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A Description of the Early Juvenile Colour Patterns of Eleven *Lethrinus* Species (Pisces: Lethrinidae) from the Great Barrier Reef, Australia

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ABSTRACT. The early post-settlement diurnal colour patterns of 11 of the 17 Lethrinus species presently known from the Great Barrier Reef are described: Lethrinus atkinsoni Seale; Lethrinus erythracanthus Valenciennes; Lethrinus genivittatus Valenciennes; Lethrinus harak Forsskål; Lethrinus lentjan Lacépède; Lethrinus nebulosus (Forsskål); Lethrinus obsoletus (Forsskål); Lethrinus olivaceus Valenciennes; Lethrinus ornatus Valenciennes; Lethrinus variegatus Valenciennes and Lethrinus xanthochilus Klunzinger. Where possible, descriptions cover the ontogenetic development of colour patterns from settlement through to attainment of the adult colouration. In addition, notes are provided on the pigmentation patterns of the late pre-settlement stage of L. atkinsoni, L. genivittatus and L. variegatus. Descriptions are based on field and aquarium observations and freshly collected specimens, with details of colour patterns retained by preserved material also included. The study is aimed as a guide to the identification of Lethrinus early juveniles, based primarily on colour patterns, with notes given on ecology and field identification. Morphological information is provided to facilitate the identification of early juveniles. Two new characters, cheek scales and maxillary serrations, are used to distinguish among recently-settled *Lethrinus* species. Juvenile lethrinids possess a complex range of colour patterns during their early juvenile period. Three general patterns are displayed by most species, based on stripes and irregular bands. These patterns and their rapid interchanges are described, and interpreted in relation to behavioural observations. Possible functions of the shared colour patterns are discussed in relation to the ecology of Lethrinus juveniles.

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The emperors (family Lethrinidae, *Lethrinus* species) are conspicuous percoid fishes found predominantly within coral reef habitats of the subtropical and tropical Indo-Pacific (Johnson, 1980; Springer, 1982; Carpenter & Allen, 1989). They often form an important component of reef-

based fisheries throughout their range (Craik, 1981; Dalzell, 1988; Carpenter & Allen, 1989; Dalzell *et al.*, 1992; Jennings & Polunin, 1995), and are of considerable management interest. Fishes on coral reefs represent an increasingly exploited fisheries resource (Russ, 1991; Johannes & Riepen, 1995), and a need exists to collect appropriate life history information for future stock assessment and management. However, a better understanding of the dynamics of these multi-species stocks will not be achieved without the ability to accurately identify the component species.

The importance of the early post-settlement period to the subsequent dynamics of reef fish populations has been increasingly recognised over the past decade (Doherty & Williams, 1988; Jones, 1991). However, information on these systems has mostly arisen from studies of sedentary taxa such as pomacentrids (damselfishes). Highly mobile species, and those which do not associate with the isolated coralline structures often employed in recruitment studies, have received scant attention. These taxa embrace some of the most valuable fisheries on Indo-Pacific coral reefs, yet knowledge of their early life histories is almost nonexistent.

Lethrinus species comprise an ideal assemblage for examining early life history in exploited species, owing to their large size at settlement (Brothers *et al.*, 1983; Leis & Rennis, 1983; author's unpublished data) and ease of capture using conventional and recently-developed techniques (Doherty, 1987; Thorrold, 1992; Wilson, in prep.). Despite the prominence of the genus on Indo-Pacific coral reefs (Carpenter & Allen, 1989; Myers, 1989; Randall *et al.*, 1990), the juvenile stages have been largely unstudied. The development of suitable taxonomic criteria for distinguishing these individuals is a crucial step in redressing this imbalance.

Taxonomic studies of juveniles need to consider the extent of ontogenetic changes in body form and colouration. The external adult morphology of many *Lethrinus* species is very similar, but the degree of interspecific overlap is even greater in juveniles. Moreover, most morphological characters vary considerably during early ontogeny. By contrast, although *Lethrinus* juveniles are capable of rapid switches between alternative colour patterns (Smith, 1959), each of these alternate patterns varies little throughout the juvenile period, and characteristic colouration is easily distinguished in the field. Detailed descriptions of colour patterns therefore represent a valuable taxonomic tool for investigating juvenile assemblages.

The most recent revision of the Lethrinidae (Carpenter & Allen, 1989) provided brief descriptions of the adult colouration of the 28 *Lethrinus* species currently recognised. In addition, the typical juvenile colouration of *L. erythracanthus* and *L. nebulosus* was also figured. Juveniles of eight species are figured elsewhere (Wheeler, 1961; Allen & Swainston, 1988; Myers, 1989; Randall *et al.*, 1990; Shao *et al.*, 1992; Kuiter, 1992, 1993, 1996; Lee, 1993; Kuiter & Debelius, 1994; Lieske & Myers, 1994; Masuda & Kobayashi, 1994), although primarily in reference to mid or late-juvenile stages. Juvenile colour patterns of the remaining 20 species have not been reported.

The present study describes the early-juvenile stage of 11 of the 17 *Lethrinus* species recorded from the Great Barrier Reef region (Carpenter & Allen, 1989; D.McB. Williams, pers. comm.). Juveniles of the remaining six species—L. laticaudis Alleyne & Macleay, L. microdon Valenciennes, L. miniatus (Schneider), L. rubrioperculatus Sato, L. semicinctus Valenciennes and Lethrinus sp. 2 (undescribed species: Carpenter & Allen, 1989)—were not knowingly observed in the field. Collections and observations concentrated on a single locality on the Great Barrier Reef, although most of the species occur throughout the Indo-West Pacific or south-east Asia. Species designations follow those of Carpenter & Allen (1989).

This study is aimed as a guide to the field identification of living and freshly collected juveniles, based on colour patterns. Additional morphological information is also provided to facilitate the separation of similar species and the identification of preserved material. Descriptions focus on the identification of early post-settlement specimens, although notes are also included on distinguishing the late pre-settlement stage of three of the 11 species. Where possible, details are given of any changes in colouration occurring throughout juvenile ontogeny. Rapid switches among diurnal colour patterns are described from field and aquarium observations, and discussed in relation to behaviour and ecology.

Materials and methods

The main study and collection areas were located within the shallow lagoon surrounding Green Island (16°45'S 145°57'E), a small mid-shelf coral cay, 26 km from the mainland and a similar distance from the outer perimeter of the Great Barrier Reef. Additional observations were made in shallow, subtidal areas at Lizard Island (northern Great Barrier Reef, 14°40'S 145°28'E), Magnetic Island (Townsville, 19°15'S 146°50'E), and two localities (Bali [8°20'S 115°28'E] and Flores [8°32'S 122°13'E]) within the eastern Indonesian archipelago. The study period extended from August 1990 to November 1994, with field work concentrated around the November to February period of peak settlement (Russell *et al.*, 1977; Milicich, 1988).

The majority of specimens were collected using a small beach-seine net, 15×1.5 m, constructed from 9.5 mm nylon mesh. A 1 m cod-end in the net's centre facilitated the collection of small specimens. Because of the relatively large size at which Lethrinus individuals settle out of the plankton (Brothers et al., 1983; Leis & Rennis, 1983; author's unpublished data), post-settlement juveniles of all developmental stages could be collected using this technique. In addition, late pre-settlement individuals, 14-21 mm, were sampled from around submerged fluorescent lights along the shoreline using a 6×1.5 m beach-seine net of 1 mm mesh. Specimens were killed by cold shock, and fixed in 10% formalin and preserved in 70% alcohol. A number of individuals were also kept alive in aquaria for periods of up to eight months to monitor ontogenetic changes in their colouration.

Photographic records were taken of both alive and freshly-killed specimens in a vertical aquarium. Fish to be photographed dead were killed by cold shock, and their fins set in an extended position using 40% formaldehyde.

Formalin was also brushed over the side of the body to be photographed in order to arrest any *post-mortem* fading of melanophore pigmentation.

In the present study, settlement refers to the transition between the pelagic and demersal phases of the life cycle. In the Lethrinus species considered here, known sizes at settlement range from 16 to 21 mm (Brothers et al., 1983; author's unpublished data). Juveniles are the life cycle phase from the time of settlement to the onset of sexual maturity. However, Lethrinus species attain the adult colouration relatively early in comparison with other groups of reef-associated fishes such as the scarids and labrids (e.g., Bellwood & Choat, 1989). As such, the scope of the present study covers the size range from settlement to attainment of the adult colouration; this having occurred by 60 mm in most species. Lethrinus adult colour patterns are described and figured in Carpenter & Allen (1989) and are not referred to in any detail here. Unless otherwise noted, all lengths refer to the standard length (SL), the straight-line distance between the tip of the snout and the posterior edge of the hypural plate.

Colour information is provided as a basis for identifying field, captive and freshly-killed specimens, as well as preserved material. Horizontal, longitudinal markings are referred to as stripes. Where relevant, stripes are further designated as either dorsal, orbital, pectoral or ventral. Near-vertical, oblique and irregular markings are termed bands. Blotches refer to distinct cuboidal or circular markings. Pale areas between stripes, blotches and bands are referred to as interspaces. "Diagnostic colour notes" summarise the main diagnostic or characteristic features of a species' colour patterns. "Diagnosis" sections list the morphological features of greatest value for confirming colour-based identifications. "Colour in alcohol" descriptions were based on specimens collected during the present study, fixed in 10% formalin and retained in 70% ethanol for at least three months.

Carpenter & Allen (1989) provide information on morphological characters useful for separating Lethrinus species, based primarily on adults. In the present study, eight of these morphometric measurements and five scalecount characters (Fig. 1) were examined for their use in separating Lethrinus species as juveniles. Ontogenetic variation in the morphometric characters was assessed using a principal component analysis (PCA). Individuals were placed into five size-classes: 15-29.9 mm, 30-49.9 mm, 50-69.9 mm, 70-89.9 mm, and "adults"; the latter class representing values given by Carpenter & Allen (1989). The five species included in the analysis were those for which replicate observations were available within each size class. Data analysed were character means for each size class. Characters displaying minimal ontogenetic variation were further analysed using a canonical discriminant analysis of their separation of the 11 species. This analysis was restricted to individuals of ≤ 60 mm. All morphological measurements were made under a stereo microscope fitted with a calibrated ocular micrometer.

Two additional morphologies, the presence of cheek scales and presence and mean number of serrations along the outer surface of the maxilla, were also examined for



Fig. 1. Schematic summary of meristic counts and morphometric measurements examined in *Lethrinus* juveniles. Symbols: SL, standard length; BD, body depth; HL, head length; SnL, snout length; CH, cheek height; OD, orbit diameter; LL, number of lateral-line scales; DSR, number of dorsal scale rows; VSR, number of ventral scale rows.

separating *Lethrinus* species during the early postsettlement phase. Both characters have previously been discounted in the identification of *Lethrinus* species, although they have been used for distinguishing lethrinid genera (Sato, 1978; Carpenter & Allen, 1989).

Bibliographic information relating to early taxonomy is given in full in Carpenter & Allen (1989).

Voucher specimens were deposited in and specimens examined from the Australian Museum, Sydney (AMS); Museum of Victoria, Melbourne (NMV); and National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM).

Juvenile distributions

Distribution patterns are only of limited use for separating early juveniles of the 11 species examined. At Green, Magnetic and Lizard Islands, *Lethrinus* juveniles occur almost solely over areas of shallow seagrass (≤ 7 m) until at least 80 mm. Furthermore, juvenile lethrinids typically co-occur in loose, multi-species schools. However, crossshelf patterns in species composition are evident, with the number of species increasing from coastal areas outwards to mid-shelf reefs containing seagrass cover (Fig. 2).

At 80-90 mm, individuals of the common species (principally L. atkinsoni, L. harak and L. obsoletus) extend their distribution to include vegetated (e.g., Sargassum species) and unvegetated (sand, coral rubble, small patch reefs) habitats adjacent to seagrass beds. Other species, particularly L. genivittatus, L. xanthochilus and L. variegatus, migrate away from the seagrass habitat altogether at this size. With the exception of L. harak, few Lethrinus individuals greater than 120 mm reside within shallow habitats at Green Island (< 3 m). At this size, species such as L. atkinsoni, L. lentjan, L. nebulosus, L. obsoletus and L. olivaceus inhabit areas of soft substrate and patch reefs (5-15 m) surrounding the reef flat (line transect and beach-seine data in Wilson, in prep.; author's unpubl. obs.). Several species, particularly L. genivittatus and L. variegatus, frequent deeper interreefal habitats (data from otter trawls, T.J. Wassenberg, pers. comm.).

