens were preserved and catalogued in the VIMS Nunnally Ichthyology Collection prior to this analysis. Therefore, an ethical statement is not applicable.

3 | RESULTS

Based on morphological characters, we identified 14 bathydraconid specimens as putatively representing *A. nudiceps* due to their overall

TABLE 1 The sampling dates, locations and map label key associated with the 14 larval specimens of *Akarotaxis nudiceps*

Label no.	VIMS no.	Count	Sampling date	Latitude	Longitude	Bottom depth
1	20913	1	3 February 1997	−67.770	−69.921	711
2	22788a, b	2	4 February 1997	−68.151	−68.978	239
3	22690	1	7 February 1997	−66.550	−67.174	398
4	41368	1	26 January 2006	−67.649	−70.277	599
5	33107	1	29 January 2011	−70.076	−76.176	336
6	23177	1	17 January 2013	−68.038	−69.595	964
7	24545	1	24 January 2015	−68.958	−73.584	215
8	24518	1	26 January 2015	−69.387	−75.795	308
9	23274	1	21 January 2016	−67.465	−70.585	760
10	43571a, b	2	14 January 2019	−67.522	−70.591	773
11	43716	1	17 January 2019	−67.781	−69.958	750
12	43240	1	18 January 2020	−67.766	−68.241	387

