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A description of late and transformation stages of larvae of the *Diaphus ostenfeldi* in the western periphery of the South Pacific Gyre

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Abstract—Postflexion and transformation stages of the *Diaphus ostenfeldi* in the southwestern Pacific Ocean are described for the first time. Identification to the species level was based on tracing characters from fully formed, large metamorphic specimens backward to smaller specimens. It was found that larval *D. ostenfeldi* ≥9.5 mm standard body length (SL) can be characterized by a unique character within the genus *Diaphus*, namely the presence of melanophores at the dorsal fin base and between branchiostegal rays. Metamorphosis in larvae of this species occurs at a much longer body length (~20 mm SL) than in larvae of other species of this genus.

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Diaphus is the most speciose genus of the mesopelagic family Myctophidae and plays a key role in oceanic food webs. Larvae of *Diaphus* are poorly known. Of the 80 species in this genus (Fricke et al., 2020), the early stages of development are known for only 10 species. These species are the *D. agassizii* (Pertseva-Ostroumova, 1975), Garman's lanternfish (*D. garmani*) (Sassa et al., 2003), *D. hudsoni* (Olivar, 1987), short-headed lantern fish (*D. brachycephalus* or *D. richardsoni*) (Olivar and Beckley, 1995), *D. diadematus* (Olivar and Beckley, 1995), *D. mollis* (Olivar and Beckley, 1995), *D. metopoclampus* (Sparta, 1952), *D. pacificus* (Moser and Ahlstrom, 1974), California headlightfish (*D. theta*) (Moser and Ahlstrom, 1996), and Malayan lanternfish (*D. malayanus*) (Tsokur, 1975). The early stages of development are known in only 2 species of the 9 species of *Diaphus* that have been observed in the southwestern Pacific Ocean: *D. hudsoni* and *D. mollis* (McGinnis, 1982; Bekker and Evseenko, 1986).

Diaphus ostenfeldi is circumglobal, is distributed in the Subtropical Convergence, a frontal zone between subantarctic and tropical water masses, and is considered to be a convergence (Krefft, 1974), notal or subantarctic (Parin et al., 1974), or transitional (McGinnis, 1982; Bekker and Evseenko, 1986) species. This species has been observed in the central eastern Pacific Ocean (McGinnis, 1982) and in the southwestern Pacific Ocean (Bekker and Evseenko, 1986), and its range is known to extend to about 23–24°S in the region of the Benguela Current (Trunov, 1968; Hulley, 1972). It has been found at depths as great as about 120 m below the sea surface (Bekker, 1983). Juveniles have been taken at depths less than 100 m; larger specimens have been found at depths 160 m below the sea surface (Hulley, 1981; McGinnis, 1982). Little is known of the ecology of this species. Specimens caught in the South Atlantic Ocean were limited between the 10°C and 15°C isotherms at a depth of 200 m; however, it has been assumed that the species can live at shallower depths, in suitable temperatures (Krefft, 1974; Hulley, 1981).

Herein, we present larval descriptions for *D. ostenfeldi* from the southwestern Pacific Ocean based on a developmental series of larvae from the postflexion stage to the transformation stage.

Materials and methods

Larvae of *D. ostenfeldi* were caught at 4 stations (stations [st.] 3049, 3052,

3054, and 3069) during the 34th expedition of the RV *Dmitry Mendeleev* to the southwestern Pacific Ocean in January–February 1985 (Fig. 1). All specimens were caught by using an Isaacs-Kidd mid-water trawl with the Samyshev-Aseev modification in the depth layers of 0–100 m, 0–200 m, and 0–600 m in the area between 35°S and 57°S. This trawl is 25 m long and has a 5-mm mesh net without nodes and with a terminal insertion of 500-µm nylon mesh and a 6-m^2 mouth area. The specimens were preserved and stored in 10% formaldehyde. We captured 62 specimens that were 8.6–20.5 mm standard body length (SL); larvae of smaller sizes were absent in samples of trawl hauls.