Further details of habitat-use by juveniles of individual species are given in the ecology sections below.

Colour patterns

The identification of juvenile lethrinids in the field was based primarily on colour patterns. Few *Lethrinus* species undergo marked ontogenetic changes in their juvenile colouration, and most can be readily identified from the time of settlement on the basis of diagnostic and characteristic patterns. Table 1 summarises the colour patterns of greatest value for distinguishing juveniles of the 11 *Lethrinus* species in the field and at capture. These patterns are also generally discernible in freshly-killed material and specimens maintained in aquaria.

Prior to settlement, body pigmentation in most Lethrinus species is restricted to yellow-orange xanthophores along the myosepta and as precursor markings to post-settlement patterns of stripes, blotches and bands. Sparse melanophores may also be visible over the body and spinous portion of the dorsal fin in some species. In late pre-settlement *L. atkinsoni, L. genivittatus* and *L. variegatus*, these form distinctive markings along the body, allowing individuals to be readily separated from other lethrinids. Following settlement, coloured stripes form rapidly from grey or tan melanophores in species such as *L. genivittatus, L. obsoletus* and *L. ornatus*. Darker body markings (e.g., bands along the dorsum) also begin to appear, although generally do not reach full intensity until individuals are 2–3 mm SL larger.

Three general colour patterns are found in most of the 11 *Lethrinus* species as early juveniles (Fig. 3), although interspecific differences exist in their intensity and form.

1-Primary stripes. Lethrinids may be placed into two groups based on the form and intensity of this pattern. The first group (L. genivittatus, Fig. 3A, Pl. 1E,F,G; L. lentjan, Pl. 2C; L. obsoletus, Pl. 2G; and L. ornatus, Pl. 3C) have pink to orange stripes. Four stripes are generally visible, hereafter referred to as the dorsal, orbital, pectoral and ventral stripes (Fig. 4: cf. Bellwood & Choat, 1989). Both the dorsal and orbital stripes originate behind the rear edge of the operculum and typically fuse near the caudal peduncle base. The dorsal stripe passes along the ventral margin of the lateral-line, while the orbital stripe extends from level with the lower half of the orbit. The pectoral stripe commences at the pectoral base and extends to midway along the caudal peduncle. The ventral stripe originates ventral to either the pectoral base (L. lentjan and L. ornatus) or medial dorsal spines (L. genivittatus and L. obsoletus), and passes along the lower flank to the ventral margin of the caudal peduncle. With the exception of L. ornatus, the dorsal stripe is seldom conspicuous, and may be obscured by overlying darker patterns (e.g., Pl. 1G). In L. genivittatus (Pl. 1E,F) and L. obsoletus (Pl. 2G), the ventral stripe is often similarly inconspicuous.

The second group comprises species possessing inconspicuous primary stripes (Fig. 3B). Clearest examples include *L. xanthochilus* (Fig. 3B; Pl. 3E), *L. erythracanthus* (Pl. 1D) and *L. nebulosus* (Pl. 2D). *Lethrinus xanthochilus* displays two irregular brown to grey stripes, generally in the pectoral and ventral positions. These typically originate on the operculum or adjacent to the pectoral base, and extend to above the second anal spine. Although inconspicuous in the field, they often intensify in response to capture or other disturbance. *Lethrinus erythracanthus* and *L. nebulosus* are exceptional within this category in displaying greater than four stripes, silver or pale blue, as a normal component of the diurnal field colouration.

Variation between the two groups is also evident in the ontogeny of their primary stripes. With the exception of *L. lentjan*, species from the first group display their stripes during both juvenile and adult phases. Species from the second group generally only retain their pattern until 60–80 mm (ca. 150 mm in *L. erythracanthus*), although *L. nebulosus* may display its primary stripes throughout the adult phase.



Fig. 2. General distribution patterns of *Lethrinus* juveniles within shallow habitats on the Great Barrier Reef. Species are listed in decreasing order of abundance and refer to the less than 80 mm size-class unless otherwise indicated. Based on observations from: Cleveland, Upstart and Princess Charlotte Bays (inshore); Magnetic Island (inner-shelf); Michaelmas Reef, Green and Lizard Islands (mid-shelf). Information from outer-shelf habitats was not available. Extent of seagrass cover indicated. *: not encountered during the present study, although common in the southern section of the Great Barrier Reef (I. Halliday, pers. comm.).

Table. 1. Characteristic and diagnostic colour patterns displayed by juvenile Lethrinus species 18–80 mm in the field and at capture. General forms of body and head colour patterns are given in Figs 3–5. †: body depth; ?: not known; *: identical colour to body background.

Character	Lethrinus atkinsoni	Lethrinus erythracanthus	Lethrinus genivittatus	Lethrinus harak	Lethrinus lentjan	Lethrinus nebulosus	Lethrinus obsoletus	Lethrinus olivaceus	Lethrinus ornatus	Lethrinus variegatus	Lethrinus xanthochilus
Primary stripes (Fig. 3A,B, 4)	2, usually absent, dark brown; interspaces off white	≥4, silver; interspaces yellow	3-4, golden orange to orange-tan; interspaces silver	absent	3–4, pale pink; interspaces off white	≥4, pale blue; interspaces yellow-tan	3–4, orange-tan; interspaces off white	absent	3–4, orange; interspaces silver	2, pale or absent, khaki; interspaces silvery off white	2, black- brown; interspaces silvery off white
Dark mid-lateral stripe (Fig. 3C)	width 4.0 in BD†	?	width 5.0 in BD	width 4.0 in BD	width 5.0 in BD	?	width 5.0 in BD	width 6.0 in BD	width 4.0 in BD	width 4.0 in BD	width 4.0 in BD
Banding (Fig. 3D)	frequent, dark brown to black	absent	frequent, black	frequent, black	frequent, pale to dark grey	frequent, pale to dark grey	frequent, black	frequent, black	rarely seen, pale to dark grey	rarely seen, pale grey	frequent, dark grey
Shoulder blotch (Fig. 3D, 5)	black, narrow vertical- rectangle	absent	black, silver halo, extending over lateral line	pale to dark grey, square, rarely seen	pale to dark grey, circle or vertical- rectangle	pale to dark grey, vertical- rectangle	grey to black, square or vertical- rectangle	black, horizontal- rectangle (Fig. 3D)	pale grey, square, rarely seen	pale grey, square, rarely seen	dark grey, square
Dorsal margin of lateral line	cryptic*	cryptic or with silvery dots	cryptic; rarely silver	cryptic	cryptic (< 31 mm) or with silvery dots	cryptic; occasionally with silvery dots	silvery cream	cryptic; rarely faded yellow-tan	cryptic	silvery cream	cryptic
Silvery mid-body interspace? (Fig. 3B)	no	no	no	no	no	no	no	no	no	no	yes (18–45 mm)
Suborbital markings (Fig. 3A,B)	none	none	2 tan bands at >35 mm	rarely dark triangle at >22 mm	rarely pale brown blotch at > 25 mm	rarely diffuse grey blotch at >38 mm	rarely 2 dark bands at >20 mm	single dark blotch at 40–60 mm	rarely broad diffuse brown blotch	single dark blotch at > 30 mm	single prominent dark blotch at 20–45 mm
Large rectangular blotch on mid- body? (Pl. 2B)	no	no	no	yes	no	no	no	no	no	no	no
Pelvic fin membrane	hyaline	hyaline or off white to pale grey	hyaline	hyaline	hyaline	off white to grey	hyaline	dark grey with underlying yellow to off white	hyaline	hyaline	dark grey with under- lying yellow
Dorsal fin margin	hyaline or off white to pale scarlet	hyaline to dusky yellow	hyaline to off white	hyaline to greyish yellow or pale scarlet	hyaline or off white to pale maroon	hyaline to greyish yellow	hyaline or off white to pale pink	dark grey over yellow	hyaline or off white to pale scarlet	hyaline	hyaline to dark grey over yellow









Fig. 3. General colour patterns displayed by *Lethrinus* juveniles: A—primary stripes-conspicuous form, based on *L. genivittatus* 25–80 mm SL; B—primary stripes-inconspicuous form, based on *L. xanthochilus* 25–45 mm SL; C—dark mid-lateral stripe, based on *L. olivaceus* 45 mm SL; D—dorsoventral banding, based on *L. olivaceus* 32–39 mm SL.



Fig. 4. Positioning and designation of the four primary stripes present in juveniles of numerous *Lethrinus* species.

2—Dark mid-lateral stripe. This pattern is only displayed in the field, and consists of a broad dark brown to black stripe originating along the rear margin of the orbit and terminating over the hypural plate (Fig. 3C; Pl. 1G; also Pl. 56E in Myers, 1989). Concomitant with its appearance is a partial or complete fading of other patterns. In *L.* genivittatus and *L. obsoletus*, a faded pectoral primarystripe (rarely orbital, pectoral and ventral stripes together; as in Pl. 1G) may remain visible. Background colouration below the mid-lateral stripe is typically uniform, and paler than the dorsum. Field observations of early juvenile *L.* erythracanthus and *L. nebulosus* were too few to determine if a dark mid-lateral stripe pattern was present, although the remaining nine species do display this pattern.

Interspecific similarities in the dark mid-lateral stripe, and the associated fading of other diagnostic patterns, may lead to difficulties during field-identification. Differences in the relative breadth and/or intensity of the dark midlateral stripe may facilitate field diagnoses.

3—Banding. This colour pattern comprises dark bands and blotches along the length of the body (Fig. 3D). From 5–8 narrow grey to black bands appear along the dorsum, between the nape and base of the caudal peduncle (Pl. 1B,G, 2C,E,F). These either extend from the body margin to the lateral-line, or to halfway between, depending on the species and size of the individual. A further 2–3 bands appear along the caudal peduncle, usually connecting both body margins. Below the lateral-line, bands extend to the belly, either directly from the lateral-line and dorsal bands (as in Pl. 1A,B) or from a series of 3–4 dark blotches along the ventral lateral-line margin (Pl. 2E,F). In both forms, the bands are often linked in a network pattern, producing the *Lethrinus* "reticulated" appearance. The ventral blotches, mostly cuboidal or rectangular in shape, extend along the body below the dorsal fin (as in Pl. 2C,E, 3D). The blotch, below dorsal spines 2-5 (5-7 in *L. olivaceus*), is generally the smallest and most intense, and designated as the "shoulder blotch". In species such as *L. atkinsoni*, this is the only blotch displayed (e.g., Pl. 1A,B).

The shoulder blotch displays some within-species variation, although its shape and intensity may nonetheless be diagnostic (Fig. 5). The shoulder blotch of species such as L. obsoletus varies from almost square to a deep rectangle. Shoulder blotches of this shape are round or square at settlement and deepen with ontogeny. Lethrinus



Fig. 5. Variations in the juvenile shoulder blotch pigmentation of selected *Lethrinus* species from the Great Barrier Reef. In species where two or more forms occur, underlined letters denote the predominant pattern(s) exhibited by freshly-killed specimens. Shoulder blotch positioning relative to the lateral-line scales is indicated. *Lethrinus genivittatus*—A; *L. lentjan*—<u>B</u>,C; *L. nebulosus*—<u>C,D</u>; *L. obsoletus*—<u>B,C,E</u>.

olivaceus is the only species with a horizontal shoulder blotch (Fig. 3D, Pl. 3A,B; Pl. 56E in Myers, 1989).

Banding is frequently displayed in the field, and also upon capture or death. In the field, species such as *L. atkinsoni, L. genivittatus* or *L. obsoletus* often display intense black banding over a uniform off-white background, obscuring other patterns (e.g., primary stripes). Banding in other species (particularly *L. ornatus* and *L. variegatus*) is generally inconspicuous or absent in the field, and only visible upon capture or after death. Both banding and mid-lateral stripe patterns are rapidly and frequently turned on or off at will, usually within 1-2seconds. Observation of individuals displaying these patterns may be necessary for several minutes before diagnostic or characteristic colouration can be fully determined. In some cases, the collection of specimens for confirmation with meristic counts may be warranted.

Field observations

Display of the 3 shared colour patterns ("Colour patterns" above) appears strongly influenced by behaviour. Throughout the early juvenile period, lethrinids occur either as solitary individuals, or in loose schools with congenerics or species from several other families. Antagonistic interactions are most frequent between non-schooling individuals. When initially disturbed, banding (Fig. 3D) is rapidly displayed, often overlying a uniformly pale background. In all species intense displays of this nature are mainly limited to individuals of 30–50 mm. In small specimens (less than 30 mm), such displays are often restricted to appearance of the shoulder blotch.

