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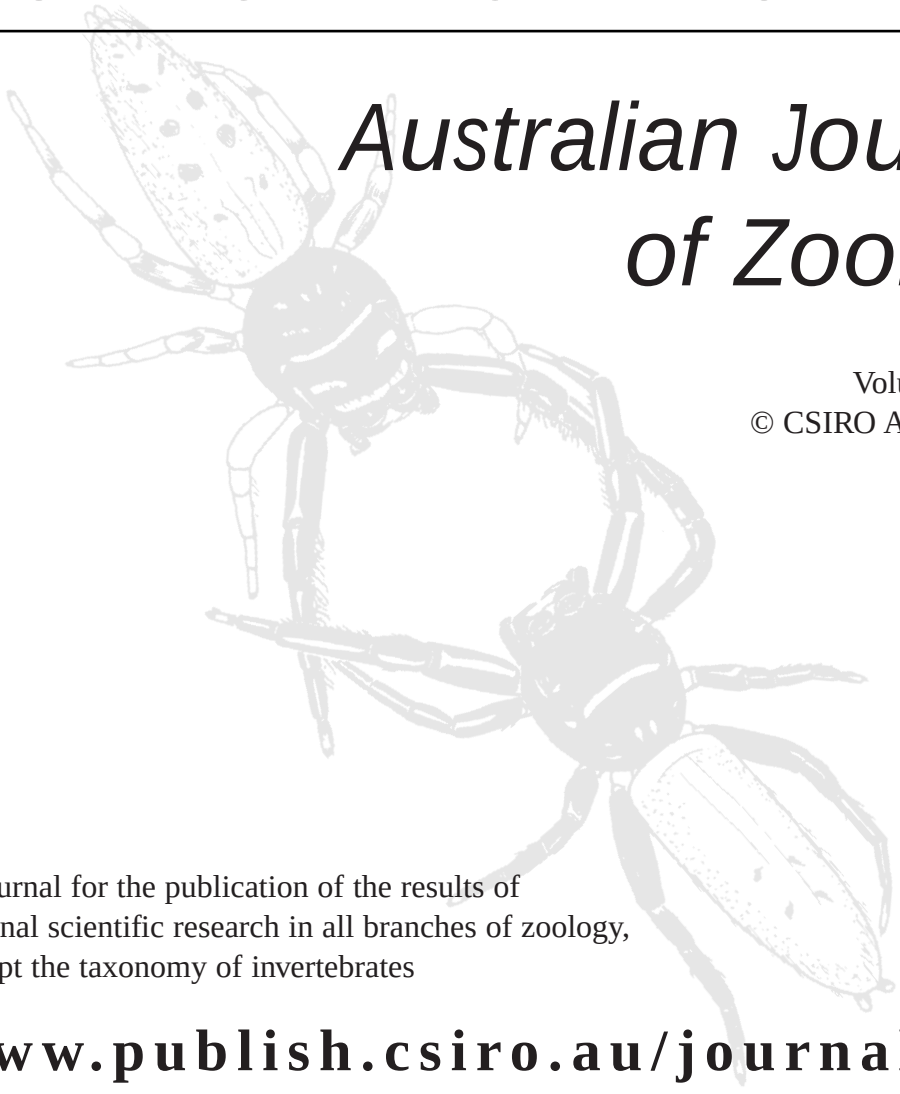

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Development and ecology of larvae of the monotypic Australian fish family Dinolestidae

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Abstract.