Information for the following features are included in the descriptions of larval stages in this paper (Moser, 1996): SL, head length (HL), body depth at pectoral fin base (BD), preanal length (PAL), predorsal length (PDL), snout length (SnL), horizontal diameter of the eye (ED), number of rays in dorsal fin (D), number of rays in anal fin (A), number of rays in pectoral fin (P_1), number of rays in pelvic fin (P_2), number of rays in caudal fin (C), number of gill rakers (GR) on the upper and lower parts of the first gill arch, and number of vertebrae (V). Descriptions include patterns of the following photophores (Bekker, 1983): branchiostegal (Br), opercular (Op), pectolateral (PLO), pectoventral (PVO), pectoral (PO), ventrolateral (VLO), ventral (VO), supraanal (SAO), anterior anal (AOa), posterior anal (AOp), and posterolateral (Pol). Also included in descriptions are the following orbital glands: dorsonasal (Dn), anteorbital (Ant), suborbital (So), and ventronasal (Vn).

Results

Identification

The identification of large specimens (>20 mm SL) as *D. ostenfeldi* was based on the following features: the number of gill rakers on the first gill arch of 25–26, So absent, Ant present, Dn and Vn connected but not extended anteriorly from the olfactory rosette, no enlarged teeth in the lower jaw inner row, head depth approximately equal to its length, VLO about midway between lateral line and base of the ventral fin. The identification of specimens smaller than 20 mm SL was based on tracing characters from fully formed, large metamorphic specimens backward to smaller specimens.

Body proportions

The larvae have a moderately deep body (BD 24–28% SL). The head is relatively small (HL 25–30% SL) but deep with

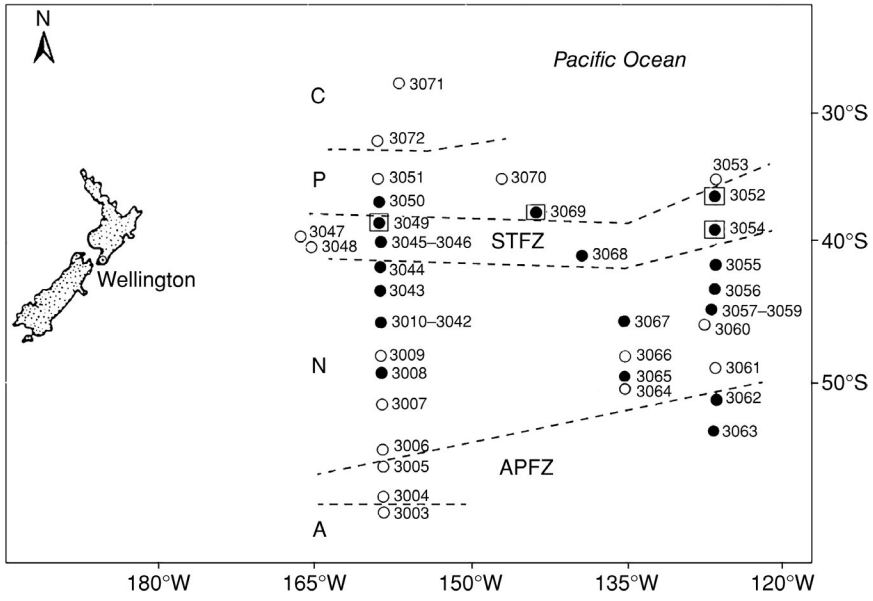

Figure 1

Schematic map of the stations (open circles) where larval (open squares) and adult (black circles) *Diaphus ostenfeldi* were sampled during the 34th cruise of the RV *Dmitry Mendeleev* in the southwestern Pacific Ocean between January and February 1985. Dashed lines indicate the positions of biogeographic borders (Becker and Evseenko, 1986) for the central water mass (C), periphery of the central water mass (P), subtropical frontal zone (STFZ), notal zone (N), Antarctic Polar Frontal Zone (APFZ), and Antarctic (A). Station numbers are given next to station markers.

a steep profile; the depth of the head at the corner of the mouth is almost equal to HL. The jaws are long and continue beyond the vertical of the eye posterior edge; both jaws have small teeth. Jaw length increases with larval size. The snout is short (SnL 19–22% HL), the eye is slightly oval at sizes up to about 16 mm SL (ED 25–30% HL). The anus opens slightly behind the midbody (PAL 57–61% SL). The dorsal fin begins almost at the middle of the body (PDL 44–48% SL). The posterior margin of the pectoral fin rays reaches the vertical of the ventral fin base, and the tips of the ventral fin rays reach the anal fin origin. The proportions are generally retained with increases in larval size.