Following initial display of the banding, primary stripes may become visible, particularly during flight from an aggressor. Often concomitant with the appearance of primary stripes is a partial fading of the banding. Prior to the appearance of primary stripes, field identification of some species (e.g., *L. genivittatus* and *L. obsoletus*) may be tenuous or impossible. However, field displays of the primary stripes are often less intense than those initiated at the time of capture, and collection of specimens for confirmatory identification may be necessary. In individuals larger than 50 mm, banding becomes progressively less prominent as a "fright colouration", and the increased clarity of the primary stripes or other characteristic colouration facilitates easier field identification.

During resting periods or when otherwise undisturbed, the dark mid-lateral stripe (Fig. 3C) is the most common pattern. Individuals switch it on while foraging among seagrass leaves or when hovering over the seagrass canopy (cf. Pl. 1G). Although most common when solitary, it may also be displayed by individuals swimming in relatively discrete schools. When disturbed, the dark mid-lateral stripe is rapidly replaced by either the primary stripes, dorsoventral banding, or a combination of the two. Upon removal of the cause of disturbance, the dark mid-lateral stripe is resumed. Solitary, resting individuals may also occasionally display an exceedingly faint pattern of primary stripes, without overlying dark markings.



Fig. 6. Results of principal component analysis of ontogenetic variation in *Lethrinus* morphometric ratios. Analysed were five size-classes across *L. atkinsoni*, *L. genivittatus*, *L. harak*, *L. obsoletus* and *L. variegatus*. Principal components 1 and 2 were plotted, together accounting for 98.9% of variance in the data. Ontogenetic variation within a character was evidenced by an elongate ordination of size-class values along either axis (e.g., SnL in HL). Ratio symbols follow those detailed in Fig. 1, except for: DS_{max}, length of longest dorsal spine. For clarity, ratios 1–4 are shown separated from 5–8.

The dark mid-lateral stripe pattern of *Lethrinus* species is extremely similar to that of *Siganus fuscescens* (Pl. 10 G in Woodland, 1990). This may lead to difficulties in separating these taxa when recently-settled (25–30 mm). Both groups also display similar behaviours: swimming in short bursts, periodically hovering to pick small food items off seagrass leaves, and often schooling together. This association is addressed further in the Discussion.



Fig. 7. Results of canonical discriminant analysis of relative body and head depths for the morphological separation of *Lethrinus* species as early-juveniles (≤ 60 mm). Canonical variates 1 and 2 are plotted; together, these account for 95% of variance in the data. The characters responsible for variation along each axis are shown. Circles surrounding species means represent 95% confidence ellipses.

The siganid pattern may be distinguished from that of *Lethrinus* species by the thin off-white border along both the dorsal and ventral margins of the mid-lateral stripe (cf. either a pale dorsal border in *L. obsoletus* and *L. variegatus* or no such pale borders in the remaining nine species described here). Juvenile siganids also possess a more ovoid body and rounded snout, with their eyes further from the head margin.

Morphological characters for distinguishing *Lethrinus* juveniles

Morphological characters may augment the colour-based identification of *Lethrinus* juveniles, particularly in preserved material where characteristic colour patterns are faded or absent. However, the application of "adult" characters (Carpenter & Allen, 1989) to the identification of juveniles must proceed cautiously. There are two principal reasons for this. Firstly, a substantial degree of allometric growth occurs during early post-settlement



Fig. 8. Maxilla ontogeny in *Lethrinus genivittatus* juveniles, showing the occurrence of serrations along the left maxilla. A,B 18.9 mm SL (pre-settlement); A—oblique lateral view, B—dorsal view. C,D—21.4 mm SL (post-settlement); C: oblique lateral view, D: dorsal view. E—42.0 mm SL; lateral view. F—82.6 mm SL; lateral view. Serrations occur along a medial ridge in A and C (arrows) and absent in F. Scale bars = 0.5 mm (A–D) and 1 mm (E–F).

development, particularly in relation to growth of fin elements and protrusion of the snout. Secondly, this period of rapid structural change is characterised by highly variable intraspecific development trajectories.

The PCA of ontogenetic variation in the eight morphometric ratios identified trends along the first two axes (Fig. 6). Variation along these axes reflected ontogenetic changes in head shape (axis 1, 96.3% of total variance) and two body-depth ratios (axis 2, 2.6%). Five characters varied among size-classes, evidenced by their elongate elipses: orbit diameter in head length, snout length in head length, cheek height in head length, snout length in cheek height and length of longest dorsal spine in body depth. By contrast, the three remaining ratios (body depth in standard length, head length in during the with body size. The latter character did, however, vary between individuals of ≤ 89 mm and the "adult" size class.

Using these three ratios, a canonical discriminant analysis of morphological differences among the 11 species indicated a differentiation of body profiles along canonical axis 1 (Fig. 7). This showed a gradation from the slenderbodied *L. variegatus* through to deep-bodied *L. atkinsoni* and *L. ornatus*. Of the two characters responsible for variation along axis 1, body depth in standard length is the simplest to discern under field conditions. Values of this ratio for individual species are provided in the species descriptions below.

Three of the five scale-count characters (LL, DSR, VSR) did not vary ontogenetically, although they may be difficult to discern in specimens without full body pigmentation. Both the pectoral axil or parietal scales (see Carpenter & Allen, 1989) were found to be unreliable for identifying early juveniles. Parietal scales appear at around the time of settlement, although their number varies with both SL and side of the fish. Scales on the pectoral axil are entirely absent until 60–80 mm.

Both the cheek scales and serrations along the maxilla may further facilitate the identification of recently-settled specimens. A full complement of cheek scales is present in all lethrinids at settlement (Leis & Rennis, 1983). In *Lethrinus* species, they are lost shortly thereafter, with the mean size (SL) at which a species looses its scales useful as a diagnostic character. Cheek scales become difficult to detect as they recede towards the preopercular angle with increasing body size. Serrations along the outer edge of the maxilla (Fig. 8) are also present at settlement, although they are progressively lost soon thereafter in most species. In *L. genivittatus*, they may be present until 70–80 mm.

Lethrinus atkinsoni Seale

Pl. 1A,B,C

Material examined. (37 specimens: 18–126 mm). AUSTRALIA Great Barrier Reef region, AMS I.20578-003 (1:114 mm), AMS I.22674-007 (1:20 mm), AMS I.34147-003 (2:61–78 mm), AMS I.34323-042 (1:78 mm), AMS I.34911-001 (2:30–35 mm), AMS I.34912-001 (3:20–25 mm), AMS I.34912-002 (1:20 mm), AMS I.34912-003 (1:22 mm), AMS I.34913-001 (1:23 mm), AMS I.34913-002 (1:38 mm), USNM 336678 (2:20–21 mm), USNM 336679 (1:33 mm), USNM 336692 (1:31 mm), not retained (12:18–55 mm); INDONESIA Ceram, AMS I.18469-066 (2:40–45 mm); PAPUA NEW GUINEA Trobriand Islands, AMS I.17099-049 (1:48 mm); SOLOMON ISLANDS New Georgia Island, AMS I.22128-153 (1:126 mm).

Diagnosis. Body relatively deep, depth 2.4–2.8 in SL; 4.5 dorsal scale rows, 14–15 ventral scale rows; maxillary serrations 3–5 (rarely 6) at 18–21 mm, 2–5 at 22–30 mm, absent at greater than 35 mm; cheek scales absent at greater than 29 mm; at 18–115 mm dorsal spine 4 or 5 the longest.

Diagnostic colour notes. Snout and dorsum yellow-tan; intermittent yellow hue along caudal peduncle and fin (at greater than 25 mm); 4 black bands below dorsal spines fusing mid-body into 2 pointed configurations (Pl. 1A,B); shoulder blotch narrow and vertical; width of dark midlateral stripe approximately 4.0 in body depth; no dark markings below orbit; fins hyaline.

Pre-settlement colour notes. At 18–20 mm: body translucent off-white, melanophore patterns overlying yellow-orange xanthophore pigmentation; banding and shoulder blotch near-identical to juveniles (Pl. 1A,B; "Colour notes" below) although less distinct and intense; dark markings on head restricted to scattered melanophores over brain and diagonal black band through orbit; fins hyaline.

Colour notes. A distinctive species, displaying several colour patterns, rapidly switching between them within 1-2 seconds, only subtle variation noted with ontogeny. At 18-80 mm: snout and nape yellow-tan, dorsum either vellow-tan (without dark bands), off-white (with banding, noted below) or pale grey-tan (freshly killed, Pl. 1B), cheek and flank off-white to pale grey-tan, belly off-white; cheek without dark markings, eye often bisected by near-vertical black band (Pl. 1B); fins mostly hyaline, anterior two thirds of spinous fins off-white, dark bands bordering dorsal fin extending onto basal half of fin, melanophores absent from inner pelvic rays, at greater than 25 mm caudal fin vellowish, hue extending in broad stripe along caudal peduncle to mid-body, usually faded during banding displays, outer margin of dorsal, anal and caudal fins often pale scarlet at greater than 50 mm (as in Masuda & Kobayashi, 1994, Pl. 7, p. 175).

Two dark intermittent patterns. (A) Banding: 8–9 sharply-defined dark brown to black bands originating along dorsal margin of body and caudal peduncle, most tapering mid-body, 2 bands between head and dorsal fin either terminating at lateral-line (Pl. 1A) or fusing at base of pectoral fin, 2 bands below dorsal spines fusing above belly, 4–5 bands between dorsal and caudal rays extending unfused to ventral body-margin; 2 ventral bands near anal-fin origin fusing mid-body and extending in pointed configuration to above lateral-line, occasionally appearing as single broad stripe; narrow vertical shoulder blotch below dorsal spines 3–4 (Pl. 1A,B,C), marginally darker

than adjacent bands. When stressed (Pl. 1C), body paler than when freshly collected, banding and shoulder blotch slightly broader and darker, medium brown blotches along snout and operculum. (B) Dark mid-lateral stripe: frequently displayed at 30–80 mm, medium brown, extending from orbit to base of caudal peduncle, width approximately 4.0 in body depth.

Colour in alcohol. At 18–55 mm, head and body uniform pale off-white tan, belly off-white; banding and shoulder blotch of variable intensity, usually dulled; fins hyaline, melanophores retained; at greater than 30 mm, subtle broad pale stripe sometimes present between caudal-fin origin and above pectoral-fin base.

Ecology. Common, settles into shallow dense seagrass cover on lagoonal or fringing coral reefs (0.2-6 m; Cymodocea, Halodule, Thalassia), an ontogenetic shift to adjacent reefflat habitats apparent at 80-100 mm, thereafter seldom observed over seagrass; at 15-30 mm, remaining close to the seagrass canopy and rapidly seek cover therein when disturbed, larger individuals (30-80 mm) escape over the seagrass canopy; settlement recorded from 17-19 mm, small individuals (less than 40 mm) solitary, larger juveniles (40-80 mm) occasionally join small (approximately 10-20 individuals) schools with similarly-sized congeners (L. genivittatus, L. harak and L. obsoletus), Lutjanus fulviflamma (Lutjanidae), Parupeneus indicus and P. barberinus (Mullidae), Stethojulis strigiventor (Labridae), and in particular, Siganus fuscescens (Siganidae); juveniles forage diurnally over and between seagrass shoots, occasional brief aggressive interactions with congeners when recently-settled, noted resting on the substrate among seagrass shoots at night, not fleeing when approached.

Field identification. Lethrinus atkinsoni can be distinguished from other Lethrinus species by a combination of its deep body profile, characteristic dark banding, yellow caudal peduncle and fin (greater than 25 mm), and vertical shoulder blotch. Bellwood & Choat (1989) note the early-mid juvenile phase of the scarid Hipposcarus longiceps to mimic the behaviour, body shape and colouration of similarly-sized Lethrinus species. Juvenile H. longiceps with a yellow mid-lateral band (Pl. 1D, Bellwood & Choat, 1989) may be confused with L. atkinsoni, although the black dot at the base of the caudal rays in H. longiceps separates these species. Juvenile L. atkinsoni, 30-80 mm, frequently exhibit a dark mid-lateral stripe pattern, and form schools with juvenile Siganus fuscescens displaying a near-identical pattern. When approached, L. atkinsoni juveniles usually revert to their distinctive banding (Pl. 1A,B) or yellow caudal-stripe patterns. The yellow-tan body of small Siganus doliatus (22-25 mm) may lead to confusion with L. atkinsoni, although the banding and pointed snout of L. atkinsoni readily separates these species.