The development and seasonal distribution of larvae of *Dinolestes lewini,* the sole species of the endemic Australian family Dinolestidae, are described for the first time using larvae 1.88–14.13 mm in body length caught in south-eastern Australia. Larvae have a moderately deep body, 27–29 myomeres, a moderate to large head, a large mouth with prominent, early-forming premaxillary teeth, small to moderate preopercular spines, a coiled and compact gut, and are moderately pigmented. Notochord flexion takes place between 4.8 and 7.0 mm and transformation at a size >14 mm. Larvae closely resemble those of *Apogonops* (Acropomatidae), *Pomatomus* (Pomatomidae) and *Scomber* (Scombridae), genera that have been postulated to be related to *Dinolestes*, but can be distinguished using a combination of myomere and fin-ray counts, and pigmentation. Larvae have been caught in marine waters off central New South Wales between January and November, and off western Victoria in late January, at depths between 30 and 0 m and within 8 nautical miles of the coast. The limited data on larval occurrence in New South Wales indicate that *D. lewini* spawns over an extended period, with a peak in autumn/winter.

Introduction

Dinolestes lewini, the sole member of the percoid family Dinolestidae, is a marine, pelagic schooling species endemic to temperate Australia between Rottnest Island (32°S, Western Australia) and Sydney Harbour (34°S, New South Wales), including Tasmania. Commonly known as long-finned pike (maximum total length to 90 cm), it is found in open as well as sheltered waters, over seagrass beds and around jetties and rocky reefs, to depths of *c*. 70 m. It is occasionally caught by recreational anglers and considered a good table fish (Paxton and Hanley 1989; Last *et al.* 1983; Gomon *et al.* 1994).

Dinolestes lewini was previously placed in the family Apogonidae (e.g. Greenwood *et al.* 1966). However, a detailed morphological study of this species by Fraser (1971) found several major anatomical differences between *Dinolestes* and apogonids that led to the formal placement of this genus in its own family, the Dinolestidae. *Dinolestes lewini* has since remained in the Dinolestidae (e.g. Eschmeyer and Bailey 1990; Nelson 1994), and it is thought to be closely related to the percoid families Acropomatidae (some genera) and Pomatomidae, and to scombroids (Johnson 1986).

Virtually nothing is known about the reproductive biology or the spawning locality and season of *D. lewini*. This paper describes for the first time the early life-history stages of this endemic Australian species using field-caught material, and provides information on the distribution and occurrence of larvae in south-eastern Australia.

Materials and Methods

Collection of larvae

Larvae examined in this study were obtained in estuarine and coastal waters off central New South Wales (NSW) and Victoria (Vic.). Larvae in NSW were collected in Botany Bay (33°59′S; 151°12′E) with

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a 0.25-m^2 epibenthic sled equipped with a 500-µm mesh net (Steffe 1991); off Bondi (33°53′S; 151°17′E) using a 0.56-m^2, 500-µm mesh neuston net at water depths of 20–30 m (Kingsford *et al.* 1996); and along the Sydney coast between Long Reef (33º45′S; 151º22′E) and Marley (34º07′S; 151°10′E) (Gray 1993, 1995). The latter studies involved sampling of surface waters, and vertically stratified sampling at six inshore stations (<1.0 km from shore) at a depth of 20 m, and six nearshore stations (1.5–3.0 km from shore) at a depth of 30 m. Samples were collected with either a 80-cm diameter, 500-µm mesh ring net or a 1-m^2 opening-closing, 500-µm mesh net (see Gray 1993 for details). Larvae in Victoria were collected immediately inside the entrance to Port Phillip Bay (38°18′S; 144°39′E) using a 1-m^2 mouth-opening, 1-mm mesh plankton net (G. P. Jenkins, unpublished data).

Material examined

A total of 67 larvae (1.88–14.13 mm body length) were used to describe morphometrics, meristics and pigmentation. Larvae had been fixed in 5% formaldehyde and later preserved in 70% ethanol. Seven late postflexion larvae were cleared and stained following Potthoff (1984) to obtain fin and vertebral counts. Representatives of the larvae examined were lodged with the Australian Museum (AMS, Sydney).