Meristic characters

D: 16–17, A: 16, P_1: 11, P_2: 8, C: 6–10+9–6(5), GR: (8)9+1+15–17=25–26, V: 37–38. Fin rays are formed in all fins at 8.6 mm SL, and larvae have a definitive number of gill rakers at 12.0 mm SL. Larvae have 37–38 myomeres.

Pigmentation

The 8.6-mm-SL larva (Fig. 2A) has one melanophore dorsally on the peritoneum near the terminus of the gut, one melanophore behind the anal fin base (these melanophores

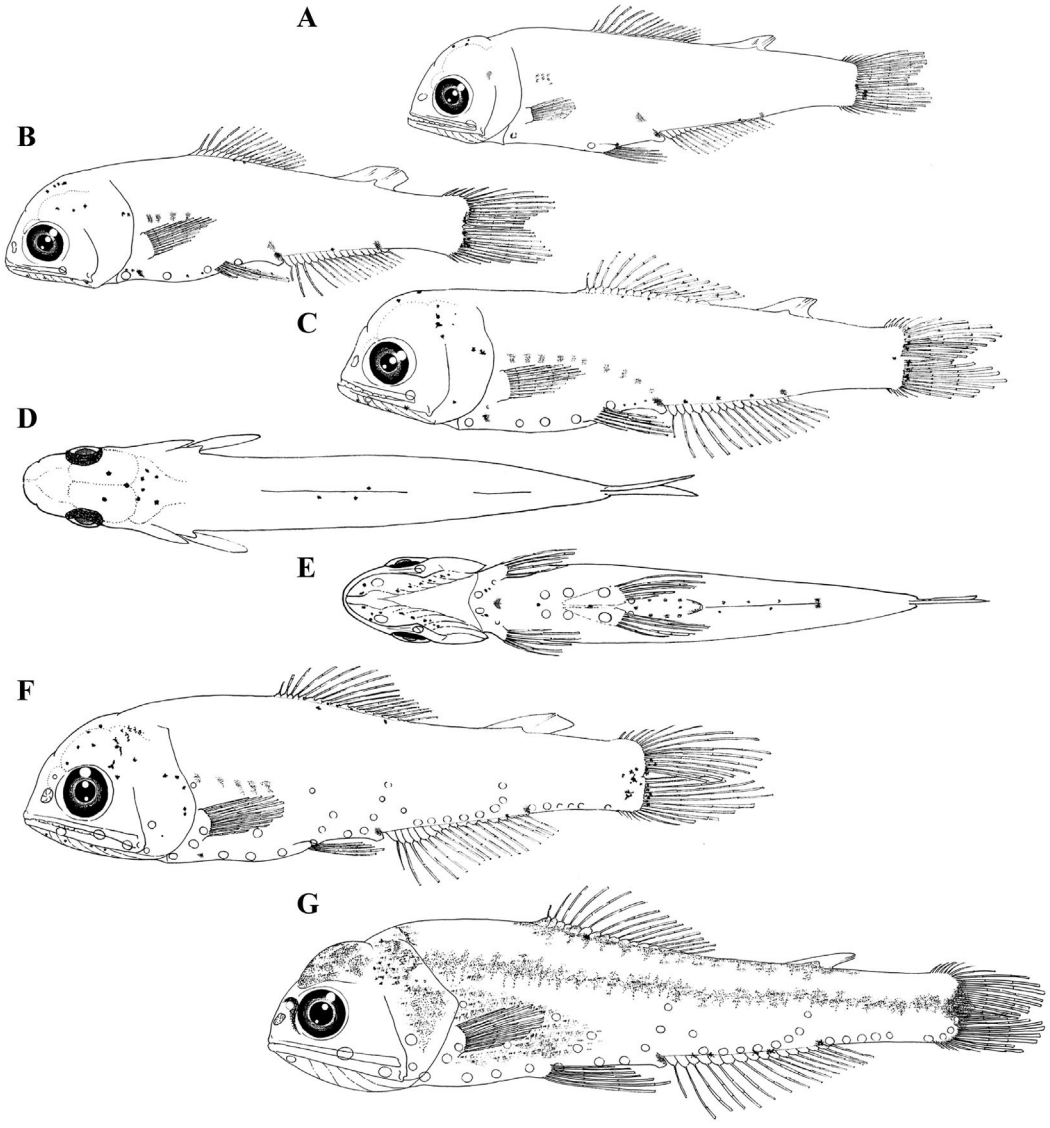

Figure 2

Illustrations of 5 larval and transformation specimens of *Diaphus ostenfeldi* caught in the southwestern Pacific Ocean in 1985: (**A**) 8.6 mm standard body length (SL), (**B**) 9.5 mm SL, (**C**) 10.7 mm SL, (**D**) 10.7 mm SL (dorsal view), (**E**) 10.7 mm SL (ventral view), (**F**) 15.8 mm SL, and (**G**) 20.5 mm SL.

are present in all specimens and noticeable to a size of 20.5 mm SL), and one melanophore above the posterior part of the anal fin base (approximately at the level of the 12th pterygiophore). Several melanophores are present proximally on the lower caudal fin rays. Internal melanophores are visible above the midbrain and above the otic capsules; melanophores are scattered on the dorsolateral part of the peritoneum. In the 9.5-mm-SL larva (Fig. 2B), melanophores are added at the dorsal fin base and at the base of some upper caudal fin rays. An unpaired internal melanophore is visible on the anteroventral part of the liver on the level of the pectoral fin base; melanophores appear above the hindbrain, on the opercle, and on the membrane between the branchiostegal rays. Pigmentation becomes more intense by