Previous descriptions. Juvenile *L. atkinsoni* of unknown size were figured by Allen & Swainston (1988) and Shao *et al.* (1992). Masuda & Kobayashi (1994) included a colour plate of a specimen 75 mm total length, displaying the characteristic yellow caudal stripe and dark banding.

Lethrinus erythracanthus Valenciennes

Pl. 1D

Material examined. (3 specimens: 25–26 mm). AUSTRALIA Great Barrier Reef region, AMS I.34914-001 (1:25 mm), AMS I.34914-002 (1:26 mm), USNM 336680 (1:25 mm).

Diagnosis. At 25–26 mm, body moderately deep, depth 2.8–2.9 in SL; 4.5 dorsal scale rows, 16 ventral scale rows; maxillary serrations 4–5; cheek scales present; dorsal spine 3 or 4 the longest.

Diagnostic colour notes. At 25–26 mm, dorsum and flanks yellow-orange, belly off-white yellow; 4 narrow silver primary stripes (4–6 at 50–100 mm, Pl. 1D), broad interspaces yellow-orange; no dark markings on body or cheeks; fins hyaline (but see "Identification note" below).

Colour notes. A species characterised by marked colour changes throughout life history, although little ontogenetic variation apparent during early postsettlement phase; no rapid colour pattern changes. At 25-26 mm, freshly collected: dorsum deep yelloworange, fading to pale orange belly, no dark banding or mid-lateral stripe patterns, silver peritoneal lining faintly visible; 4 narrow silver stripes below lateral-line, originating behind operculum and pectoral fin base, orbital stripe extending to base of caudal rays, other stripes terminating near base of caudal peduncle, interspaces broader than stripes and of similar colouration to rest of body; cheek and operculum off-white to silver, no dark markings, snout and lips grey to pale yelloworange, nape slightly reddish; fins hyaline, spinous fins with moderately-dense melanophores, yellow tinge distally, inner pelvic membranes without dense melanophores (but see "Identification note" below).

At 50–80 mm, in field (Pl. 1D): body yellow-orange, dorsal scales pale-centred, lateral-line denoted by row of silver dots, head yellowish grey; pectoral fins hyaline, caudal, dorsal and anal fins dusky yellow, fading posteriorly, pelvic fins off-white; 5–8 narrow silver stripes along flanks, medial stripe of greatest intensity, extending from lower margin of orbit to base of caudal rays, remaining stripes running from operculum to base of caudal peduncle.

Colour in alcohol. At 25–26 mm, head and body uniform off-white yellow, peritoneum off-white; silver primary stripes inconspicuous, initially darker than surrounding body, faded after ca. 2 years; fins hyaline, melanophores retained.

Ecology. Settlement and nursery sites unknown, rare at Green Island, three recently-settled specimens were collected from a sheltered seagrass bed (0.5-2.0 m; Cymodocea and Thalassia) adjacent to the shoreline; field behaviours unknown.

Field identification. Early-juvenile L. erythracanthus



Plate 1. A—Lethrinus atkinsoni, 23 mm SL, AMS I.34915-001, live, Green Island. B—Lethrinus atkinsoni, 23 mm SL, AMS I.34915-001, dead, Green Island. C—Lethrinus atkinsoni, 50 mm SL, live (stress colouration), Green Island. D—Lethrinus erythracanthus, 80 mm SL, underwater photograph by R.H. Kuiter, Flores (Indonesia). E—Lethrinus genivittatus, 30 mm SL, AMS I.34919-001, dead, Green Island. F—Lethrinus genivittatus, approx. 30 mm SL, underwater photograph by R.H. Kuiter, Sydney Harbour. G—Lethrinus genivittatus, approx. 40 mm SL, underwater photograph by R.H. Kuiter, Sydney Harbour. H—Lethrinus harak, 20 mm SL, AMS I.34920-002, live, Green Island.

individuals are rarely encountered in the field; no underwater observations were made during the present study. At the size examined, *L. erythracanthus* field colouration could be confused with both *L. genivittatus* and *L. atkinsoni* juveniles of a similar size. All three species may be yellow-orange over at least the snout and dorsum. The lack of dark intermittent patterns in *L. erythracanthus* may distinguish it from other species.

Identification note. The density of pigmentation on the innermost pelvic membranes varies among *L. erythracanthus* individuals (Carpenter & Allen, 1989). In the specimens examined, this ranged from a faint covering of fine melanophores to absence. Although the small sample and narrow size range did not allow ontogenetic effects to be distinguished from variation at the individual or population level, this character may be useful for separating *L. erythracanthus* from other lethrinid juveniles.

Previous descriptions. The *L. erythracanthus* juvenile stage has been figured by Carpenter & Allen (1989; length not given) and Lieske & Myers (1994; length not given), and colour plates included in Myers (1989; 150 mm), Randall *et al.* (1990; length not given), Kuiter (1992; 80 mm, reproduced here in Pl. 1D) and Masuda & Kobayashi (1994, 50 mm total length).

Lethrinus genivittatus Valenciennes

Pl. 1E,F,G, Figs 3A, 5A, 8, 9

Material examined. (38 specimens: 17–99 mm). AUSTRALIA New South Wales, AMS I.17458-004 (1:32 mm), AMS I.26438-003 (4:17–34 mm), AMS I.30814-007 (1:25 mm); Great Barrier Reef region, AMS I.20786-012 (3:18–23 mm), AMS I.32476-003 (2:18–19 mm), AMS I.34911-002 (7:20–26 mm), AMS I.34911-003 (1:39 mm), AMS I.34911-004 (1:25 mm), AMS I.34915-001 (2:18–21 mm), AMS I.34916-001 (1:19 mm), AMS I.34917-001 (1:31 mm), AMS I.34917-002 (1:19 mm), AMS I.34919-001 (1:30 mm), AMS (I.33287-001) (1:20 mm), USNM 336681 (6:21–32 mm); Queensland south of Great Barrier Reef, AMS IB.1023 (4:46–70 mm), AMS E.1359 (1:99 mm).

Diagnosis. Body depth variable, 2.6–3.8 in SL, deepening with increased SL; 4.5 dorsal scale rows, 15 (rarely 16) ventral scale rows; maxillary serrations 5–7 (occasionally 4) at 16–40 mm, fewer at greater than 40 mm, absent by 80–90 mm; cheek scales retained until 25–27 mm; dorsal spine 2 relatively elongate, its length \geq dorsal spine 3 at greater than 30–35 mm (occasionally 25–30 mm).

Diagnostic colour notes. Dorsum yellow-tan, 4–6 distinct narrow black bands extending to lateral-line, body off-white tan to silver ventrally; intense cuboidal shoulder blotch, surrounded by silvery halo (Pl. 1F), pointed tip crossing lateral-line (Fig. 5A); 3–4 orange stripes below lateral-line, of equal intensity and width, interspaces silver;

at greater than 35 mm, 3 broad tan bands on suborbit and preoperculum (Pl. 1G); fins hyaline.

Pre-settlement colour notes. Pre-settlement pigmentation variable with SL (16-21 mm), complete by 22 mm (Fig. 9): dorsum and flank translucent off-white to pale tan, belly and cheek silver; prior to appearance of melanophores, pigmentation restricted to yellow-orange xanthophores along myosepta and horizontal septum, sparse melanophores first appear over caudal peduncle and 1-3 scales below dorsal spines 4-5 forming early shoulder blotch (Fig. 9A), later increasing to 4-6 scales; 3-4 cuboidal blotches appearing between lateral-line and horizontal septum, behind shoulder blotch (Fig. 9B), followed by banding along dorsum and 2-3 indistinct blotches below horizontal septum (Fig. 9C), interspaces silver to pale blue; head with few markings, melanophores scattered over brain, dark band forming between orbit and maxilla; fins mostly hyaline, sparse melanophores and underlying xanthophores visible along spines.

Colour notes. A distinctive species with few ontogenetic changes in juvenile colouration, capable of rapid pattern changes within 1-3 seconds. At 20-30 mm: snout and dorsum intense yellow-tan, head and body abruptly silvery off-white ventrally, lateral-line cryptic; 4 narrow primary stripes along flank, of similar widths, terminating near base of caudal peduncle, golden orange in captivity or when freshly killed (Pl. 1E), orange (rarely orange-tan) in field with dorsal stripe concealed by 3-4 pale brown to grey blotches (Pl. 1F,G), interspaces silver (rarely pale blue, Pl. 1F); intense banding frequently displayed in field with concomitant partial-fading of primary stripes (Fig. 3A), dulled in captivity and after death (cf. Pl. 1E and 1G), 4-6 narrow bands along dorsum, series of blotches along ventral margin of lateral-line, further banding between blotches and belly (Pl. 1G); blotch below dorsal spines forming diagnostic shoulder blotch (Fig. 5A), cuboidal with pointed tip extending over lateral-line and surrounded by silvery halo (Pl. 1F); intense dark mid-lateral stripe prevalent in field, width approximately 5.0 in body depth, rarely accompanied by banding or primary stripes; snout and cheek without dark markings, intermittent near-vertical black band bisecting eye in field; fins mostly hyaline, dorsal fin often similar hue to dorsum in field, sparse offwhite and dark patches over anterior half of spinous fins. At 20-30 mm, individuals in field frequently display background and primary-stripe colourations either with distinct shoulder blotch alone or without dark markings (as in Pl. 6, p. 173 in Masuda & Kobayashi [1994]).

At 30–80 mm: mostly as in smaller individuals, dorsum greyish tan, banding more intense than when smaller, shoulder blotch and orange primary stripes prominent; two vertical dark tan bands visible on suborbital at greater than 35 mm (Fig. 3A, Pl. 1G), third similar band along rear margin of preoperculum.

Colour in alcohol. At 16–21 mm, late pre-settlement: body translucent off-white to pale straw, xanthophore





Fig. 9. Ontogenetic changes in the external melanophore pigmentation of *Lethrinus genivittatus* prior to settlement. Typical length ranges: A—16–20 mm SL; B—17–20 mm SL; C—18–21 mm SL. Details of scalation, myomeres and internal pigmentation not shown. Based on six specimens from Green Island, including AMS I.34915-001, AMS I.34916-001, AMS I.34917-002 and 2 specimens not retained.

pigmentation lost, melanophores retained in similar patterns to when freshly killed, fins hyaline. At greater than 20 mm, post-settlement: body and head pale greytan, belly off-white; dorsal banding slightly dulled, dark blotches below lateral-line indistinct; shoulder blotch faded from when freshly killed, halo absent; primary stripes lost; fins hyaline.

Ecology. At less than 90 mm, common in dense shallow seagrass beds on coral reefs and in coastal embayments (0.2–3.0 m; *Cymodocea, Halodule, Halophila, Thalassia, Zostera*); settlers recorded from 16 mm although typically 19–22 mm, mostly solitary, individuals 20–30 mm hover over the seagrass canopy, periodically picking food items off seagrass blades, occasional aggression noted towards conspecifics and congeners of a similar size; not appearing site-attached although seldom moving further than 1 m when disturbed, at less than 30 mm will rapidly seek shelter at base of canopy if closely approached; at greater than 30 mm occasionally joining loose multi-species schools with *Scarus* species (Scaridae), *Parupeneus indicus, Siganus fuscescens* and congeners of a similar size.

Field identification. Although distinctive when freshly killed, may be easily confused with L. obsoletus under field conditions, particularly at less than 40 mm. Both species are capable of rapid changes in their overlying dark colour patterns and display 3-4 coloured primary stripes. When recently-settled (18-25 mm), L. genivittatus and L. obsoletus often display an almost uniform yellow-tan to grey-tan hue, and observation for several minutes is necessary before other patterns can be discerned. The shoulder blotch's form is useful for distinguishing these species (Fig. 5.): the L. obsoletus shoulder blotch is mostly vertically-rectangular, does not cross the lateral-line and is seldom surrounded by a pale halo. This contrasts with the square shoulder blotch with pointed extension over the lateral-line and pale halo in L. genivittatus. At less than 40 mm, dorsal bands tend to be narrower and of sharper definition in L. genivittatus than L. obsoletus (cf. Pl. 1G and 2E). In many cases, it may be necessary to collect smaller specimens for confirmation with morphological characters or freshly-killed colour patterns.

