Larval Distributions of Some Commercially Valuable Fish Species Over the Sydney Continental Shelf

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The cross-shelf and vertical distributions of larvae of 12 species of commercially valuable marine fish are described from continental shelf waters off Sydney, south-eastern Australia. Depth stratified sampling was conducted along a shore-normal transect on 3 and 4 consecutive nights in January and April, respectively, 1994. Larvae of the commercially valuable species *Hyperolius vitatus*, *Sardinops sagax*, *Engraulis australis*, *Argyrosomus japonicus*, *Pseudocaranx dentex*, *Trachurus novaezelandiae*, *Liza argentea*, *Sillago flindersi*, *Acanthopagrus australis*, *Pegasor harrisi*, *Rhabdosargus sarba* and *Gerres subfasciatus* together represented 11947 of the 50781 total fish larvae in samples. Species distributions extended to the outer shelf or slope, although the majority of larvae occurred in subsurface waters of the nearshore mixed layer. The majority of larvae were at a preflexion stage of development. Where present, later stage larvae tended to exhibit a different distribution to that of earlier stage larvae, although trends were variable among species. Results are discussed in relation to existing information on the larval distributions and spawning times of each species.

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INTRODUCTION

Studies of early life history can provide valuable information to managers of fisheries resources. The spatio-temporal distribution of planktonic larvae, at various developmental stages, can help to infer the timing and location of spawning, and may assist in the interpretation of juvenile recruitment variability. Such information is most useful when coupled with oceanographic data (e.g. Caputi et al. 1996).

Australian marine ichthyoplankton communities are typically diverse but numerically dominated by species of low fisheries value (Leis 1991; Gray 1993; Smith and Suthers 1999). The low abundances of species of higher value often preclude their individual attention in final analyses and published reports, contributing to a dearth of information on the early life history of many of Australia’s commercially valuable fish species (hereafter ‘commercial species’). The limited number of continental shelf ichthyoplankton studies, compared with those conducted within estuaries, is also a contributing factor.

Several ichthyoplankton studies have been conducted in south-eastern Australian shelf waters (Miskiewicz 1987; Gray et al. 1992; Gray 1993, 1996, 1998; Dempster et al. 1997; Smith and Suthers 1999; Smith et al. 1999; Smith 2000). Although generally not targeted, larvae of numerous commercial species have been encountered in these studies. However, only some of the larval distributions and developmental stages of commercial species captured in shelf waters during previous studies have been described (Gray 1993, 1998; Smith 2000).

Some commercial species occurring off south-eastern Australia are also distributed in other shelf regions, suggesting inferences about early life history may be drawn in the absence of local information. However, widespread intra-specific differences in spawning patterns and modes of larval dispersal among geographic regions and oceanographic regimes demonstrate the importance of local observations (e.g. Juanes et al. 1996). The aim of this paper is to provide local observations on the cross-shelf distributions and larval developmental stages of 12 species of commercial fish found in shelf waters off Sydney during two surveys in 1994. The
COMMERCIAL Y IMPORTANT FISH LARVAE OF THE SYDNEY SHELF

outer shelf occurrence of larvae of these species has not been previously described off Sydney. Samples described in this paper constitute a valuable contribution to the limited body of knowledge concerning the early life history of commercial fish in Australian marine waters.

MATERIALS AND METHODS

Location and time of study

Data were collected in continental shelf waters adjacent to Sydney, on the south-eastern coast of Australia (Fig. 1). Currents over the shelf are predominantly southward, due to the influence of the East Australian Current (EAC) and associated eddies (Nilsson and Cresswell 1981). Compared to along-shore currents, cross-shelf currents are small, usually <10 cm/s (Middleton 1987). Density variability in the Sydney coastal ocean is primarily the result of changes in temperature (Griffin and Middleton 1992). During the summer months, shelf waters generally exhibit strong temperature stratification (White and Church 1986).