Terminology used to describe head spines and morphometric measurements of larvae follows Neira *et al.* (1998). Measurements were made to the nearest 0.01 mm using a dissecting microscope fitted with an eyepiece micrometer. Body length (BL) corresponds to notochord length (tip of snout to tip of notochord) in preflexion and flexion larvae, and to standard length (tip of snout to posterior margin of hypurals) in postflexion larvae. Measurements of body depth (BD), head length (HL), preanal length (PAL) and gap between the anus and the origin of the anal fin (VAFL) were converted to percentage (%) of BL, and the ranges and means (± 2 s.e.) given for each of the preflexion, flexion and postflexion stages (Table 1). Values given throughout the text are means (% BL). Pigment described refers solely to melanin. Illustrations were made with the aid of a camera lucida.

Results

Identification of larvae

Late postflexion larvae were identified as those of *Dinolestes lewini* (Griffith, 1834) using fin meristics provided for the adults in the literature, and whose combination is found only in this species across temperate Australia (D IV–V [visible], III [hidden] + I, 15–19; A I, 25–29; P_1 16–18; P_2 I, 5: Fraser 1971; Last *et al.* 1983; Gomon *et al.* 1994). Two of our cleared and stained larvae had 20 and 22 rays on the second dorsal fin. A developmental series through to the smallest preflexion larva was assembled using body shape, head spines and pattern of pigmentation.

Description of larvae

Development and morphology

Larvae are moderately deep (mean BD 24.1–25.7%; Table 1). The snout is pointed and relatively elongate, and the head moderate to large (mean HL 32.4–33.7%). The gill membranes are free from the isthmus. The large mouth reaches to below midpupil and is functional in the smallest larva examined (1.88 mm), having several prominent canine-like teeth along the premaxilla (6 on each side) and a few (4) on the dentary. Teeth increase in number along both jaws during development but become less conspicuous in late postflexion larvae (Fig. 1). The moderate-sized eyes are round and pigmented. A prominent, inflated gas bladder is present in all larvae examined. The gut is moderate in length (mean PAL 45.6–48.2%), and coiled and compact (triangular-shaped) from the early preflexion stage. A short preanal membrane is present in some late preflexion larvae but is no longer visible by the flexion stage. A prominent gap between the anus and the anal-fin origin is visible from the time the anal-fin anlagen starts to form, i.e., the late preflexion stage (mean VAFL 4.2–6.9%). The smallest and largest larvae undergoing notochord flexion measured 4.80 and 6.25 mm, respectively, whereas the smallest postflexion larva measured 7.00 mm (Table 1; Fig. 1). There are 27–29 (7–10 + 17–20) myomeres (10 + 17 = 27 vertebrae; Fraser 1971). Scales were absent in the largest larva examined (14.13 mm).

Table 1. Range of body length (mm), and range and mean values (± 2 s.e.) of selected body proportions (given as a percentage of body length) of *Dinolestes lewini* larvae

n, sample size; BL, body length; HL, head length; BD, body depth; PAL, preanal length; VAFL, gap between anus and anal-fin origin