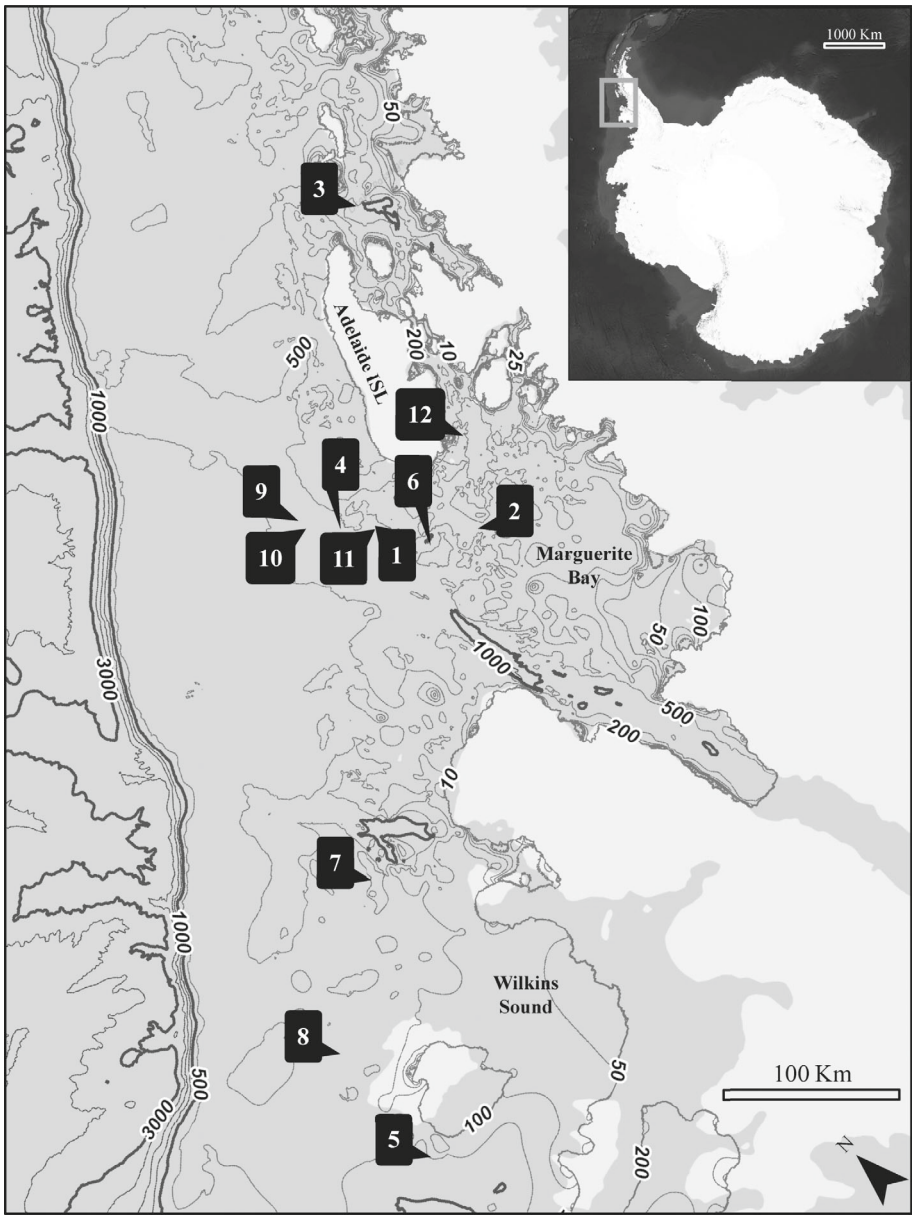

FIGURE 1 Map of a portion of the western Antarctic Peninsula showing the capture sites of the 14 larval specimens of *Akarotaxis nudiceps* examined herein with depth contours in meters. The inset shows Antarctica with the grey box indicating the map region. The specimens were collected by the Palmer Antarctica Long-Term Ecological Research (Palmer LTER) programme during austral summer (January–February). The corresponding VIMS catalogue numbers to each of the shortened labels are given in Table 1

TABLE 2 Morphometric and meristic data of the 14 *Akarotaxis nudiceps* larvae examined herein, including total length (L_T), standard length (L_S), notochord length (L_N), prepectoral length (L_{PP}), predorsal length (L_{PD}), preanal length (L_{PA}), head length (L_H) and preorbital length (L_{PO})

VIMS no.	Stage	L_T	L_S	L_N	L_{PP} (%L_T)	L_{PD} (%L_T)	L_{PA} (%L_T)	L_H (%L_T)	L_{PO} (%L_T)	C	P
43571a	Preflexion	10.8	–	10.1	2.26 (21.0)	0.95 (8.8)	5.7 (52.9)	2.18 (20.2)	0.45 (4.2)	Broken	19/19
43716	Preflexion	10.9	–	10.7	Broken	Broken	Broken	Broken	Broken	Broken	Broken
24545	Preflexion	11.4	–	11.0	2.27 (19.9)	1.66 (14.5)	5.36 (46.9)	2.15 (18.8)	0.53 (4.6)	Broken	Broken
24518	Postflexion	11.8	11.3	–	2.01 (17.1)	Broken	Broken	1.63 (13.8)	0.27 (2.3)	Broken	9/Broken
43571b	Preflexion	11.8	–	11.8	2.44 (20.7)	1.01 (8.6)	5.69 (48.2)	2.28 (19.3)	0.6 (5.1)	8	19/18
23274	Postflexion	13.2	12.6	–	2.5 (19.0)	1.26 (9.6)	Broken	2.22 (16.9)	0.42 (3.2)	5	15/15
23177	Postflexion	13.4	12.1	–	2.99 (22.3)	2.13 (15.9)	6.62 (49.3)	2.92 (21.8)	0.69 (5.1)	13	20/21
41368	Preflexion	14.9	–	14.4	2.95 (19.9)	1.85 (12.4)	7.42 (49.9)	2.7 (18.2)	0.61 (4.1)	11	Broken/22
20913	Postflexion	17.3	16.7	–	3.49 (20.1)	2.65 (15.3)	8.53 (49.2)	3.14 (18.1)	0.77 (4.4)	11	19/19
33107	Postflexion	18.5	17.2	–	4.79 (25.8)	3.34 (18.0)	8.4 (45.3)	4.39 (23.7)	1.21 (6.5)	15	21/21
43240	Postflexion	19.2	17.2	–	4.15 (21.6)	2.84 (14.8)	9.04 (47.1)	3.94 (20.5)	1.13 (5.9)	13	19/18
22788b	Postflexion	19.5	17.6	–	3.77 (19.3)	2.14 (11.0)	8.22 (42.1)	3.24 (16.6)	1.06 (5.4)	12	21/20
22690	Postflexion	19.7	18.6	–	4.85 (24.6)	2.76 (14.0)	9.96 (50.6)	4.54 (23.0)	1.09 (5.5)	13	21/21
22788a	Postflexion	22.7	20.7	–	4.48 (19.7)	2.85 (12.5)	9.56 (42.1)	4.33 (19.1)	1.03 (4.5)	15	21/21