Data were collected during two 10-d cruises, in January and April, 1994, aboard the research vessel, R. V. Franklin. On both cruises, data were collected from five stations along a cross-shelf transect. The transect began 2.7 km offshore and ended 40 km from the coast. Plankton sampling stations A, B and C were within shelf waters (bottom depths less than 150 m). Station D was at the shelf break, (bottom depth 250m), and station E occurred over the continental slope (bottom depth 600 m) (Fig. 1, Table 1). Plankton was collected on 22, 23 and 25 January and on 5, 6, 7 and 8 April. Some locations were not sampled on 7 April due to bad weather. Plankton was collected at night between 2030 and 0500 hours in January, and 1900 and 0600 hours in April. Sunrise and sunset were at approximately 0600 and 2000 hours in January, and 0600 and 1745 hours in April, respectively.

Collection and processing of samples

Surface plankton was collected by a 75 x 75 cm square mouth net (330 μm mesh), fitted with a General Oceanics flow meter. Two surface hauls, each of 6 minutes duration, were conducted at each station per night. Average volume of water filtered by the surface net was 291 m³.

Subsurface plankton was collected by a multiple, opening and closing net with a square mouth of 1 m² and mesh size of 330 μm. The net was fitted with temperature, conductivity and depth sensors and two General Oceanics flow meters - one inside and one outside the net mouth. Real time data were communicated to an operator onboard ship who electronically triggered each net release. At each station, three subsurface depth strata were sampled. Strata were designed to sample above (shallow), within (middle) and below (deep) the thermocline where possible at each station. Actual sampling depths varied according to hydrography and water depth at each station (Table 1). Subsurface haul durations were 10 minutes and each depth stratum was obliquely sampled once per station per night. Average volume of water filtered by the subsurface net was 429 m³.

Plankton samples were immediately placed into seawater and 5-10% formalin. Fish were removed from samples between 1 and 24 months after

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**TABLE 1.**

<table>
<thead>
<tr>
<th>Distance offshore (km)</th>
<th>Bottom depth (m)</th>
<th>Depth of sampling intervals (m)</th>
<th>Surface</th>
<th>Shallow</th>
<th>Middle</th>
<th>Deep</th>
</tr>
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<tbody>
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<td>15-30</td>
<td>30-40</td>
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<tr>
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<td>0-1</td>
<td>15-40</td>
<td>40-60</td>
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<td>C 16</td>
<td>130</td>
<td>0-1</td>
<td>15-40</td>
<td>40-80</td>
<td>80-120</td>
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<tr>
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<td>0-1</td>
<td>15-40</td>
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<td>E 40</td>
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collection, counted, identified and then stored in 95% ethanol. Larvae were assigned a developmental stage of preflexion, flexion, or postflexion. Flexion is the stage during which the notochord tip turns upward (Neira et al. 1998). Fin development is largely completed at the end of flexion.

Larvae of twelve commercially valuable fish species were identified by descriptions in Leis and Trnski (1989) and Neira et al. (1998). Some other commercially valuable species, which were present in samples, were excluded due to very low abundance or difficulty in identification to species level. A summary of the Australian distribution and seasonality of each larval species can be found in Neira et al. (1998).

Raw abundances per sample were standardised to density of larvae 100 m$^{-3}$ of water filtered. Mean density of each stage of each species was calculated for each sampling location (i.e. depth within station) during each sampling period.

RESULTS AND DISCUSSION

During both sampling periods, a mixed layer of 23 °C and 20-50 m depth, overlay the shelf. The mixed layer extended over the entire shelf region during January but, during April, was displaced from the nearshore region by cooler, upwelled water (Fig. 2). There was a tendency for the distributions of some species to extend further from the coast in April compared with distributions in January. This tendency was most pronounced in the eulcyclids, Pseudocaranx dentex (silver trevally) and Trachurus novaezelandiae (yellowtail scad), and coincided with the offshore displacement of the nearshore mixed layer (Fig. 2). For a full description of this coastal upwelling event see Smith and Suthears (1999).