Identification notes. Carpenter & Allen (1989) report the degree of outward-curvature of the lower canine teeth, along with the greater length of the second dorsal spine over the third, to be the most useful means for separating *L. genivittatus* from other lethrinids. However, dentition is of little value for distinguishing *L. genivittatus* at less than 80 mm. Although the second dorsal spine is shorter than the third until 30–35 mm in most cases ("Diagnosis" above), it is still relatively elongate in individuals greater than 23 mm in comparison with other *Lethrinus* species, and may be a useful diagnostic character. The number of scale rows above the lateral-line also differentiates *L. genivittatus* (4.5) from similar species such as *L. obsoletus* (5.5).

Previous descriptions. Early life history stages of *L. genivittatus* have been described and/or figured in several works. The larval development of laboratory-reared individuals 2.7–16.4 mm was described and figured (as *L. nematacanthus*) by Mori (1988), although few details of pigmentation were given. Juvenile colour plates were provided by Kuiter (1993, length not given), Masuda & Kobayashi (1994, 35 mm total length) and Kuiter & Debelius (1994, 40 mm, reproduced here in Pl. 1G). Sato (1984) noted the prolonged occurrence of maxillary serrations in *L. genivittatus* juveniles (under *L. nematacanthus*) as "maxillary ornamented with row of tubercles in younger individuals".

Lethrinus harak (Forsskål)

Pl. 1H, 2A,B

Material examined. (38 specimens: 19–96 mm). AUSTRALIA Cocos-Keeling Islands, AMS I.33529-002 (1:73 mm); Great Barrier Reef region, AMS I.20773-026 (2:93–96 mm), AMS I.34911-005 (5:24–56 mm), AMS I.34912-004 (1:19 mm), AMS I.34912-005 (1:21 mm), AMS I.34920-001 (1:20 mm), AMS I.34920-002 (1:20 mm), USNM 336682 (3:23–34 mm), USNM 336683 (2:19– 21 mm), not retained (9:25–67 mm); PAPUA NEW GUINEA Trobriand Islands, AMS I.17102-048 (6:45–84 mm), AMS I.17075-003 (1:43 mm); SOLOMON ISLANDS Guadalcanal, AMS I.17482-020 (5:62–76 mm).

Diagnosis. Body moderately deep, depth 2.7–3.1 in SL; 5.5 dorsal scale rows, 14–15 ventral scale rows; maxillary serrations 1–3 at 22–25 mm, absent at greater than 35 mm; cheek scales retained until 45 mm; dorsal spine 5 (occasionally 4) the longest.

Diagnostic colour notes. Dorsum olive to off-whitetan, silvery blue interspaces prominent at 18–22 mm (Pl. 1H); dark horizontal blotch below dorsal spines 8– 10, inconspicuous at 18–22 mm, seldom switched off; shoulder blotch square, usually inconspicuous; dark midlateral stripe moderately-intense, seldom obscuring horizontal blotch, width approximately 4.0 in body depth; fins mostly hyaline.

Colour notes. A relatively distinctive species, capable of rapid colour changes within 1–3 seconds. At 18–22 mm (Pl. 1G): dorsum and nape yellowish olive, series of diffuse black markings (3 bands followed by 3 blotches) above lateral-line, 2–3 exceedingly-faint black bands along caudal peduncle, 3–4 yellowish olive blotches along lower lateral-line margin, interspaces silvery blue, rectangular blotch below dorsal spines 8–10 beginning to form characteristic *L. harak* "thumb-print" blotch, series of indistinct blotches of similar hue between pectoral and anal fins, belly silvery off-white; snout and lips dusky olive, cheek silvery off-white, without dark markings, eye often bisected by near-vertical black band



Plate 2. A-Lethrinus harak, 55 mm SL, live (stress colouration), Green Island. B-Lethrinus harak, 50 mm SL, dead, Green Island. C-Lethrinus lentjan, 50 mm SL, live, Green Island. D-Lethrinus nebulosus, 30 mm SL, dead, Ken-Ting National Park (Taiwan), reproduced from Shao et al. (1992). E-Lethrinus obsoletus, 25 mm SL, AMS 1.34913-004, live, Green Island. F-Lethrinus obsoletus, 56 mm SL, live, Green Island. G-Lethrinus obsoletus, 27 mm SL, AMS 1.34913-005, dead, Green Island. H-Lethrinus obsoletus, approx. 250 mm SL, underwater photograph, Green Island.

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in field; fins mostly hyaline, off-white with diffuse dark blotches over anterior half of spinous fins. After death, patterns retained though faded.

At 23-80 mm (Pl. 2A,B): body and head olive to greytan dorsally, belly off-white; dark banding and blotches more distinct, intensifying when stressed (Pl. 2A), most fading after death (Pl. 2B), rapidly switched on or off, "thumb-print" blotch distinct, cuboidal shoulder blotch below dorsal spines 4-5, rarely conspicuous, dark blotches between pectoral and anal fins now as series of 3-4 short bands, terminating mid-body; dark mid-lateral stripe often displayed in field, dark khaki, seldom fully obscuring "thumb-print" blotch, width approximately 4.0 in body depth; cheek silver to off-white, series of dark bands when stressed (Pl. 2A), intermittent dark band through eye until 60 mm; fins hyaline greyish yellow, margins often pink to pale scarlet in field. At greater than 80 mm, dark midlateral stripe absent, banding faded or absent, "thumbprint" blotch distinct.

Colour in alcohol. Body and head pale off-white-tan, belly off-white; dark body and head markings dulled, "thumb-print" blotch often inconspicuous at less than 23 mm; fins hyaline, melanophore patterns retained.

Ecology. Common, restricted to reef seagrass cover at less than 80 mm, without preference for particular seagrass species or canopy structures, larger juveniles also found over adjacent sand/coral rubble and sparse vegetative growth (*Halimeda, Sargassum*); settlers 16–18 mm, mostly solitary, not appearing site attached, rapidly seek cover within the seagrass canopy when disturbed; at greater than 40 mm, occasionally found with similarly-sized juveniles of *Parupeneus barberinus* and *P. indicus, Siganus fuscescens* and congeners (particularly *L. atkinsoni, L. obsoletus, L. genivittatus*) in small loose schools, no aggressive interactions noted; observed resting on the substrate among seagrass shoots after dark, not fleeing when approached.

Field identification. Generally an easily identified species, distinguished at greater than 25 mm by presence of the dark "thumb-print" blotch and the absence of coloured primary stripes. If intense banding is displayed, then the horizontal blotch is always visible. At less than 25 mm (Pl. 1H), the series of khaki blotches below the lateral-line, pale blue interspaces, and lack of primary stripes and intense mid-lateral stripe is diagnostic of *L. harak.* Small individuals often need to be followed for several minutes to confirm their identification.

Previous descriptions. The early juvenile stage of *L. harak* has not been described previously. Masuda & Kobayashi (1994) included a colour plate of a specimen 40 mm total length.

Lethrinus lentjan (Lacépède)

Pl. 2C, Fig. 5B,C

Material examined. (8 specimens: 24–105 mm). AUSTRALIA Great Barrier Reef region, AMS I.22700-041 (1:78 mm), AMS I.34144-001 (2:75–105 mm), AMS I.34911-006 (1:24 mm), AMS I.34911-007 (1:39 mm), AMS I.34912-006 (1:27 mm), AMS I.34920-003 (1:46 mm), AMS I.34921-001 (1:31 mm).

Diagnosis. Body moderately deep, depth 2.5–3.0 in SL; 5.5 dorsal scale rows, 15–16 ventral scale rows; maxillary serrations 3–5 at 24 mm, 1–2 at 31 mm, absent by 39 mm; cheek scales absent at greater than 26 mm; dorsal spine 4 (rarely 5) the longest at 24–105 mm.

Diagnostic colour notes. Body and head silvery olive to greyish tan, belly off-white; dark markings moderatelyintense, often inconspicuous, shoulder blotch small, cuboidal or circular, width of dark mid-lateral stripe approximately 5.0 in body depth; 3–4 narrow primary stripes of similar widths, pale pink to orange-pink, often inconspicuous (as in Pl. 2C), interspaces silver; rear margin of operculum with narrow scarlet patch at greater than 40 mm (Pl. 2C); fins mostly hyaline.

Colour notes. A relatively drab species, possessing only subtle differences in juvenile colouration from several other species ("Field Identification" below), capable of rapid pattern changes within 2-3 seconds. At 25-31 mm: dorsum pale olive, belly off-white, lateral-line cryptic, 3-4 narrow primary stripes along flank, of similar width and intensity, pale pink to orange-pink with silver interspaces, often inconspicuous (as in Pl. 2C), intermittent dark patterns on body less intense than similar species (e.g., L. obsoletus), 5-6 indistinct dark bands along dorsum between head and caudal peduncle, most extending to lateral-line, 2-3 similar bands along caudal peduncle, dorsal bands may connect with diffuse banding and series of 3-4 blotches along midbody, first blotch below dorsal spines 3-4 forming diffuse cuboidal or circular shoulder blotch (Fig. 5B), never with pale halo; head similar to body, operculum and cheek silvery off-white, near-vertical black band often bisecting eye in field, may join diffuse grey blotch below eye, rear margin of preoperculum occasionally with narrow dark band (or as several dark blotches); fins mostly hyaline, few dark markings, outer margins pale pink in field, scattered off-white and dark patches in captivity (as in Pl. 2C) or after death.

At 40–60 mm (Pl. 2C): body pale grey-tan, lateral-line cryptic or lined either side by row of silver dots, dark banding and blotches along body more distinct; dark midlateral stripe occasionally displayed in field, dark grey, width approximately 5.0 in body depth; snout pale tan, occasionally several silvery bands across snout, narrow scarlet patch along the rear margin of operculum, distinguishable in field though often faded in captivity (Pl. 2C) or after death; primary stripes more distinct (faded in Pl. 2C); fins mostly hyaline, often deep pink hue along fin margins in field, darkening to pale purple after death, diffuse patches of melanophores along dorsal and anal spines.

At 60–100 mm: dorsum olive, belly off-white, few or no dark markings, banding and shoulder blotch faint or absent when alive, diffuse after death, dark mid-lateral stripe absent, primary stripes faded or absent, scarlet operculum margin bright.

Colour in alcohol. At 24–60 mm, body and head creamy tan, scattered with fine black flecks, slightly paler ventrally; shoulder blotch retained, other dark markings on body faint or lost, lateral-line cryptic; primary stripes lost, at 40–80 mm may be replaced by stripes slightly darker or paler than adjacent body in specimens preserved for less than 1 year; fins hyaline, dark markings retained though faint. Preserved specimens (20–80 mm) may be indistinguishable from *L. obsoletus* and *L. nebulosus*, precluding diagnoses beyond *L. lentjan/obsoletus/nebulosus*.

Ecology. Uncommon at Green Island, settles into shallow seagrass cover, remaining there until 80–100 mm, at 100–140 mm only recorded within shoreline seagrass habitats after dark; not appearing site attached, mostly solitary although occasionally joining small (approximately 10–15 individuals) multi-species schools with congeners (principally *L. atkinsoni*, *L. harak* and *L. obsoletus*), siganids and mullids of a similar size; other field behaviours unknown.

Field identification. A difficult species to identify in the field, displaying similar colouration to both *L. obsoletus* and *L. nebulosus*. All three species possess a similar body profile and may join multi-species schools together. The colouration differences for distinguishing these species in the field are summarised below:

Lethrinus lentjan (Pl. 2C, Fig. 5B,C): dark body markings moderately-intense, shoulder blotch circular or square, rarely vertically-rectangular; 3–4 primary stripes, narrow, of similar widths, pink to orange-pink, often indistinguishable at less than 35 mm, interspaces silver; rear margin of operculum scarlet at greater than 40 mm; spinous fin membranes mostly hyaline.

Lethrinus nebulosus (Pl. 2D, Fig. 5C,D): dark body markings moderately-intense, shoulder blotch circular or square; more than 4 narrow primary stripes, pale blue, mostly indistinguishable at less than 40 mm, interspaces off-white to yellow-tan; operculum off-white silver or yellow-tan; spinous fin membranes with moderately-dense melanophores.

Lethrinus obsoletus (Pl. 2E–G, Fig. 5B,C,E): dark body markings usually intense; shoulder blotch square or vertically-rectangular; primary stripes 3–4, orange-tan, pectoral stripe wider than others, visible at greater than 20 mm, interspaces off-white; operculum silvery off-white; spinous fin membranes mostly hyaline.