Note: The stage and number of caudal (C) and pectoral (P) fin rays are also listed.

similarity to previous descriptions of larger individuals (Kellermann, 1990). The relatively long guts and slender body shape of the specimens suggested they were larval bathydraconids. Specimens were also heavily pigmented all over, but we ruled out the morphologically similar *P. evansii* based on the lack of dorsolateral and ventrolateral spines (Kellermann, 1990). The 14 specimens were collected between 1997 and 2020 (Table 1) by the Palmer LTER (Figure 1) and ranged from 10.8 mm total length (L_T) to 22.7 mm L_T, with a mean length of 15.4 mm L_T ± 4.0 SD (Table 2).

We sequenced DNA from 2 of the 14 specimens (VIMS 43571a, 10.8 mm L_T and VIMS 43240, 19.2 mm L_T), and obtained *mt-nd2* and *mt-co1* sequences, trimmed to a final length of 1048 and 693, respectively. The *mt-nd2* region for both specimens most closely aligned with two *mt-nd2* sequences for *A. nudiceps* in GenBank from the same analysis (HQ170108.1 and HQ170109.1) with >99% identity and 97% query coverage (accessed on 3 July 2022), supporting the initial morphologically based identification. As these results provided sufficiently clear support to the initial morphological identification of *A. nudiceps*, we opted to restrict genetic analysis to two specimens to limit the dissection of these rare specimens. To confirm the morphological identification of preflexion *P. evansii* larvae, we also obtained an *mt-ND2* sequence (trimmed to a final length of 1048) from a preflexion specimen (VIMS 42468) which most closely aligned with *P. evansii mt-nd2* sequences in GenBank (HQ170126.1 and HQ170127.1) with >99% identity and 91% query coverage (accessed 28 September 2022).

The *mt-co1* region of both specimens also most closely aligned with a *mt-co1* sequence of *A. nudiceps* (OK493722.1) with 96.9% identity and 94% query coverage (accessed on 3 July 2022). We are performing a separate concurrent analysis to evaluate population connectivity of *A. nudiceps* based on the relatively large gap in sequence identity observed between the *A. nudiceps* larvae and the closest sequences available in GenBank for the *mt-co1* region.

The two smallest preflexion larvae (VIMS 43571a, 10.8 mm L_T and VIMS 43716, 10.9 mm L_T) were collected in 2019 near the mouth of Marguerite Bay over bottom depths ranging from 750–773 m (Figure 1). Two other small, preflexion larvae were also collected near the mouth of Marguerite Bay in 2006 (VIMS 41358, 14.9 mm L_T) and 2019 (VIMS 43571b, 11.8 mm L_T). One additional preflexion larvae (VIMS 24545, 11.4 mm L_T) was collected farther south, near Wilkins Sound, over a bottom depth of 215 m (Figure 1).

The preflexion specimens all have a similar pigmentation pattern. Their bodies are heavily and uniformly pigmented from their jaw to their caudal peduncle (Figure 2). Pigmentation extends onto the base of the pectoral fins, although it is less dense than on the body. There is also pigmentation along the base of the dorsal and anal fin folds (Figure 2). The pectoral fins are well developed in preflexion larvae, with pectoral-fin rays (P) ranging from 18 to 22 (Table 2). Fin rays were also present on the caudal fins of these preflexion specimens, ranging from 8 to 11 (Table 2). Nonetheless, the dorsal (D) and anal (A) fin folds are less developed and lack fin rays. The pelvic fins are not clearly visible at the preflexion stage.

