Notothenioidea: Development and Relationships

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Notothenioidea comprises 5 families with 35 genera and about 100 species (Table 140). These familes are endemic to the Antarctic and Subantarctic regions (DeWitt, 1971; Norman, 1938a; Wyanski and Targett, 1981). Adults, ranging from 100 to 900 mm SL, occupy several habitats from the surface to several hundred meters depth and are often associated with continental and island slopes and shelves. Some species are adapted for living close to the undersurface of ice.

Discussions of the systematic position of notothenioids are found in Gosline (1968) and Norman (1938a), who consider them Perciformes or perciform relatives on the basis of the adult cranial osteology; the jugular position of the pelvic fins, which have one spine and five rays; and the caudal fin ray number, usually 14. Both note the reduced number of pectoral radials found in Notothenioidea. Gosline (1968) unites the notothenioids with trachinoids and blennioids using characters such as the one to one ratio of vertebrae to dorsal and anal fin rays, more than 25 vertebrae, and fewer than 15 branched caudal rays. Gosline (1968), Norman (1938a), and other recent workers (i.e., Andersen and Hureau, 1979) separate Nototheniidae and Harpagiferidae making a total of five families (this classification is used here), whereas Nelson (1976) follows Berg (1940) and

Table 141. Notothenioidea: Egg Diameter (mm) and Larval Size at Selected Developmental Stages (mm SL).

Family	Egg diameter	Hatching	Notochord flexion	Juvenile
Bovichthyidae	Unknown	Unknown	Unknown	ca. 25
Nototheniidae	1.2–4.0	6–14	9–20	25–60
Harpagiferidae	2.4–3.0	7–13	ca. 9–13	35–38
Bathydraconidae	1.5–3.0	Unknown	18–24	24–34+
Channichthyidae	2.8–4.5	ca. 14	18–42	50–60+

Table 140. Notothenioidea: General Summary and Early Life History Information.

Family	Number of genera	Approximate number of species	Distribution	Early life history		
				Descriptions		Illustrations
				Genera	Species	Species
Bovichthyidae	3	12	Antarctic, Subantarctic	0	0	0
Nototheniidae	8	50	Antarctic, Subantarctic	5	16	12
Harpagiferidae	5	15	Antarctic, Subantarctic	2	4	3
Bathydraconidae	10	14	Antarctic	7	8	6
Channichthyidae	11	17	Antarctic	8	8	7