These combinations of field colours will allow most *L. lentjan* juveniles to be separated from *L. obsoletus* at greater than 20 mm, and from *L. nebulosus* at greater than 40 mm. Nonetheless, at less than 40 mm, the collection of

specimens for examination of colours displayed when freshly killed, or to allow them to be grown to a larger size in aquaria, is recommended.

Lethrinus lentjan is one of the few lethrinids to occur as recently-settled or older juvenile stages in coastal seagrass habitats throughout northern Australia (Blaber *et al.*, 1992). In such localities its identification is facilitated by the absence of *L. obsoletus*, although it should be noted that *L. nebulosus* juveniles are also known from similar areas (Blaber, 1980).

Identification note. The presence of cheek scales may distinguish *L. lentjan* and *L. obsoletus* as early juveniles. Cheek scales were only noted on a single *L. lentjan* specimen of 24 mm (absent at 26–46 mm, cf. present until 30–39 mm in *L. obsoletus*).

Lethrinus nebulosus (Forsskål)

Pl. 2D, Fig. 5C,D

Material examined. (4 specimens: 38–62 mm). AUSTRALIA Great Barrier Reef region, AMS I.34924-001 (1:62 mm), AMS I.34925-001 (1:38 mm). Provisional identification: Great Barrier Reef region, AMS I.431 (2: 47–48 mm).

Diagnosis. At 38–62 mm, body moderately deep, depth 2.6–3.0 in SL; 5.5 dorsal scale rows, 15–16 ventral scale rows; maxillary serrations absent; cheek scales absent; dorsal spine 4 or 5 the longest.

Diagnostic colour notes. Dorsum grey-tan at 30–38 mm, yellow-tan at 62 mm; lateral-line cryptic or with dorsal row of silvery dots; shoulder blotch vertically-rectangular or square; more than 4 narrow primary stripes, pale blue, indistinct at 30–38 mm; 2 pale blue stripes between mouth and orbit; spinous fins greyish yellow anteriorly, dark grey when folded at rest.

Colour notes. A distinctive species throughout most of the juvenile period, although difficult or impossible to distinguish when recently-settled, capable of rapid colour pattern changes, details of dark mid-lateral stripe pattern unknown. At 30-62 mm (Pl. 2D): dorsum grey-tan to yellow-tan, shading ventrally to off-white belly, lateralline cryptic, bordered dorsally by row of diffuse silvery dots; dark banding moderately intense in field, may fade after death (Pl. 2D), rapidly switched on or off within 1-3 seconds, 3-5 indistinct dorsal bands between head and caudal peduncle, most connecting with diffuse banding below lateral-line, 2-3 bands along caudal peduncle; shoulder blotch below dorsal spines 4-5, square or vertically-rectangular (Fig. 5C,D), indistinct when alive, not bordering lateral-line; from 38 mm, primary stripes forming along flank as more than 4 rows of faint pale blue dots, between operculum or pectoral-base and caudal peduncle, may appear as faint stripes when freshly collected or killed; head similar to body, rear margin of preoperculum dark grey after death (Pl. 2D), cheek pale yellow-tan, near-vertical intermittent black band through orbit in field, faded at death, 2 silvery blue stripes between mouth and lower orbit margin; fins mostly hyaline, spinous fins greyish yellow anteriorly, dark grey when folded at rest.

Colour in alcohol. Body pale off-white tan, belly offwhite; dark head and body markings retained, shoulder blotch distinct, primary stripes faint, dorsal row of pale dots along lateral-line grey; dense melanophores retained on fins, other hues lost. After preservation, *L. nebulosus* juveniles of less than 80 mm are often indistinguishable from *L. lentjan* and *L. obsoletus*. Identification of such material should at most be considered provisional (see also *L. obsoletus* "Identification note"). The moderate to dark grey hue of spinous fin membranes may separate preserved *L. nebulosus* from *L. obsoletus/lentjan*.

Ecology. Juveniles uncommon at Green Island, occasionally observed over the shoreline seagrass habitat at 40–120 mm, never over non-seagrass habitats; mostly solitary, occasionally joining small schools of similarly-sized congeners, particularly *L. obsoletus* and *L. harak*, no aggressive interactions noted, other field behaviours unknown; a 62 mm specimen was collected over sand adjacent to fringing reef, 3 m, Lizard Island lagoon; also known from inshore habitats (Blaber, 1980).

Field identification. At 30–38 mm, difficult to distinguish in the field, the characteristic primary and preorbital stripes may be faintly visible when freshly collected (as in Pl. 2D). At 62 mm, the pale blue preorbital stripes, yellowtan body, and to a lesser extent the primary stripes, are clearly visible and diagnostic. However, individuals 30– 100 mm readily display dark intermittent banding which may obscure any underlying colouration. In most cases, specimens will need to be observed for at least several minutes before their identification can be accurately discerned.

At less than 40 mm, distinguishing *L. nebulosus* juveniles from *L. lentjan*, and occasionally *L. obsoletus*, is difficult or impossible prior to development of distinct primary stripes. It is often necessary to collect such individuals for maintenance in aquaria to allow examination of colour patterns displayed with subsequent growth. The combinations of colour patterns most useful for separating *L. nebulosus* juveniles from these congeners are summarised in the "Field Identification" section of *L. lentjan*.

Previous descriptions. Wheeler (1961) sketched and briefly described the colour patterns displayed by two "small" captive individuals, and Carpenter & Allen (1989) included a brief juvenile colour description and accompanying colour plate (length of specimen not given). Allen & Swainston (1988) and Kuiter (1993) also provided juvenile colour plates. Shao *et al.* (1992) included a colour plate of a 30 mm juvenile (reproduced here in Pl. 2D), illustrating the early appearance of the characteristic primary stripes. Two further juveniles from Taiwan (83 and 105 mm) are shown in Lee (1993).

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Lethrinus obsoletus (Forsskål)

Pl. 2E-H, Fig. 5B,C,E

Material examined. (72 specimens: 17–81 mm). AUSTRALIA Great Barrier Reef region, AMS I.20772-027 (1:81 mm), AMS I.34911-008 (4:18–27 mm), AMS I.34911-009 (3:36–39 mm), AMS I.34911-010 (1:33 mm), AMS I.34912-009 (1:33 mm), AMS I.34913-003 (1:25 mm), AMS I.34913-004 (1:25 mm), AMS I.34913-005 (1:27 mm), AMS I.34913-006 (1:43 mm), AMS I.34913-005 (1:27 mm), AMS I.34913-006 (1:43 mm), AMS I.34919-002 (2:31–35 mm), AMS I.34919-003 (1:31 mm), AMS I.34926-001 (1:18 mm), AMS I.34927-001 (1:58 mm), USNM 336685 (1:20 mm), USNM 336686 (3:26–34 mm), USNM 336687 (4:37–40 mm), not retained (45:17–63 mm).

Diagnosis. Body moderately deep, depth 2.5–3.0 in SL; 5.5 dorsal scale rows, 15–16 ventral scale rows; maxillary serrations 5–7 at 16–18 mm, 1–4 at 25–29 mm, 0–2 at 30–39, absent thereafter; cheek scales present at 16–30 mm, variable at 31–39 mm, absent at less than 39 mm; dorsal spine 4 or 5 the longest at less than 35 mm.

Diagnostic colour notes. Body and head cream to pale grey-tan; banding intense, shoulder blotch cuboidal or vertically-rectangular, seldom with pale halo, not crossing lateral-line; dorsal margin of lateral-line silvery cream; 2–4 orange-tan primary stripes, pectoral stripe of greatest width and intensity; dark mid-lateral stripe frequently displayed (20–80 mm), intense, width approximately 5.0 in body depth; fins mostly hyaline.

Colour notes. Minimal change in colour patterns throughout juvenile ontogeny, frequently displays dark intermittent patterns, able to switch colour patterns in 1–3 seconds. At 17–19 mm, recently-settled: body cream, abdomen silver, lateral-line cryptic; 4–7 indistinct grey bands along dorsum, may join faint ventral bands at lateral-line; shoulder-blotch dark grey, often inconspicuous, cuboidal (Fig. 5B), never crossing lateral-line, without pale halo, rapidly switched on or off within 2–3 seconds; 2–3 indistinct primary stripes, pale orange-tan, dorsal and ventral stripes often indistinguishable, pectoral stripe marginally wider than orbital stripe; nape and snout yellow-tan, cheek silver without dark markings; fins hyaline.

At 20–80 mm (Pl. 2E–G): body pale grey-tan, belly off-white, lateral-line usually distinct, dorsal margin off-white; banding and shoulder blotch distinct and intense when alive (Pl. 2E,F), fading after death (Pl. 2G), medial dorsal bands usually joining 2–3 cuboidal blotches below lateral-line (Pl. 2E,F), ventral bands extending diagonally between blotches and belly, shoulder blotch distinct, mostly vertically-rectangular (Fig. 5C,E, Pl. 2F,G), occasionally cuboidal (Fig. 5B, Pl. 2E), seldom bordering lateral-line, rarely with pale halo; dark mid-lateral stripe frequently seen in field, dark brown to black, width approximately 5.0 in body depth; primary stripes orange-pink to orange-tan, dorsal stripe seldom conspicuous, pectoral stripe

slightly wider than others (as in Pl. 2G); head similar to body, nape and snout uniform or mottled tan, black nearvertical band often bisecting orbit in field, grey blotch below orbit from 22 mm (inverted v-shaped band from 45 mm) and dark grey to brown blotches along rear margin of preoperculum and operculum in captivity; fins mostly hyaline, pale pink distally in field, anterior half of spinous fins off-white with scattered brown patches.

Colour in alcohol. At 17–20 mm, body off-white, dark banding and shoulder blotch dulled, primary stripes lost, fins hyaline; at greater than 25 mm, body and head olive to grey-tan, belly off-white, banding and dark head markings distinct though dulled, primary stripes lost; fins hyaline. After preservation, *L. obsoletus* juveniles (18–80 mm) are often indistinguishable from *L. lentjan* and *L. nebulosus*, preventing identification beyond *L. obsoletus/ lentjan/nebulosus*.

Ecology. Common, mostly solitary, occasionally joins small (approximately 10–15 individuals) multi-species schools with similarly-sized congeners (*L. atkinsoni, L. genivittatus, L. harak, L. variegatus*), Stethojulis strigiventor, Parupeneus barberinus and P. indicus, and particularly Siganus fuscescens; settles at 16–18 mm into shallow seagrass cover (0.2–4 m; Halodule, Thalassia, Cymodocea) on fringing and lagoonal reefs, an ontogenetic shift apparent to adjacent reef-flat habitats at 70–90 mm, individuals 90–140 mm only occasionally encountered within shallow areas; forages diurnally off seagrass leaves (18–30 mm) or on benthic items (at greater than 30 mm), no aggressive interactions noted, individuals 18–25 mm rapidly seek shelter within the seagrass canopy when disturbed.

Field identification. Generally an easy species to identify in the field, although can be confused with L. genivittatus, L. lentjan and L. nebulosus (Table 1). Small specimens (18-25 mm) can be distinguished from L. nebulosus and L. lentjan by their intense shoulder blotch (Fig. 5) and orange to orange-tan primary stripes. At this size, L. obsoletus and L. genivittatus can be reliably separated by their primary stripes, dorsal bands, and shoulder blotch. At greater than 25 mm, L. obsoletus can be distinguished from other species by the prominent orange-pink to orangetan pectoral stripe. During display of the dark mid-lateral stripe, the off-white dorsal border of the lateral-line, in combination with a moderately-deep body profile (cf. pale dorsal border with slender body in L. variegatus), is diagnostic. At all sizes, individuals may need to be observed for several minutes before the full range of colour patterns can be ascertained. At less than 40 mm, the collection of specimens for examination of freshly-killed colours may also be necessary. Further notes on separating these species in the field are given in the "Field Identification" sections of L. genivittatus and L. lentjan. Lethrinus obsoletus appears unique among GBR lethrinids in continuing to display a dark mid-lateral stripe pattern throughout the adult stage (Pl. 2H).

Previous descriptions. Wheeler (1961) included a colour sketch of a captive 88 mm TL specimen (as *Lethrinus ramak*) along with brief descriptions of the stress, resting and freshly-killed colouration displayed by "very young" specimens (sizes not given). Masuda & Kobayashi (1994) provided a colour plate of a specimen 35 mm total length.