Pigmentation pattern changes little during ontogeny (Figure 2). The largest specimen studied (VIMS 22788a, 22.7 mm L_T) was pigmented similarly to the smaller stages, with pigment evenly covering the body. In postflexion specimens, pigmentation extends slightly past the caudal peduncle and onto the caudal-fin rays (Figure 2). The largest specimen examined (VIMS 22788a) had 21 pectoral-fin rays, but its anal and dorsal fins remained undeveloped, with no fin rays clearly present (Kellermann, 1990) (Table 2). Adult *A. nudiceps* are known to have 29–33 D, 25–28 A, 22–24 P and 56–65 vertebrate (V) (Gon & Heemstra, 1990). We were unable to obtain a myomere count from any individual due to the condition of the specimens. Nonetheless, we combined the preanal myomeres (17) from VIMS 24545 and the postanal myomeres (37) from VIMS 20913 to obtain a combined estimate

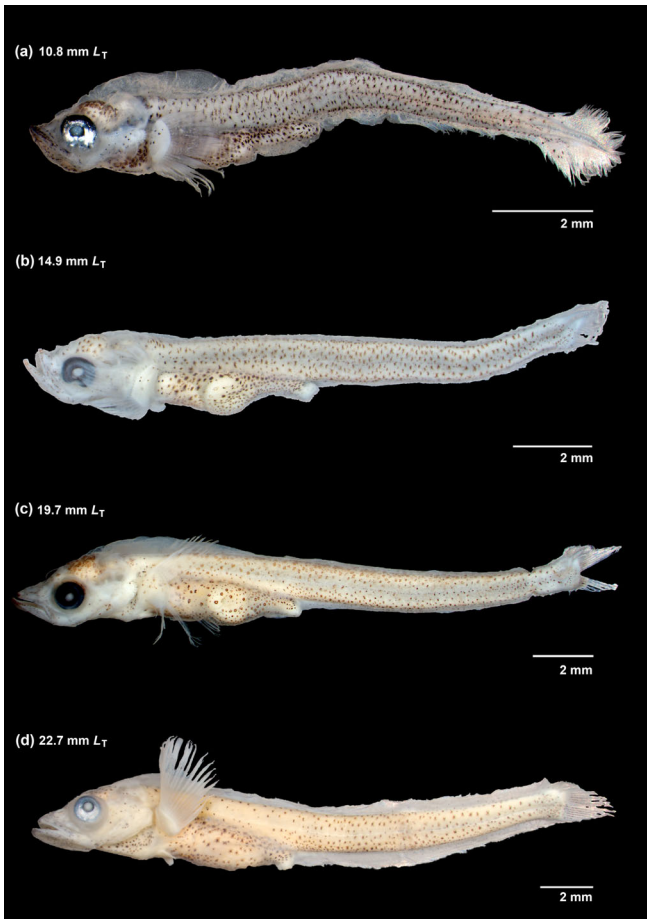

FIGURE 2 Development of *Akarotaxis nudiceps* in left lateral view. (a) VIMS 43571, 10.8 mm total length (L_T), preflexion. (b) VIMS 41368, 14.9 mm L_T, postflexion. (c) VIMS 22690, 19.7 mm L_T, postflexion. (d) VIMS 22788a, 22.7 mm L_T, postflexion

of 54 myomeres (including those associated with three occipital myomeres).