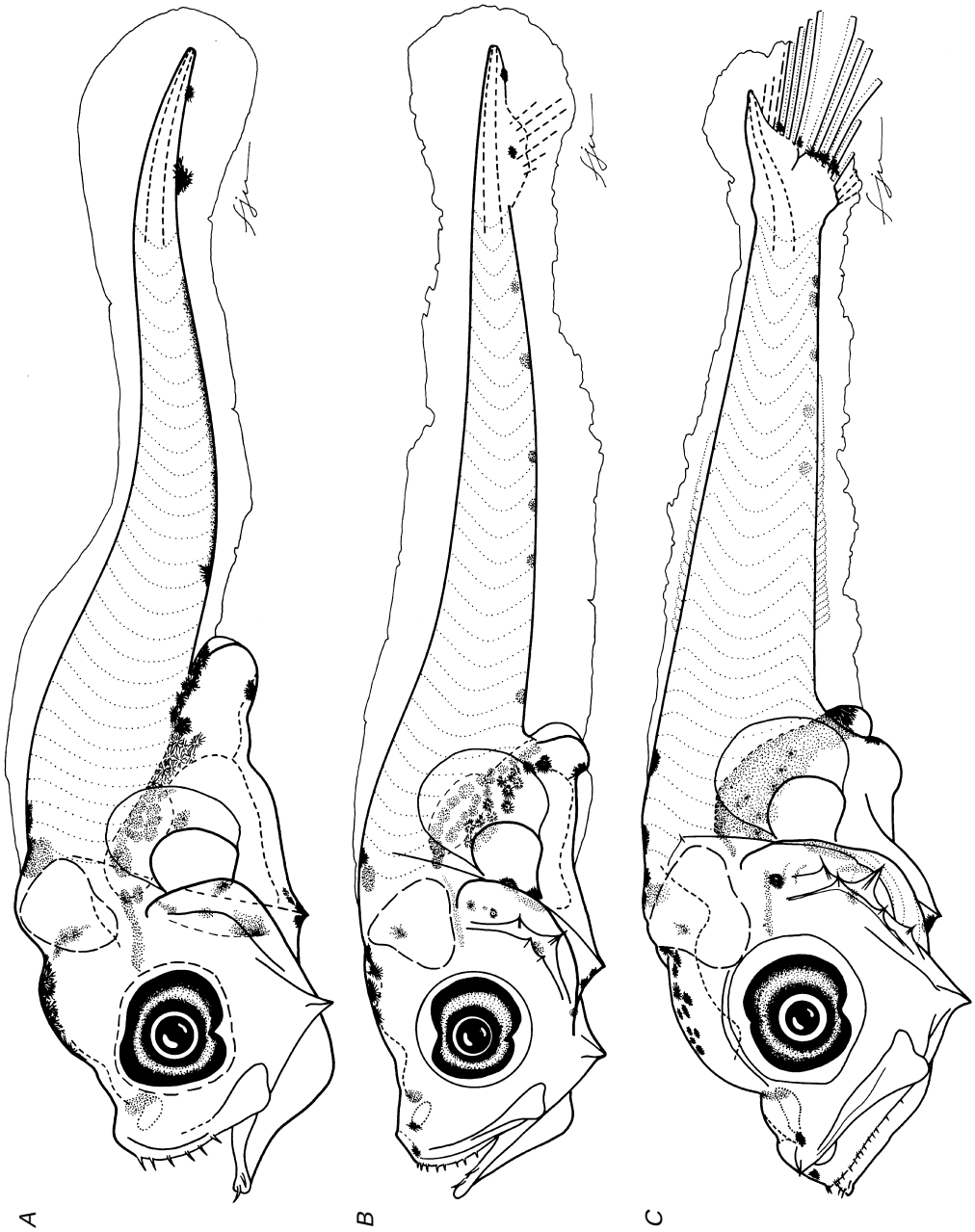
	Preflexion (n = 26)	Flexion (n = 11)	Postflexion (n = 30)
BL (mm)	1.88–5.20	4.80–6.25	7.00–14.13
HL (% BL)	23.6–40.0 (32.4 ± 1.8)	29.7–40.6 (33.7 ± 2.0)	25.4–42.3 (33.7 ± 1.0)
BD (% BL)	21.4–35.1 (25.7 ± 1.2)	20.7–27.1 (24.8 ± 1.2)	20.3–33.0 (24.1 ± 0.9)
PAL (% BL)	41.3–51.7 (46.7 ± 1.2)	42.1–50.8 (45.6 ± 1.6)	44.3–52.2 (48.2 ± 0.8)
VAFL (% BL)	2.2–7.4 (4.2 ± 2.3; n = 4)	2.2–11.6 (8.4 ± 1.8)	4.1–10.2 (6.9 ± 0.7)