Identification notes. Carpenter & Allen (1989) note the presence of a "knob" on the outer surface of the maxilla in L. obsoletus to be useful for separating this species from other lethrinids. This character is indistinguishable at less than 80 mm. Alternative meristic and morphological measurements (particularly the number of dorsal scale rows, presence of cheek scales and number of maxillary serrations), along with the shoulder blotch and primary stripes, represent the easiest means of distinguishing smaller L. obsoletus from other close species.

Lethrinus olivaceus Valenciennes

Pl. 3A,B, Fig. 3C,D

Material examined. (15 specimens: 32–124 mm). AUSTRALIA Great Barrier Reef region, AMS I.34919-004 (1:36 mm), AMS I.34928-001 (1:38 mm), AMS I.34929-001 (1:39 mm), AMS I.34930-001 (1:32 mm), AMS I.34931-001 (1:40 mm), AMS I.34931-002 (1:63 mm), USNM 336688 (1:34 mm), USNM 336689 (1:53 mm), USNM 336690 (1:32 mm), not retained (5:44–124 mm); INDONESIA Eastern Archipelago, NMV 46333 (1:111 mm).

Diagnosis. Body moderately elongate, body depth 2.9– 3.2 in SL; 5.5 dorsal scale rows, 16–17 ventral scale rows; maxillary serrations absent at greater than 32 mm; cheek scales retained until 40 mm; dorsal spine 3 or 4 the longest.

Diagnostic colour notes. Dorsum pale olive-grey, shading to silvery off-white ventrally; dark markings intense, shoulder blotch horizontally-rectangular, ventral bands diagonal (Fig. 3D, Pl. 3B), width of dark mid-lateral stripe approximately 6.0 in body depth; single dark blotch below orbit at 40–63 mm, 2 blotches below orbit and 2 bands between mouth and orbit at 124 mm; spinous fins with dense melanophores, appearing dark grey when folded at rest.

Colour notes. At 32–63 mm: dorsum off-white tan to olivaceus tan, body silvery off-white ventrally, lateral-line mostly cryptic, occasionally faded yellow-tan stripe along ventral margin; dark markings prominent, particularly in field (as in Pl. 3B), rapidly switched on in 1–3 seconds when approached or otherwise disturbed, 5–7 indistinct dark bands along dorsum between head and caudal peduncle, 2–3 similar bands along caudal peduncle, 2–3 dark blotches below lateral-line, first blotch of greatest intensity forming a horizontally-rectangular shoulder blotch below dorsal spines 5–7 (Fig. 3D, visible though faded in Pl. 3A,B), network of diagonal dark bands between blotches and belly (Fig. 3D); intense dark mid-lateral stripe

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Plate 3. A—Lethrinus olivaceus, approx. 250 mm SL, underwater photograph by R.H. Kuiter, Bali (Indonesia). B—Lethrinus olivaceus, approx. 400 mm SL, underwater photograph by R.H. Kuiter, Papua New Guinea. C—Lethrinus ornatus, 36 mm SL, AMS I.34932-001, live, Green Island. D—Lethrinus variegatus, 39 mm SL, live, Green Island. E—Lethrinus xanthochilus, 26 mm SL, AMS I.34923-001, dead, Green Island.

common in field, banding switched off, narrower than that of other lethrinids, width 6.0 in body depth, switched on or off rapidly; lips, snout and nape mottled grey, preoperculum and ventral half of operculum silvery white with indistinct dark blotches along posterior margins, further dark blotch forming below orbit; fins mostly hyaline, anterior half of spinous fins with off-white and yellow patches interspersed by dark grey blotches, pale orange-pink distally at greater than 40 mm, appearing dark grey when folded at rest.

At 124 mm, as in smaller specimens, dark markings on head and body more intense, 5-6 dark blotches on

operculum, 2 dark blotches below orbit and 2 bands between mouth and orbit; fins with oblique maroon bands, interspaces off-white yellow, pale scarlet distally.

Colour in alcohol. Dorsum pale off-white tan, shading to off-white belly; distinctive markings on body and head slightly faded; dense melanophores retained on fins.

Ecology. Uncommon at Green Island, restricted to shoreline seagrass areas (0.2–1.5 m; *Cymodocea*, *Halodule*, *Thalassia*), occurring over shallow (2–4 m)

open sand/coral rubble at greater than 100 mm; not appearing site-attached, a single 35 mm individual was observed swimming in a loose multi-species school with similar-sized *Siganus fuscescens*, *Halichoeres* species (Labridae) and congeners (*L. atkinsoni*, *L. harak*, *L. obsoletus*), periodically picking food items off seagrass blades and adjacent substratum; no aggressive interactions noted, other field behaviours unknown.

Field identification. Rarely encountered in the field as early juveniles, a combination of the slender body and snout profiles, horizontal shoulder blotch, narrow mid-lateral stripe, ventral diagonal banding and absence of coloured primary stripes may distinguish this species. The intense fin pigmentation characteristic of dead specimens was not noted in field observations, although is faintly visible in the colour plate of a 150 mm juvenile given in Myers (1989). During display of the dark mid-lateral stripe pattern, *L. olivaceus* may be confused with numerous species, particularly *L. genivittatus*. Individuals may need to be followed for several minutes before other patterns are displayed.

Previous descriptions. Kuiter & Debelius (1994) included a colour plate of *L. olivaceus* (as *L. microdon*) showing the characteristic horizontal shoulder blotch and ventral banding. A 150 mm juvenile (as *L. semicinctus*) is shown in Myers (1989, Pl. 56E), displaying the intense shoulder blotch and narrow mid-lateral stripe characteristic of field observations. Lieske & Myers (1994, Pl. 53) also figured the *L. olivaceus* dark mid-lateral stripe pattern.

Remarks. Freshly collected *L. olivaceus* juveniles are unlikely to be confused with other *Lethrinus* species of a similar size. Specimens retained frozen or in alcohol for extended periods were noted to display near-identical banding to *L. genivittatus*, particularly if the orange primary stripes in the latter species had faded. Such material may be reliably separated using the number of dorsal scale rows, shape of the shoulder blotch, and intensity of pelvic-fin pigmentation.

Lethrinus ornatus Valenciennes

Pl. 3C

Material examined. (11 specimens: 20–91 mm). AUSTRALIA Great Barrier Reef region, AMS I.34917-001 (1:32 mm), AMS 1.34932-001 (1:36 mm), not retained (6:20–69); INDONESIA Maumere Bay (Flores), not retained (2:20 mm); SOLOMON ISLANDS New Georgia Island, AMS I.22128-154 (1:91 mm).

Diagnosis. Body relatively deep, its depth 2.5–2.8 in SL; 5.5 dorsal scale rows, 15 ventral scale rows; maxillary serrations 2–4 at 20 mm, absent at greater than 28 mm; dorsal spine 5 the longest at 20–60 mm (rarely 4 at greater than 50 mm).

Diagnostic colour notes. Primary stripes 4, bright orange, of similar width and intensity, interspaces silvery off-white;

fins hyaline, pink to pale scarlet distally; pale scarlet band along rear margin of operculum at greater than 28 mm; dark markings seldom displayed.

Colour notes. A striking species with few differences in colouration between adults and juveniles, difficult to confuse with other Lethrinus species. At 20-80 mm (Pl. 3A): dorsum and nape pale grey-tan, flank silvery offwhite, belly off-white; 4 prominent bright orange primary stripes, of similar width and intensity, fine grey borders, interspaces grey-tan or silvery off-white, dorsal stripe extending to below medial dorsal rays, remaining stripes terminating at base of caudal peduncle; black banding and cuboidal shoulder blotch seldom displayed in field although common at capture (Pl. 3C) and after death, rapidly switched on or off, 6-7 bands along dorsum, most connecting with further banding between lateral-line and belly, 2-3 similar bands along caudal peduncle; dark midlateral stripe occasionally displayed in field, dark grey, width approximately 4.0 in body depth, obscuring dorsal and orbital stripes, pectoral and ventral stripes usually remaining visible though dulled; head similar to body, snout yellow-brown, cheek silvery off-white, may have diffuse tan blotch, eye often bisected by near-vertical black band in field, pale scarlet band developing along rear margin of operculum from 28 mm (faded in Pl. 3C); fins mostly hyaline, caudal and pectoral fins pale pinkish yellow, anterior half of spinous fins off-white with dark grey patches basally, deep pink to scarlet distally in field, diffuse pink at capture (as in Pl. 3C) and when freshly-killed.

At greater than 80 mm, body, head and fins as in smaller specimens, dark mid-lateral stripe and banding absent.

Colour in alcohol. Dorsum pale grey-tan with 5–6 dark bands; ventral half of body and primary stripes faded to off-white, dark banding below lateral-line dissected by primary stripes into 3–6 series of square blotches; banding retained along caudal peduncle; fins hyaline.

Ecology. Uncommon at Green Island, settles at 19–21 mm into shallow reef seagrass habitats, remaining there until 70–80 mm; solitary, not appearing site attached, seldom in close association with other fishes, occasionally joining small loose schools with juvenile *Stethojulis strigiventor, Siganus fuscescens, Parupeneus indicus* and congeners of a similar size, particularly in the presence of piscivorous carangids or lutjanids; at 40–70 mm periodically resting briefly at the base of the seagrass canopy in tall-dense *Cymodocea* and *Halodule*, fleeing over the canopy when disturbed.

Field identification. Juvenile *L. ornatus* are best distinguished in the field by their deep body profile, intense orange primary stripes and rarity of conspicuous dark banding or mid-lateral stripe patterns (cf. frequent displays in other species with bright primary stripes). Recently-settled specimens display near-identical colouration to later stages, although less conspicuously.

Pl. 3D, Fig. 10

Material examined. (29 specimens: 14–114 mm). AUSTRALIA Great Barrier Reef region, AMS I.32476-004 (2:16 mm), AMS I.34911-011 (1:30 mm), AMS I.34911-012 (1:25 mm), AMS I.34933-001 (2:14 mm), AMS I.34934-001 (2:28–47 mm), AMS I.34935-001 (3:34–35 mm), AMS I.34936-001 (1:32 mm), AMS I.36201-001 (1:15 mm), AMS I.37803-001 (1:16 mm), USNM 336691 (3:26–35 mm), not retained (9:24–69 mm); FUI Suva, AMS I.22232-016 (1:114 mm); INDONESIA Eastern Archipelago, NMV 46329 (1:73 mm); PAPUA NEW GUINEA Trobriand Islands, AMS I.17102-015 (1:38 mm).

Diagnosis. Body slender, body depth 3.1–3.5 in SL; 4.5 dorsal scale rows, 13–14 ventral scale rows; maxillary serrations absent at greater than 23 mm; cheek scales retained until 47–50 mm; dorsal spine 4 the longest.

Diagnostic colour notes. Dorsum finely-mottled grey-tan, seldom with dark banding, dorsal margin of lateral-line off-white; dark mid-lateral stripe semi-permanent, yellowish brown, width approximately 4.0 in body depth, shoulder blotch inconspicuous or absent; ventral half of body abruptly silvery off-white; dark suborbital blotch at greater than 30 mm; fins hyaline.

Pre-settlement colour notes. At 14–16.5 mm (Fig. 10): head and body translucent off-white, melanophores overlying yellow-orange xanthophore pigmentation; distinct dark stripe extending from lips to orbit margin, continuing as dark mid-lateral stripe between posterior margin of orbit and caudal peduncle, may appear as series of irregular blotches; lateral-line cryptic, 3–5 irregular blotches along dorsum, interspaces silver, occasionally 3–6 less-distinct blotches extending below dark mid-lateral stripe from pectoral fin to mid-way along caudal peduncle, further 2–3 irregular blotches adjacent to anal fin; fins hyaline.

Colour notes. A distinctive species with minimal ontogenetic variation following settlement, few differences noted between field and captive or freshly-killed colouration. At 25-50 mm: dorsum and nape finely-mottled grey-tan, 4-6 narrow dark bands above lateral-line and 2-3 similar bands along caudal peduncle, often switched off in field, lateral-line bordered dorsally by silvery off-white interspace in field; yellow-brown mid-lateral stripe extending from lips through orbit to base of upper caudal rays, semi-permanent (cf. intermittent stripe in other species), width 4.0 in body depth, may appear as series of dark blotches in captivity (Pl. 3D), blotch below dorsal spines 3-4 forming diffuse cuboidal shoulder blotch; ventral half of body and head abruptly silvery white, without dark markings in field, often 2-3 diffuse brown stripes or bands between pectoral and anal fins in captivity

(Pl. 3D) or after death, 3–4 dark blotches on cheek and operculum from 25 mm; fins mostly hyaline, anterior half of spinous fins with diffuse dark patches over off-white to pale yellow, caudal fin pale yellow with 2–3 indistinct dark bands at greater than 40 mm.