a size of 10.7 mm SL (Fig. 2, C–E) and is added ventrally at some myosepta on each side along the anal fin base. Melanophores at the dorsal fin base and above the anal fin base are not located symmetrically on each side. This pigmentation pattern persists up to a size of 20.5 mm SL (Fig. 2, F and G). Ventrally, almost all individuals larger than 10.7 mm SL have a row of 2–4 melanophores: approximately at the level of the future PO_2, PO_5, VO_1, and VO_5. Pigmentation of the caudal fin persists to a size of 20.0 mm SL.

Photophore formation

The 8.6-mm-SL larva has Br_2, PO_1, PO_5, and VO_1 beginning to form. At a size of 11.0 mm SL, Br_1 and $PO_{2–3}$ are added. Larvae at a size of 13.0 mm SL have $Br_{1–3}$, $Op_{1–2}$, $PO_{1–5}$, $PVO_{1–2}$, $VO_{1–5}$, and $AOa_{2–7}$. At a size of 16.0 mm SL, formation of PLO, VLO, $SAO_{1–3}$, Pol, and $AOp_{1–5}$ ends (Fig. 2). By a size of 20.0 mm SL, specimens have a definitive photophore pattern, but formation of the orbital luminous glands is not yet complete: So absent, the dark tissue at the future Ant is triangular, roundish Dn connected with the dark tissue of the future Vn and Ant, and Vn reaches the anteroventral part of the eye (Fig. 3).

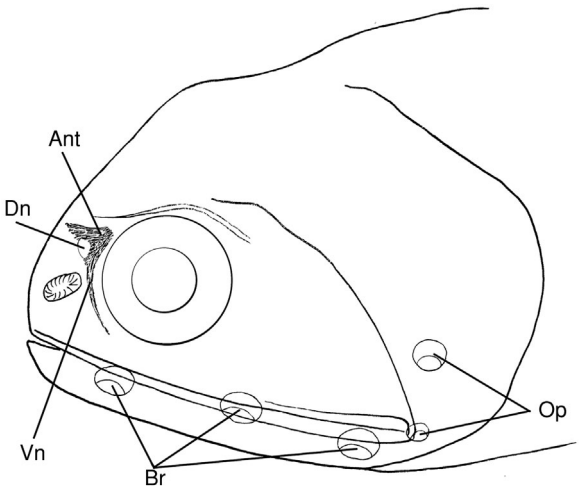

Figure 3

Illustration of the locations of the orbital luminous organs in a transformation specimen of *Diaphus ostenfeldi* that has a standard body length of 20.5 mm and was caught in the southwestern Pacific Ocean in 1985. Locations of the following organs are shown: dorsonasal (Dn), anteorbital (Ant), ventronasal (Vn), branchiostegal (Br), and opercular (Op).