Head spines

Larvae possess small to moderate head spination comprising spines on the anterior (= inner) and posterior (= outer) margins of the preopercle, single spines on the opercle, interopercle and supracleithrum, and a low, smooth supraocular ridge. A small posterior preopercular spine appears during the mid-preflexion stage by 3.1 mm, followed by a small anterior preopercular spine by 3.5 mm. Anterior and posterior preopercular spines increase to 4–5 and 5–6 spines, respectively, by the late postflexion stage, and both sets are present in the largest larva examined; the preopercular spine at the angle is the longest but remains shorter than the pupil. The supracleithral spine forms during the flexion stage by 5.6 mm, and it is still visible in the late postflexion stage. Both the interopercular and opercular spines develop during the early postflexion stage by 7.0 mm and remain throughout development. The smooth supraocular ridge forms during the flexion stage and remains low thereafter. All head spines are present in the largest larva examined (14.13 mm). Juveniles examined (55 mm BL) (AMS IB. 2682) have no head spines whereas adults examined (AMS I.15917, I.17033 and I.17178) have a very tiny spine on the infraorbital and serrations along the anterior preopercular margin. The spines in the adults are not homologous with those present in the larvae.

Development of fins

None of the fins except the caudal fin are completely developed in the largest postflexion larva examined (14.13 mm). Pectoral-fin buds are present in the smallest preflexion larva examined and rays start forming sequentially from the top by the end of the flexion stage; 13 of the 16–18 pectoral-fin rays are formed in the largest larva examined. Caudal-fin rays start forming prior to notochord flexion by 3.7 mm and the full complement (9 + 8) is present by the postflexion stage; procurrent caudal-fin rays develop from the early postflexion stage and are still forming in the largest larva. The second dorsal- and anal-fin anlagen appear just before notochord flexion by about 4.0 mm and bases of both fins are visible from 5.1 mm; the anterior-most pterygiophores of the second dorsal and anal fins are directly opposed whereas the posterior-most dorsal-fin pterygiophore is well in front of the posterior-most anal-fin pterygiophore, i.e. the anal-fin base is longer than the second dorsal-fin base and contains more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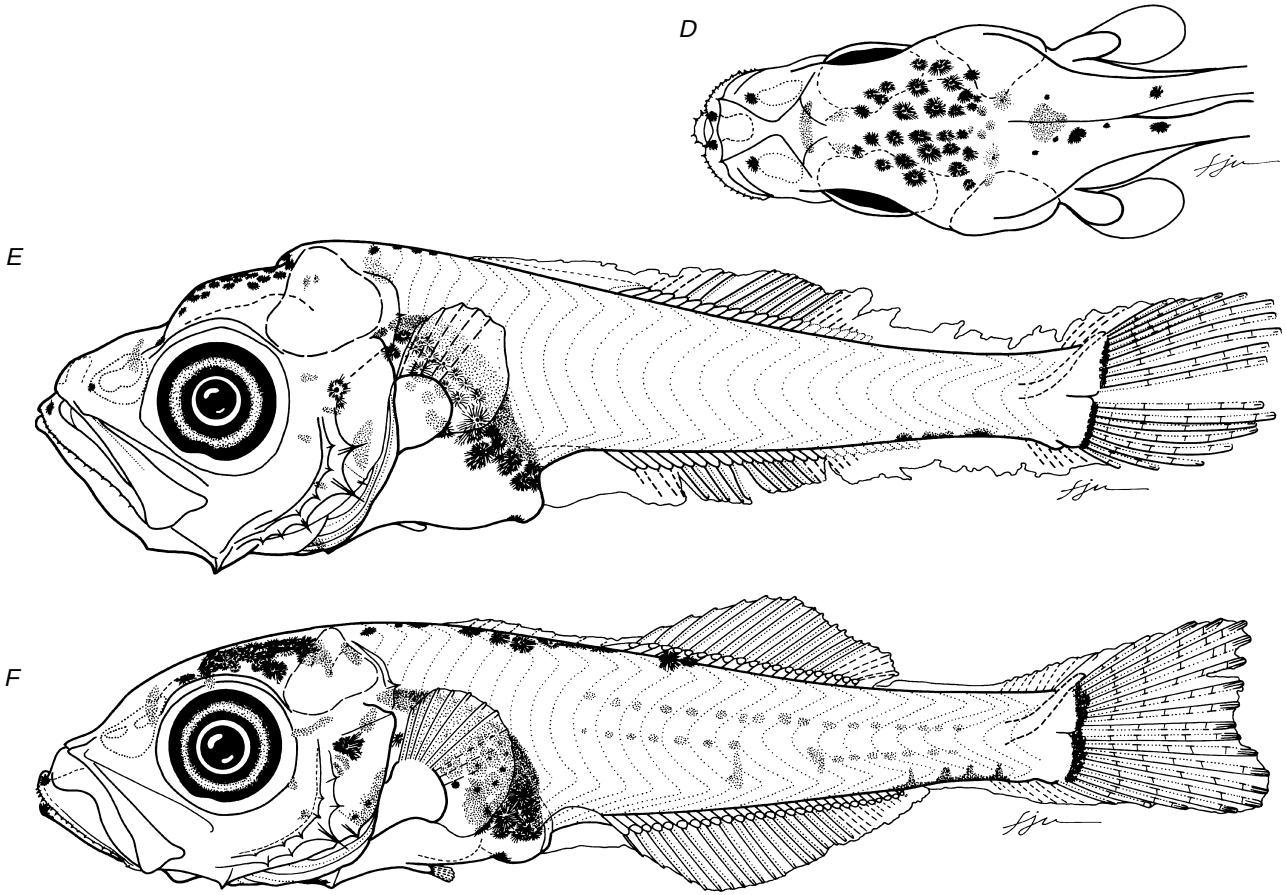