Colour in alcohol. At 25–50 mm, dorsum and nape uniform pale tan; lips and snout with dense melanophores, dark dorsal bands retained though dulled, often connecting with broad blotches on flank, dark mid-lateral stripe identical hue to dorsum, shoulder blotch usually visible; body abruptly off-white ventrally, faintly mottled; fins hyaline, sparse melanophores retained along spines.

Ecology. Moderately common in shallow seagrass beds on lagoonal or fringing coral reefs (*Cymodocea, Halodule, Thalassia*; 0.2–4 m), absent from non-seagrass areas at Green Island at less than 100 mm; solitary when recently-settled (20–40 mm), larger juveniles occasionally join small multi-species schools with congeners, particularly *L. atkinsoni, L. genivittatus, L. harak*, and *L. obsoletus*; observed resting on the substrate among seagrass shoots at night, not fleeing when approached.

Field identification. Distinguished from other *Lethrinus* species by its elongate body and snout profile, and prominent yellow-brown mid-lateral stripe. When observed from behind, may be confused with species such as *L. obsoletus* or *L. genivittatus* on the basis of their similar dark mid-lateral stripes. When freshly collected, particularly at night, may appear a uniform pale olivaceus cream; the dark mid-lateral stripe and shoulder blotch becoming visible after 10–30 seconds.

Previous descriptions. Colour plates of juveniles were included in Kuiter & Debelius (1994) and Kuiter (1996) (size not given in each case), and Lee (1993) (specimen 147 mm, misidentified as *L. semicinctus*).

Lethrinus xanthochilus Klunzinger

Pl. 3E, Fig. 3B

Material examined. (10 specimens: 19–92 mm). AUSTRALIA Great Barrier Reef region, AMS I.34912-007 (1:19 mm), AMS I.34912-008 (1:22 mm), AMS I.34922-001 (1:73 mm), AMS I.34923-001 (1:26 mm), USNM 336684 (1:25 mm), lost (1:48 mm); PAPUA NEW GUINEA Trobriand Islands, AMS I.17102-081 (1:44 mm), AMS I.17099-005 (3:66–92 mm).

Diagnosis. Body moderately deep, depth 2.6–3.2 in SL; 4.5 dorsal scale rows, 15–16 ventral scale rows; maxillary serrations 7 at 18–19 mm, 1–4 (usually 2–3) at 20–28 mm, absent at greater than 28 mm; cheek scales retained until 44 mm; dorsal spine 5 the longest at 18–19 mm, 3 or 4 the longest at greater than 20 mm.



Fig. 10. *Lethrinus variegatus* 13.9 mm SL, late pre-settlement stage. Composite drawing based on AMS I.34933-001 (2 specimens), Green Island. Details of scalation, myomeres and internal pigmentation are not shown.

Diagnostic colour notes. At 18–75 mm, dorsum cream to pale bronze, body abruptly silvery off-white ventrally, silvery off-white interspace along mid-body (22–45 mm) with 2–3 short brown stripes below; black suborbital blotch at 20–45 mm; shoulder blotch inconspicuous; pectoral base scarlet at greater than 50 mm, spinous fins with dense melanophores at greater than 19 mm, appearing black when folded at rest.

Colour notes. A species with distinctive early-juvenile colour patterns which differ markedly from the adult colouration, capable of rapid colour pattern changes. At 18-20 mm, recently-settled: snout, nape and dorsum cream to pale tan, ventral half of head and body abruptly silvery off-white, lateral-line cryptic, prominent silvery off-white interspace along mid-body between cheek and base of caudal rays (Pl. 3E), diffuse grey to brown banding and blotches along body, 4-6 irregular bands forming along dorsum, 2-3 similar bands (or single broad band) on caudal peduncle, usually bisected by mid-lateral interspace; series of 3-4 exceedingly faint grey blotches between lateralline and mid-lateral interspace, 2 short primary stripes in approximately pectoral and ventral configurations (Pl. 3E, Fig. 3B,4), may fuse below dorsal spines 8-10 and extend onto caudal peduncle as single stripe; diffuse dark markings forming on head as small blotch below orbit, blotches along rear margin of preoperculum and operculum, and band passing through lips; fins mostly hyaline, anterior half of spinous fins with black patches over off-white to yellow, appearing black when folded at rest.

At 20–73 mm (Pl. 3E): background of body gradually darkening with growth to pale bronze dorsum and off-white belly; dark markings on head and body more intense, particularly in field, dark brown to black (Pl. 3E), shoulder blotch more distinct although only at capture or after death,

ventral network of indistinct bands joining blotches along lateral-line with belly at greater than 50 mm, 2–3 diffuse bands across snout and nape (Pl. 3E); silvery off-white interspace becoming clearer (20–45 mm) then indistinct (50–73 mm); dark mid-lateral stripe occasionally displayed in field, width approximately 4.0 in body depth, moderately-intense; pigmentation on fins more intense, pectoral fin pale pink at greater than 50 mm, scarlet patch at pectoral base from 50 mm.

Colour in alcohol. At 18–20 mm, body off-white, dark markings on head, body and fins distinct although faded; 21–92 mm (Pl. 3E), dorsum off-white to pale tan, silvery off-white ventrally, dark patterns along body, head and fins distinctly retained, silvery white mid-lateral interspace usually prominent (21–50 mm), red pectoral base (50–92 mm) indistinguishable.

Ecology. Uncommon at Green Island, settlement and nursery habitat preferences uncertain, at 20–73 mm only found over shoreline seagrass cover (0.2–2.0 m; *Cymodocea, Halodule, Thalassia*), specimens 44–92 mm from the Trobriand Islands (Papua New Guinea) collected over sand near patch reefs, 0–1 m; a solitary 35 mm individual at Green Island was noted sheltering amongst epiphytic algae at the base of the seagrass canopy, two 40 mm individuals were noted foraging with congeners (*L. obsoletus* and *L. variegatus*), *Halichoeres miniatus, Lutjanus fulviflamma* and *Siganus fuscescens* of a similar size, fleeing over the seagrass canopy when closely approached; not appearing site attached, other field behaviours unknown.

Field identification. A distinctive species, easily recognised in the field by its prominent silvery white midlateral interspace (20-50 mm) and black suborbital markings. The red patch at the pectoral-fin base may be a reliable character for the field identification of individuals greater than 55 mm, along with the presence of intense black fin pigmentation (but see "Identification note" below).

Identification note. The intense black pigmentation on spinous fins of preserved specimens may lead to confusion with *L. miniatus*. No confirmed juvenile records exist for the latter species on the GBR, although two specimens are known from Sydney Harbour (Australian Museum, I.19103-010 and I.24474-002). Morphological differences distinguishing *L. miniatus* and *L. xanthochilus* at less than 110 mm include a concave interorbital area in *L. xanthochilus* (at greater than 40 mm) (flat or convex in *L. miniatus*), a slight to moderately-humped interorbital margin in *L. xanthochilus* (straight in *L. miniatus*) and deeper body profile of *L. miniatus*.

Remarks. Carpenter & Allen (1989) queried the occurrence of *L. xanthochilus* in Australian waters, although Williams & Russ (1994) noted several records from the central and northern regions of the GBR. The individuals described here represent the first confirmed juveniles to be collected from Australian waters.

Discussion

The juvenile descriptions presented above indicate the occurrence of complex juvenile colour patterns in a suite of 11 *Lethrinus* species from the Great Barrier Reef. In considering the consequences of these patterns to the ecology of *Lethrinus* juveniles, two points are salient. Firstly, each of the three shared colour patterns is associated with a particular suite of behavioural interactions. Secondly, a characteristic feature of *Lethrinus* early juvenile colouration is the degree of interspecific conservatism within each shared pattern.

The first shared pattern, the primary stripes, is notable in that two groups based on this pattern were evident within the species examined; namely species displaying conspicuous and well defined stripes of an orange or pink colour (*L. genivittatus, L. lentjan, L. obsoletus* and *L. ornatus*) and the remainder with inconspicuous stripes of varying hues (as in *L. erythracanthus* and *L. xanthochilus*). Display of primary stripes in the former group is concentrated during incidents of disturbance or when fleeing from aggressors, suggesting them to represent a "fright" or "stress" response. In turn, their ultimate function may be to visually alert other individuals to the presence of danger (Rowland, 1979). A similar explanation may also pertain to species with inconspicuous stripes, although this remains unclear.

The second shared pattern, dominated by the dark midlateral stripe, is (a) displayed in undisturbed individuals when schooling or solitary, (b) rapidly disappears in the presence of aggressors, and (c) shows a striking resemblance to similar patterns in juvenile siganids and some mullids and labrids of a similar size. It has been inferred that conspicuous striation in other reef fishes acts to visually confuse piscivores (Barlow, 1972; Ehrlich & Ehrlich, 1973; Bellwood & Choat, 1989). A similar predation-avoidance utility may also apply to this pattern in juvenile lethrinids, particularly given the exposure to predators when swimming or hovering over the seagrass canopy. Alternatively, the correspondence of this pattern with siganid juveniles may indicate it to act as an aposematic model; thereby, conferring a protective advantage through an avoidance by piscivores of siganids and their toxic spines.

The third shared pattern, dark banding, is utilised during antagonistic interactions with conspecifics and congenerics; usually displacing the dark mid-lateral stripe pattern. Such displays are effected through the rapid and contrasting appearance of intense dark banding over a pale background. Conspicuous patterns of this nature have been interpreted as "startle displays", functioning as visual warning or alarm signals (Hamilton & Peterman, 1971; Baylis, 1979). Alternative forms of this pattern in *Lethrinus* juveniles, such as displays of low contrast and intensity, and the appearance of broad bars after dark, probably renders individuals cryptic against the seagrass canopy background (e.g., Barlow, 1972). Both the dark mid-lateral stripe and banding patterns are typified by *L. atkinsoni*, *L. genivittatus*, *L. harak* and *L. obsoletus*.

The degree of interspecific similarity seen in Lethrinus juvenile colour patterns is not unprecedented among reef fish assemblages. In both Caribbean (Ehrlich & Ehrlich, 1973) and western-Pacific (Bellwood & Choat, 1989) assemblages, such coordination appears associated with multi-species schooling. On the GBR, juvenile lethrinids, siganids, mullids and labrids may all display similar darkly-striped patterns while schooling together over seagrass. The formation of multi-species schools by reef fishes is generally believed to function in predation avoidance (e.g., Ehrlich & Ehrlich, 1973; Hobson, 1978; Wolf, 1985; Bellwood & Choat, 1989). Indeed, schooling over open seagrass near reefs invokes considerable exposure to piscivorous carangids, lutjanids, serranids and synodontids (Baelde, 1990; Blaber et al., 1992; Sweatman & Robertson, 1994; author's pers. obs.). In this environment, lethrinids would undoubtedly benefit from shared patterns through increased signalling efficiency among species, as well as the "disruptive" value of dark stripes.

Similarities in Lethrinus juvenile field colouration, and rapid and frequent interchanges between colour patterns, also allude to the problematical nature of identifying small individuals in the field. Although specimens may be conspicuous and easily detected, subtle differences in colour pattern between many species, and their tendency to change patterns when approached, makes lethrinid juveniles difficult for inexperienced observers to separate. Nevertheless, colour patterns represent the most accurate means of identification. Most species can be readily distinguished, particularly if individuals are followed for several minutes to allow their full range of colour patterns to be determined. The L. lentian/nebulosus species pair is exceptional, with separation often tentative or impossible below a minimum size. In other cases, meristic counts and freshly-killed colour patterns from collected material may be used for subsequent confirmation.

Simultaneous investigations of juvenile colour patterns and behaviour may provide an insightful means of increasing our knowledge of early post-settlement regulatory mechanisms and evolutionary history in reef fish populations. Although the capability of comparative studies to identify adaptive traits has been questioned (e.g., Leroi *et al.*, 1994), observations of characters, such as colour patterns, shared between unrelated species may nevertheless yield useful information. Similarities in behaviour and colour pattern between lethrinid and siganid early juveniles are of particular interest in this regard, and worthy of further attention. Juvenile colour patterns and their ontogeny can also contribute valuable information for exploring phylogenetic relationships among reef fishes (e.g., Bellwood, 1994).

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