4 | DISCUSSION

4.1 | Early life history of *A. nudiceps*

To our knowledge, there are four reports of the early life stages of *A. nudiceps* in the literature. Kellermann (1990) describes two transforming juveniles (37.0 and 39.1 mm L_S) that were caught during early March and mid-February in the northeastern Weddell Sea. Fin-ray and vertebrate counts for the 39.1 mm L_S specimen were reported as D 26+, A 25+, P 24, V 49. The pigmentation for these transforming specimens was described as being uniformly heavy on the body and lighter on the head. Voskoboinikova (2001) also describes one juvenile (43.1 mm L_S) caught in the Weddell Sea during late February. Fin-ray counts for this specimen were D 29, A 25, P 22, and the heavy pigmentation had begun transitioning to a greyish-brown coloration. Flores *et al.* (2008) found one larva from the Lazarev Sea during April 2004, but the description, length and location were not reported. Finally, Vacchi *et al.* (1999) collected a small, 14 mm L_S specimen that they identified as *A. nudiceps* in the coastal Ross Sea near Zucchelli Station (74° 48′ 75 S, 164° 36′ 90″ E); nonetheless, this specimen was not described or illustrated. This larva was caught with a 5 m^2 Hamburg Plankton Net (500 mm mesh-size) towed to 30 m over a bottom depth of 320 m (Vacchi *et al.*, 1999).

Each of the 14 larval *A. nudiceps* identified in this study was collected at locations that are relatively nearshore, with most ($n = 10$) occurring just outside Marguerite Bay (Figure 1). The Palmer LTER sampling grid extends *c.* 240 km offshore in this area (see Smith *et al.*, 1995), but *A. nudiceps* larvae have not been found in any other net tows during the more than 30-year time series. This suggests that adult *A. nudiceps* are likely spawning in neritic areas along the WAP. This is supported by the coastal association of the only other small *A. nudiceps* larva reported by Vacchi *et al.* (1999). In addition, histological analysis and nesting behaviour of *Parachaenichthys charcoti* in the South Shetland Islands region also indicates that spawning occurs in nearshore habitat (Novillo *et al.*, 2018).

In the relatively ice-free austral summer (*i.e.*, December–February), one of the dominant currents of this region, the Antarctic Peninsula Coastal Current (APCC), is flowing in a southwest direction along the coast of the WAP (Moffat *et al.*, 2008). The circulation pattern is less characterized within Marguerite Bay, but the APCC likely creates a cyclonic surface flow within the bay (Moffat & Meredith, 2018). Based on the congregation of larval *A. nudiceps* across years and APCC flow, we hypothesize that there is a recurring nesting area for *A. nudiceps* somewhere around the perimeter of Adelaide Island (Figure 1). With the limited data, it is not possible to determine whether the larvae collected farther north (VIMS 22690) and south (VIMS 33107, 24545 and 24518) originated from the Marguerite area or if there are multiple spawning sites along the coast. Yolk-sac lengths of *P. evansii* [12.0–14.2 mm standard length (L_S)], *Racovitzia glacialis* (12.0–13.2 mm L_S) and *Gymnodraco acuticeps* (not reported), captured in similar areas along the WAP in November, suggest that hatching occurs in late spring (October–November) (Kellermann, 1990). The mid-January sampling date for the seven larvae smaller than 14 mm L_T (Table 1) in this study suggests that hatching may occur in December. We also did not observe yolk remains on any larvae, indicating *A. nudiceps* may have a smaller length at hatch than other reported bathydraconids, or absorb their yolk sac more quickly.

4.2 | Differences between *A. nudiceps* and *P. evansii*

Several specimens of *A. nudiceps* identified in this study were previously misidentified as *P. evansii*. Although the pigmentation patterns of the two species are similar at early larval stages (Figure 3), a few