Fig. 1. Larvae of *Dinolestes lewini* from south-eastern Australia. *A*, early preflexion larva (2.80 mm BL). *B*, preflexion larva (4.60 mm BL). *C*, flexion larva (5.64 mm BL). *D*, Dorsal view of head of flexion larva illustrated in *C*. *E*, early postflexion larva (7.00 mm BL); note developing pelvic-fin buds. *F*, postflexion larva (9.65 mm BL); note posteriormost dorsal- and anal-fin rays still developing. Illustrated by F. J. Neira.

rays. Developing dorsal- and anal-fin rays are present in the smallest postflexion larva examined, with those in the center of both fins developing first, followed by those towards the anterior portion of both fins; the posterior-most rays in both fins form last. Pelvic-fin buds appear during the flexion stage, and all I,5 fin elements are still forming in the largest larva. Dorsal-fin spines start to form in postflexion larvae from 8.0 mm. Considering the size of development of all elements in each fin, the sequence of fin formation can be expressed as: $C \rightarrow D$, $A \rightarrow P_2 \rightarrow P_1$.

Pigmentation

Larvae are moderately pigmented (Fig. 1). External pigment is present on the snout tip (from 3.5 mm), fore- and midbrain, opercular area, isthmus, anus, dorsally on the nape and anterior of the trunk, and ventrally on the tail. Internal pigment consists of a large melanophore anteriorly on the forebrain, pigment at the junction of the mid- and hindbrain and ventrally along the hindbrain, over the gas bladder, anteriorly and dorsally over the gut, along the notochord (late postflexion larvae only), and under the notochord tip. There are one or two melanophores anteriorly along the isthmus and one just anterior to the anus. A melanophore forms on the upper opercle by the late preflexion stage and remains prominent thereafter. The melanophore at the nape in early preflexion larvae becomes internal in late preflexion larvae and remains conspicuous (Fig. 1*D*); this and the internal forebrain melanophore are diagnostic characters to identify small preflexion larvae. Pigment along the ventral midline of the tail in the early preflexion stage consists of a continuous pigment stripe and one or two melanophores under the notochord tip; the pigment stripe differentiates into 3–6 widely-spaced melanophores by the late preflexion stage, and the notochord melanophores increase in number and remain along the hypural margin. The anterior-most ventral melanophores on the tail disappear during the flexion stage, whereas those ventrally along the caudal peduncle reduce to about 1–4 by the late postflexion stage and extend upwards internally. Melanophores dorsally on the trunk extend posteriorly along the second-dorsal fin base in late postflexion larvae. All fins are unpigmented.