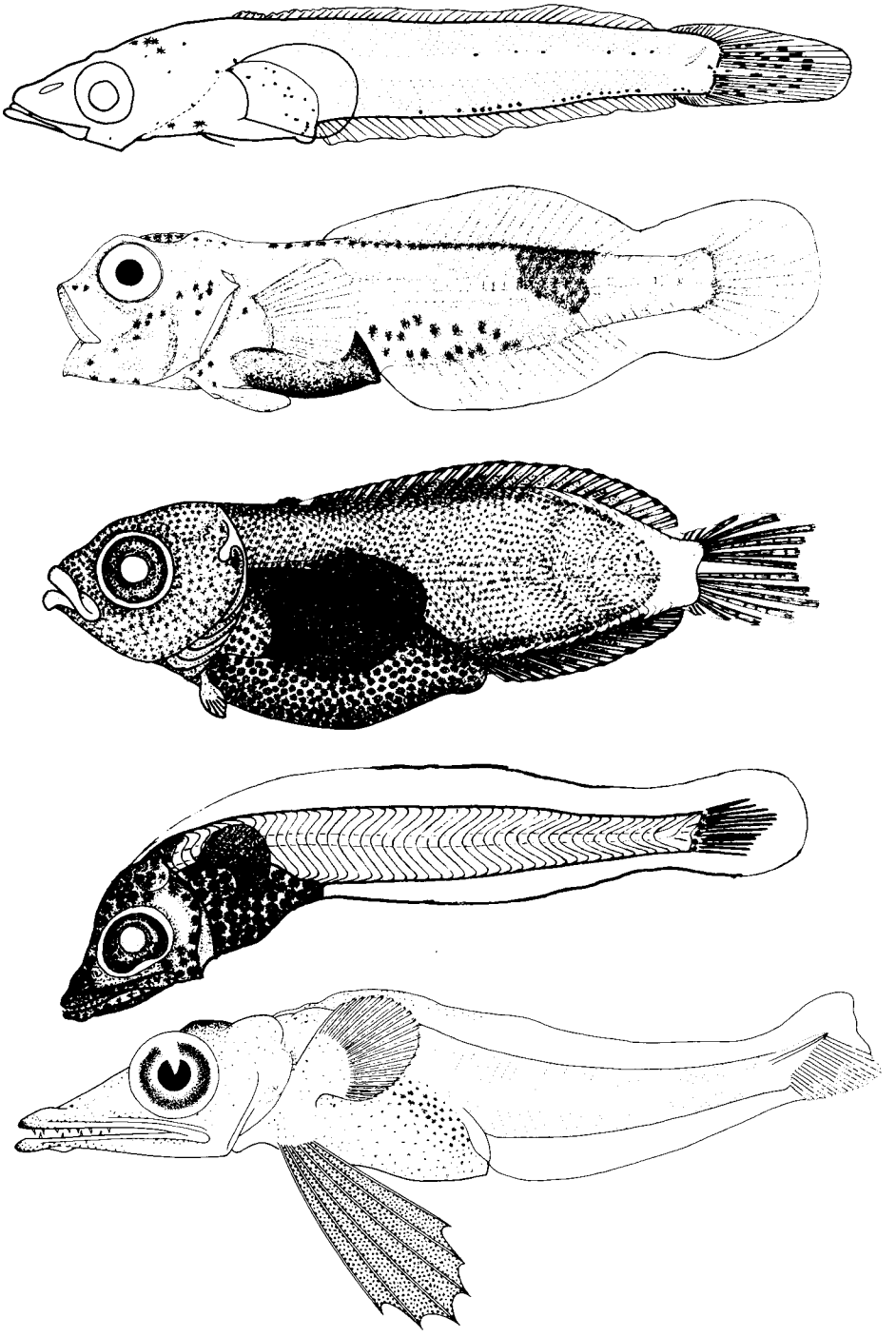

Fig. 301. Notothenioid larvae (from top to bottom): Nototheniidae: *Patagonotothen larseni,* 35 mm, from North and White (1982); Harpagiferidae: *Harpagifer bispinis,* 18.2 mm, from Everson (1968); Harpagiferidae: *Artedidraco mirus,* 24.0 mm, from Efremenko (1983); Bathydraconidae: *Psilodraco breviceps,* 16.9 mm, from Efremenko (1983); and Channichthyidae: *Pagetopsis macropterus,* 19 mm, redrawn by H. Orr from Regan (1916).

TABLE 142. NOTOTHENIOIDEA: SELECTED MERISTICS. Sources listed here do not include the following cited in the text: Andriashev (1959); DeWitt (1970); Norman (1937, 1938); Nybelin (1947, 1951); Regan (1913d, 1916); Yefremenko (1979a, b). Omissions indicate no data were found in the literature. While this paper was in press a revision of the Nototheniidae was published (Anderson, 1984).