Discussion

The larvae described herein belong to a moderately deep body morphotype (Moser and Ahlstrom, 1972, 1974; Moser et al., 1984). They have a few melanophores on the postanal ventral midline (Fig. 2) and have no So photophore (Fig. 3). In total, 9 species of *Diaphus* can be found in our study area in the southwestern Pacific Ocean: *D. anderseni*, *D. danae*, *D. effulgens*, *D. hudsoni*, small lantern fish (*D. meadi*), *D. mollis*, Taaning's lantern fish (*D. termophilus*), *D. parri*, and *D. ostenfeldi* (McGinnis, 1982; Bekker and Evseenko, 1986). Larvae are known for 2 of these species, *D. hudsoni* and *D. mollis* (Olivar, 1987; Olivar and Beckley, 1995), and they belong to a different morphotype that is moderately slender. In addition, they clearly differ from our larvae by the absence of pigmentation at the dorsal fin base and at the branchiostegal rays. Among the remaining 7 species, only 3 species, *D. effulgens, D. danae*, and *D. ostenfeldi*, have no So photophore as we observed in our transformation specimens. One of these species, *D. effulgens*, has fewer gill rakers on the first gill arch than we observed in our specimens (17–22 versus 24–25); another of those species, *D. danae*, has more gill rakers on the first gill arch (27–30) (Nafpaktitis, 1978; Bekker, 1983). For these reasons, the *Diaphus* larvae in the developmental series presented herein were identified as larvae of *D. ostenfeldi*.

Comparative notes

There are several common features in the pigmentation between our *Diaphus* larvae and those described in earlier reports (Sparta, 1952; Moser and Ahlstrom, 1974, 1996; Pertseva-Ostroumova, 1975; Tsokur, 1975; Olivar, 1987; Olivar and Beckley, 1995; Sassa et al., 2003): melanophores behind the cleithrum symphysis, at the peritoneum near the terminus of the gut, behind the anal fin base, and proximally on the lower caudal fin rays. At the same time, larval *D. ostenfeldi* can be distinguished from all known *Diaphus* larvae by the presence of pigment on the dorsal fin base and the branchiostegal rays at lengths ≥9.5 mm SL. One more difference between the larvae of *D. ostenfeldi* and the other *Diaphus* species is that parietal and peritoneal pigmentation appears earlier in development in the *D. ostenfeldi* than in its congeners. In addition, the transformation of larvae described in this article was still not complete even at a length of 20.5 mm SL; our larvae have a full complex of photophores typical for adults, but the formation of orbital glands was not yet completed. In all

Diaphus larvae described earlier by others (Sparta, 1952; Moser and Ahlstrom, 1974, 1996; Pertseva-Ostroumova, 1975; Tsokur, 1975; Olivar, 1987; Olivar and Beckley, 1995; Sassa et al., 2003), photophores are formed by a size of about 11–15 mm SL. This length may correlate with the size of adults. The *Diaphus ostenfeldi* attains a length of about 120 mm SL (Hulley, 1981), but the sizes of other species whose early stages are known do not exceed 90 mm SL (Hulley, 1981; Bekker, 1983).

Distribution

In the southwestern Pacific Ocean between 35°S and 57°S, adults of this species were encountered at the 18 stations sampled during the 34th expedition of the RV *Dmitry Mendeleev* in different water masses, from the central masses in the north of the study area across the subtropical frontal zone and the notal zone of the South Pacific Ocean to the Antarctic Polar Frontal Zone in the south of the study area (Bekker and Evseenko, 1986). Larvae of *D. ostenfeldi* were found at 4 stations in a narrow range of latitudes between 35°S and 39°S in the subtropical frontal zone. This area was located on the western periphery of the vast anticyclonic South Pacific Gyre.

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