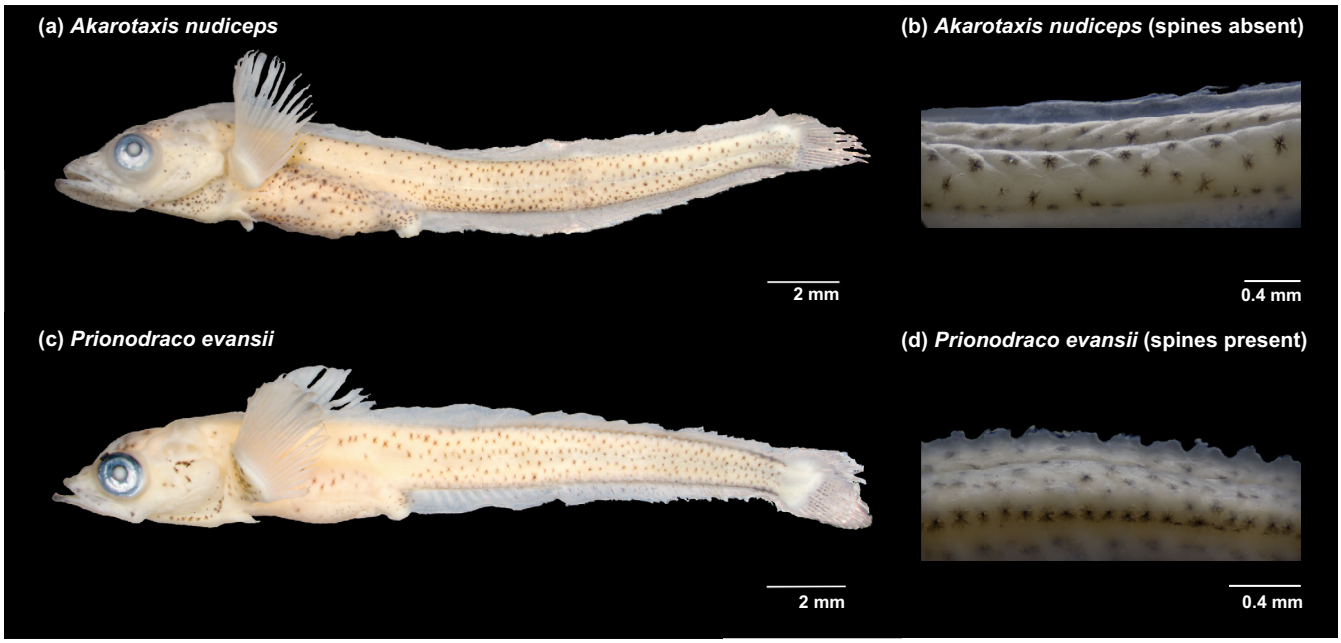

FIGURE 3 Comparison of (a) left lateral view and (b) dorsal view of lower tail of *Akarotaxis nudiceps* [VIMS 22788a, 22.7 mm total length (L_T)] to (c) left lateral view and (d) dorsal view of lower tail of *Prionodraco evansii* (VIMS 43603, 19.4 mm L_T). Anterior faces left in both (b) and (d)