Occurrence of larvae

Larvae have been caught in relatively low numbers in coastal waters off Sydney (NSW) between January and November, with the highest abundances in May and July (Gray 1995). Almost 99% of the larvae caught by Gray (1995) in coastal waters off Sydney (n = 215) were from samples taken at 20 and 30 m depths at the inshore and nearshore stations, respectively (Fig. 2), with only two larvae caught in surface waters. Larvae have also been caught in surface waters off Sydney (Kingsford *et al.* 1996), and near the bottom, both in Botany Bay (NSW) (Steffe 1991) and Port Phillip Bay (Vic.) (G. P. Jenkins, unpublished data) in August. In addition, an ongoing vertically-stratified larval fish sampling along the coast of eastern South Australia (SA) and Victoria using 500-µm-mesh plankton nets towed at different depths has found a few preflexion *D. lewini* larvae in samples taken between 25 and 0 m at stations within 8 nautical miles off Port MacDonnell (SA; 37°49′–55′S; 140°17′E), and 4 nautical miles off Port Campbell (Vic; 38°41′–43′S; 143°04′E) in late January (F. J. Neira, unpublished data).

Discussion

Taxa with similar larvae

Larval *D. lewini* can be identified by the moderate to large head, the large mouth with prominent, early-forming canine-like teeth, the head spines, 27–29 myomeres, the gut which is compact and triangular-shaped from the preflexion stage, the dorsal- and anal-fin counts, the longer anal than dorsal fin-base, and the internal forebrain and nape pigment. Larval *D. lewini* are likely to be confused with those of the acropomatid *Apogonops anomalus,* the pomatomid *Pomatomus saltatrix* and the scombrid *Scomber australasicus*, all of which occur within the distributional range of *Dinolestes* in temperate Australia (Gomon *et al.* 1994), and whose larvae

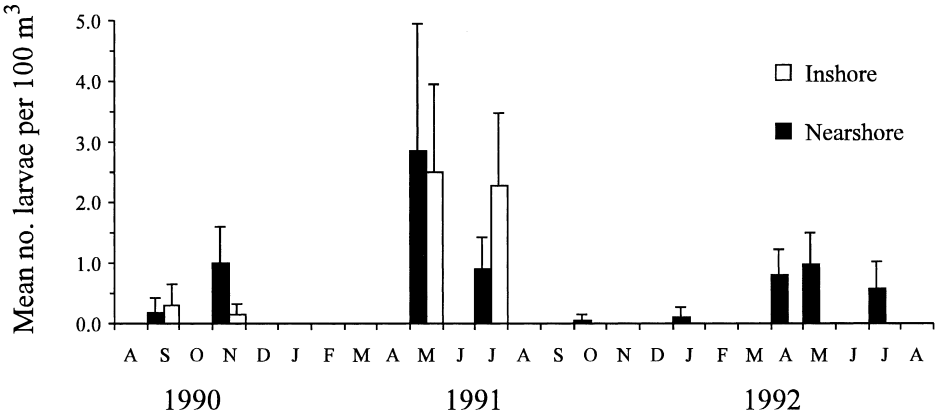

Fig. 2. Mean monthly concentrations (numbers per 100 m^3, ± 2 s.e.) of *Dinolestes lewini* larvae caught at a depth of 20 m in inshore stations (<1.0 km from shore; open bars) and at a depth of 30 m in nearshore stations (1.5–3.0 km from shore; black bars) in waters off central New South Wales between August 1990 and 1992 (data from Gray 1995).