Family Genus	Number of species	Fin rays						Vertebrae			Sources
		D_1	D_2	A	Pec.	Pel.	Principal caudal	Pre-caudal	Caudal	Total	
Bovichthyidae											
Bovichthys	10	VII–VIII	18–21	13–19	14–16	I, 4–5				41 (1sp.)	Hureau and Tomo, 1977
Cottoperca	1	VI–VIII	21–24	20–24	17						
Pseudophrites	1–2	VII–VIII	19–20	23–25	18	I, 5					Scott, 1962
Nototheniidae											
Dissostichus	2	VIII–X	25–29	25–30	25–29	I, 5		18–20		54–55	de Ciechomski and Weiss, 1976
Eleginops	1	VIII–IX	24–26	22–24	22–24	I, 5		12	30–31	42–43	de Ciechomski and Weiss, 1976
Pleuragramma	1	VI–VIII	33–38	36–39	20–21	I, 5		18–20		53–55	
Aethotaxis	1	VII	34	30	27–28	I, 5		16	36	52	DeWitt, 1962b
Cryothenia	1	IV–VI	34–36	33–35	24–26	I, 5	14–17	13–18	33–37	50–53	Daniels, 1981
Pagothenia	2	IV–VI	30–37	26–33	23–24	I, 5	14				DeWitt, 1964b
Patagonotothen	16	IV–VIII	27–38	27–37	24–28	I, 5				54–55 (1sp.)	
Notothenia	ca. 27	III–VIII	25–41	21–36	16–30	I, 5	14–16	14–22	27–37	44–58	
Harpagiferidae											
Artedidraco	5	II–IV	24–30	16–21	14–17	I, 5					
Dolliodraco	1	II–III	22–25	14–15	16–18	I, 5		13	21–22	34–35	DeWitt and Tyler, 1960
Histiodraco	1	II–III	26	17	18–19	I, 5					
Pogonophryne	7	II–III	25	16–18	19 (1sp.)	I, 5		15	23	38 (1sp.)	
Harpagifer	1	III–V	21–26	16–21	15–18	I, 5		10–11	24–25	35–36	
Bathydraconidae											
Bathydraco	4	0	34–40	29–31	22	I, 5				52–53	
Gerlachea	1	0	45–47	34–35	26–28	I, 5		25	38	63	
Racovitzia	1	0	30–37	27–31	22–25	I, 5		19–20	32–34	52–54	DeWitt, 1964a
Prionodraco	1	0	34–38	29–33	21–22			16	33–34	49–50	
Cygnodraco	1	0	61–66	35–38	22–23						
Parachaenichthys	2	0	42–46	30–33	21–23						
Psilodraco	1	0	27–30	27–29	25–27			16		48	
Gymnodraco	1	0	28–30	22–26	21–22	I, 5	13	20–21	28	48–50	DeWitt and Tyler, 1960
Akarotaxis	1	0	31–33	27–28	22–23	I, 5	12–13	17	33	50	DeWitt and Hureau, 1979
Vomeridens	1	0	34	32	31–33	I, 5	12	18	36	54	DeWitt and Hureau, 1979; DeWitt, 1964a
Channichthyidae											
Champsocephalus	2	VII–XI	32–41	31–40	22–29	I, 5		16–18		60–64	Kock, 1981
Pagetopsis	2	IX–XV	26–31	24–27	22–23	I, 5		18–20		56–58	
Pseudochaenichthys	1	VIII–XI	28–32	27–31	22–25	I, 5		16–18		51–55	Kock, 1981
Neopagetopsis	1	XIV	34	29	26						
Dacodraco	1	III	32	29	24	I, 5					
Chaenichthys	2	VI–IX	30–35	27–34	18–22	I, 5				54–56	
Chaenocephalus	1	V–IX	37–42	36–40	23–26	I, 5		18–20		60–64	Kock, 1981
Cryodraco	2	III–V	40–45	39–46	23–25	I, 5		20–22		63–65	
Chionodraco	3	V–VII	37–51	33–38	21–24	I, 5		16–18		60–64	
Chaenodraco	1	VI–VIII	38–42	32–35	22–25	I, 4		18–20		60–62	
Chionobathyscus	1										

Greenwood et al. (1966) in placing Harpagiferinae as a subfamily of Nototheniidae (Table 140).

Development

The first work on the early life history of these fishes was undertaken with material collected on the polar expeditions of the early 20th century. Regan (1916) illustrated larvae of seven notothenioid species. Additional early life history data were sparse until the Antarctic expeditions of the second half of the century. In the last 30 years efforts have been directed toward understanding the biology, ecology, population dynamics, and physiological adaptations of these fish. In these investigations some early life history data have been acquired. Larvae of 36 species have been described (Table 140). The most comprehensive summaries are the key in North and White (1982), the papers of Yefremenko (1979b, c) and the atlas of Efremenko (1983a).[1] No early life history data are available for the family Bovichthyidae except for a brief description of the behavior and an illustration of a 25 mm prejuvenile of *Bovichthys variegatus* (Robertson and Mito, 1979).