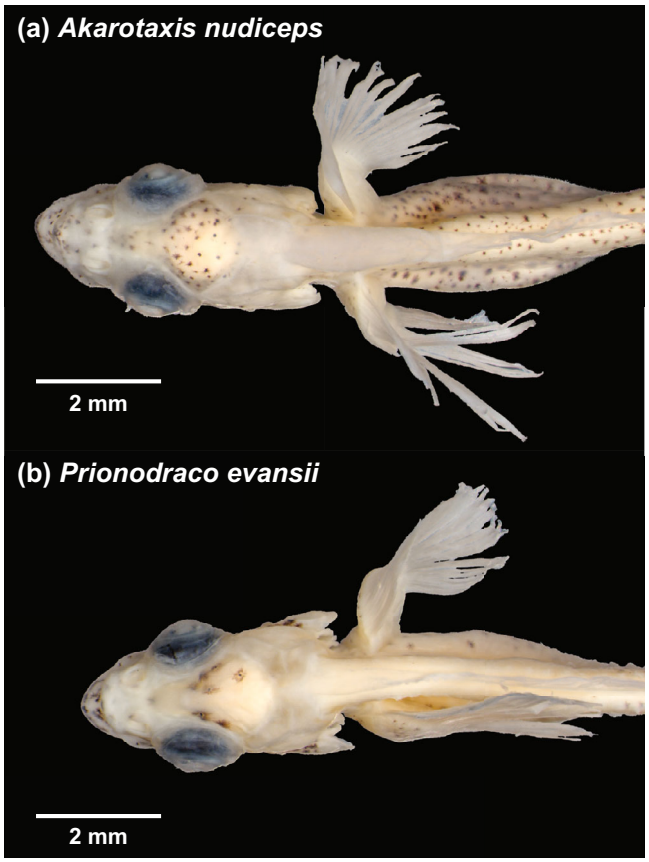

FIGURE 4 Comparison of (a) *Akarotaxis nudiceps* [VIMS 22788a, 22.7 mm total length (L_T)] and (b) *Prionodraco evansii* (VIMS 43603, 19.4 mm L_T). Dorsal view

key differences separate the two species. *P. evansii* has two parallel rows of ventrolateral spiny scales that run from their hindgut to the caudal peduncle and two parallel rows of dorsolateral spines running from the nape to peduncle (Kellermann, 1990). Nonetheless, at early preflexion stages, or in the wrong light, these spiny scales are easily overlooked. The gut and abdomen are less pigmented in the larval stages of *P. evansii* when compared to the condition in *A. nudiceps* (Figure 3), although this difference is difficult to quantify. A second distinguishing characteristic between the two species involves their cranial pigmentation. Each of the 14 larval *A. nudiceps* examined had dense, uniformly spaced pigmentation on the occipital region of the head (Figure 4a). In contrast, *P. evansii* is known to have a few large pigment spots on either side of the posterior portion of the head (Kellermann, 1990) (Figure 4b). We have not yet conducted a thorough developmental analysis of *P. evansii*, but we estimate that most stages have 2–6 large pigment spots.

5 | CONCLUSION

Through the study of an existing collection of preserved larval fishes, we identified and described the early life-history stages of the least fecund notothenioid, *A. nudiceps*, based on morphological and genetic criteria. We provide the first documentation of preflexion and small postflexion larvae for this species. Although relatively few specimens were collected in the more than 30-year time series that we examined, we conclude that spawning occurs near coastal islands and bays along the WAP. Future research is necessary to establish baseline information about the biology and life history of this important

member of the benthic ecosystem. Given the paucity of understanding of the early life history of most Antarctic fishes, we suggest that archived larval collections such as this hold an under-sampled wealth of information on the biology, taxonomy and distribution of this unique ichthyofauna.

AUTHOR CONTRIBUTIONS

A. D. Corso initiated the project, sorted and identified the fishes, measured and photographed the specimens, performed the genetic analysis, processed genetic data, created figures and prepared the manuscript. J. R. McDowell and E. E. Biesack assisted with genetic analysis and data processing. S. C. Muffelman assisted with morphological analysis. E. J. Hilton led morphological analysis, helped with figure development, oversaw the project and acquired funding. All authors edited and developed the manuscript.

ACKNOWLEDGEMENTS

We thank Sarah K. Huber for curatorial assistance, Mario La Mesa for discussion and Miguel Montalvo for photographic assistance. This work was funded by the National Science Foundation Antarctic Organisms and Ecosystems Program (PLR-1440435 for specimen and environmental data collection) and Division of Biological Infrastructure (DBI-1349327 for specimen preservation and analysis), Explorers Club, and the VIMS John Olney Fellowship.

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How to cite this article: Corso, A. D., McDowell, J. R., Biesack, E. E., Muffelman, S. C., & Hilton, E. J. (2023). Larval stages of the Antarctic dragonfish *Akarotaxis nudiceps* (Waite, 1916), with comments on the larvae of the morphologically similar species *Prionodraco evansii* Regan 1914 (Notothenioidei: Bathydraconidae). *Journal of Fish Biology*, *102*(2), 395–402. https://doi.org/10.1111/jfb.15267