have similar body shapes. However, larval *A. anomalus* posses 25 myomeres, a more extensive head spination and lower dorsal- and anal-fin counts (D IX + I, 10; A III, 10), larval *P. saltatrix* have 25–27 myomeres and a higher dorsal-fin count (VII–VIII+I, 23–28), whereas larval *S. australasicus* are generally more heavily pigmented and have no preopercular spines. In addition, larvae of *A. anomalus* have no ventral tail melanophores until the late postflexion stage, those of *P. saltatrix* have numerous early-forming melanophores dorsally and laterally on the tail whereas those of *S. australasicus* have early-forming melanophores along the dorsal midline of the tail (Leis and Trnski 1989; Miskiewicz and Bruce 1998; Trnski and Neira 1998; Trnski *et al.* 1998).

Relationships based on larval characters

The development of larval *Dinolestes lewini* is similar to that found in most generalised percoids (Johnson 1984). This includes the formation of the caudal, dorsal and anal fin anlagen shortly before the start of the notochord flexion, a size at flexion between 4 and 7 mm which ends with the attainment of the full complement of caudal-fin rays, and the presence of spines on bones of both the opercular (preopercle, opercle, and interopercle) and pectoral (supracleithrum) series (Johnson 1984). The head spines, and possibly the early-forming premaxillary teeth, constitute the only apparent specialisations of *Dinolestes* to pelagic larval life.

Although the decision by Fraser (1971) of removing *Dinolestes* from the Apogonidae and placing it in the Dinolestidae was based purely on adult characters, the marked differences between apogonid and *Dinolestes* larvae (short-based dorsal and anal fins, and 23–24 myomeres in the former) clearly support the change (Leis and Rennis 1983; Neira and Bruce 1998). Fraser (1971) also discussed a possible relationship of *Dinolestes* with the Sciaenidae based on adult characters, but the distinct larval form of sciaenids (Leis and Trnski 1989) certainly does not support such a relationship.

A detailed study of scombroid phylogeny by Johnson (1986) identified a small group of percoid genera as scombroid outgroups on the basis of their possession of a unique specialised premaxillary adult dentition. Among others, this group included *Dinolestes*, *Apogonops* (Acropomatidae) and *Pomatomus* (Pomatomidae). As discussed previously, larval *Dinolestes* share similarities with the larvae of some scombroids (e.g. *Scomber*) and with those of *Apogonops* and *Pomatomus*, including a moderately elongate body, a moderate to large head, early-forming (preflexion stage) premaxillary teeth**,** a small to large gap between anus and anal-

fin origin, and pigment on the head and nape. Although the above characters are also present in the larvae of many other groups (Johnson 1984; Leis and Trnski 1989; Neira *et al.* 1998), these shared features provide support for Johnson's (1986) proposal of a possible relationship between these taxa. However, establishing relationships among these taxa on the basis of larval characters is problematic. Thus, resolution of whether larval characters will help in determining the relationship between *Dinolestes* and these taxa may require more detailed comparative studies including, for example, the development of the dentition in larvae of these taxa.

Seasonal and spatial distribution of larvae

The limited data on the occurrence of larval *D. lewini* in New South Wales indicate that spawning takes place over a protracted period with a peak in autumn/winter, with larvae generally occurring in coastal waters within 8 nautical miles of the coast, at depths between 30 and 0 m. The absence of *D. lewini* larvae in coastal waters off Lake Macquarie (*c*. 95 km north of Sydney) despite an extensive larval survey (Miskiewicz 1987) suggests that the north-eastern-most limit of spawning lies somewhere between this system and Sydney. In addition, the finding of a few larvae in coastal waters off eastern South Australia and western Victoria in late January (F. J. Neira, unpublished data) suggests a much larger spawning area in south-eastern Australia. The few postflexion *D. lewini* larvae caught within Botany Bay (NSW) and Port Phillip Bay (Vic.) in August can be regarded as stragglers, as juveniles are rarely found in bays and inlets in temperate Australia (SPCC 1981; Jenkins *et al.* 1997; Valesini *et al.* 1997) and therefore do not utilise these systems as nurseries.

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