Eggs

Eggs of four notothenioid families have been described including some known only from studies of ovaries (Table 141). Eggs are moderate to large (1.2–4.5 mm diameter) with large yolks, no oil globules, and small perivitelline spaces (Marshall, 1953; Andriashev, 1965; Dearborn, 1965). In one species, *Notothenia* (*Trematomus*) *bernacchii*, eggs are bright yellow to deep brown. Most species are demersal spawners; nesting behavior has been observed in *N. bernacchii* (Moreno, 1980) and *Harpagifer bispinis* (Daniels, 1978). However, *Notothenia microlepidota* eggs have been reported from plankton collections (Robertson, 1975a). The demersal eggs are sticky, clinging to substrate or algae. One species, *N. neglecta*, reared in the laboratory from artificially fertilized eggs, has an incubation time of 103–150 days and hatches with a well-developed, heavily pigmented body, black eyes, and a large yolk sac (White et al., 1982). Daniels (1978) reports an incubation time of 14 to 18 weeks for *H. bispinis*.

Larvae

Morphology.—The described larvae of 36 species display some morphological similarity (snout–anus length), and some diversity (snout length and body shape). Preflexion larvae, ca. 6–18 mm SL, are elongate with large pectoral fins and moderate to wide finfolds. Channichthyid larvae have well developed pelvic fins at this stage and more elongate snouts than larvae of other notothenioids. Some species have large yolk sacs which persist after notochord flexion has begun. Preanal lengths range from slightly under to slightly over 50% of body length.

During flexion and postflexion stages most larvae maintain their elongate shape (Fig. 301). However the larvae of the harpagiferid genera *Artedidraco* and *Pogonophryne* become very robust (North and White, 1982; Efremenko, 1983a). Notochord flexion occurs between 9 and 42 mm with larval Harpagiferidae and Nototheniidae flexing at the shortest lengths, Channichthyidae at the longest, and Bathydraconidae at intermediate lengths (Table 141). Size at transformation to the juvenile stage also spans a wide range with *Harpagifer bispinis* settling at 18.3 mm (Everson, 1968) and pelagic larvae of other species reaching 24–60 mm (de Ciechomski and Weiss, 1976; North and White 1982; Yefremenko, 1979b, c).

Larvae of all species develop pelvic fins. Channichthyid larvae retain their elongate snouts and develop teeth and preopercular and rostral spines not reported for other notothenioids (Fig. 301).

Pigmentation.—Pigment patterns of all known larvae are highly specific and are useful identification criteria. The amount and location of pigment varies within families and the amount usually increases with development. A few species have general body pigment, but most exhibit patterns in one or more of the following areas: dorsal body margin, ventral body margin, body midline, peritoneum, gut, and along the myosepta. The occipital and parietal areas typically are pigmented; many species have snout, opercular, and jaw pigment as well. The paired fins are usually pigmented. Pigment is found at the base of the caudal fin in most species, associated with the posterior margin of the hypural elements or the bases of the caudal rays.

Meristics.—Meristics are from counts given for adults by Regan (1913d, 1916), Norman (1937, 1938a), Nybelin (1947, 1951), Andriashev (1959), and DeWitt (1970) (Table 142). Vertebral counts are especially useful diagnostic features within and between families. The dorsal, anal, pectoral, and vertebral counts have been the most significant characters linking larvae to adults (Yefremenko, 1979b, c). The sequence of fin formation is the same in Nototheniidae, Harpagiferidae, and Bathydraconidae with pectoral and caudal fins forming first, followed by pelvics, with dorsal and anal last to ossify. In Channichthyidae the pelvics are precocious and are present in yolk-sac larvae.

Relationships

Knowledge of the early life history of Notothenioidea has not contributed to understanding relationships between Blennioidei and other perciform suborders, but does offer some clues to relationships within the suborder. The lengthy ovarian egg development (Dearborn, 1965; Everson, 1970) is probably related to the cold environment. In other aspects of spawning, i.e., nesting behavior, long incubation time, and laying of demersal adhesive eggs, this infraorder resembles other cold-water blennioids. The well developed state of newly hatched larvae and the sequence of fin development as well as the general lack of specialized larval structures are also blennioid features. Further study of developmental characters, such as the sequence of ossification, might contribute to better understanding of the relationships among the Blennioidei. Superficial morphological and meristic resemblances exist among notothenioid larvae and those of other blennioid species, for example, the notothenioid *Patagonotothen larseni* (Fig. 301), the trachinoid *Trichodon trichodon* (see Trachinoidea, this volume) and the blennioid *Heterostichus rostratus* (see Blennioidea, this volume). As relationships among the blennioids become better known, their relationship with other perciforms might become clearer.

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[1] Efremenko and Yefremenko are alternative transliterations of the name of the same author.