A high density (298 larvae 100 m$^{-3}$) of Hyperlopus vittatus (sandy sprat) occurred in a single deep sample taken at station A on 22 January (Fig. 3a, Table 2). Densities in other January samples were relatively low. Few individuals were taken in April and these mostly occurred at shallow depths over the inner shelf. Flexion and postflexion H. vittatus were rare during both sampling periods and no trends were apparent in the vertical distribution of these stages.

The occurrence of Hyperlopus vittatus off Sydney in January is consistent with spawning by this species during late summer and early autumn off eastern Australia (Ramm 1986; Miskiewicz 1987). The occurrence of preflexion H. vittatus off Sydney (this study) and to the north of Sydney (Miskiewicz 1987), suggest a large potential spawning area. Off Western Australia, spawning also occurs over a long length of coastline (Gaughan et al. 1996). The extremely patchy, coastal distribution of H. vittatus larvae observed off Sydney may be typical for this species (Gaughan et al. 1996).

Engraulis australis (anchovy) were less abundant in April than in January. Spawning peaks between spring and autumn throughout the species distribution, and a decline in larval density off Sydney between January and April is consistent with decreasing

Figure 2. Average temperature (°C) profile across Sydney continental shelf during sampling on a) 22-25 January, and b) 5-8 April, 1994. Sampling stations A-E shown along top of profile.
Spawning activity between these times. Spawning occurs in estuaries and shelf waters of temperate and sub-tropical Australia (Miskiewicz and Neira 1998). Low densities of larvae over the outer shelf off Sydney (this study, Fig 3b) and elsewhere (Hoedt and Dimmlieh 1995) suggests that spawning is restricted to the inner shelf.

Densities of preflexion and flexion stage Engraulis australis larvae were highest in shallow and middle depths, and low at the surface (Fig. 3b). The highest density of preflexion E. australis was 78 larvae 100 m$,^3$, occurring at shallow depth at station A in January (Table 2). Postflexion larvae occurred at similar densities in surface and subsurface waters in January, but mainly at the surface in April. Previously, Gray (1993, 1996) found E. australis larvae most abundant in subsurface waters in November, but equally abundant in surface and subsurface waters in April/May and August/September. Given the tendency of older larvae to dominate surface samples in the present study, previously noted variability may reflect ontogenetic changes in vertical distribution.

Sparids were rare in shelf waters during January and April, 1994 (Fig. 3c). Acanthopagrus australis (yellowfin bream) spawns throughout the year along the eastern Australian coast, although there are regional peaks in activity, including a local peak in autumn. This is consistent with a slight increase in larval abundance between January and April. A. australis observed during this study were caught within 7 km of the coast. Spawning occurs at the mouths of estuaries and most previous observations of A. australis larvae within eastern Australian shelf waters have been within 1 km of the coast (Gray 1993; Miskiewicz and Neira 1998). Additional larvae may have been present in coastal waters in 1994 but distributed inshore of station A.

Pre- flexion and flexion Acanthopagrus australis larvae occurred in subsurface samples but were absent at the surface. Densities of A. australis were < 1 larvae 100 m$,^3$, in all samples (Table 2). A single postflexion larva, which appeared competent to settle, was taken at the surface at station A in January. This is consistent with observations of settlement stage larvae.
laurae at the surface in estuarine waters (T. Trnski, pers. comm.).

In January, a single preflexion stage *Rhabdosargus sarba* (tarwhine) was taken, at shallow depth over the inner shelf (Fig. 3d). In April, *R. sarba* was more abundant in samples. Spawning by *R. sarba* occurs during most months of the year off eastern Australia, but local larval abundance and recruitment rates peak in autumn/winter (Miskiewicz and Neira 1998; Smith and Suthers 2000). The increase in larval abundance between January and April, 1994, was consistent with these patterns. A single larva in January, and the presence of early and late stage larvae in April, 1994, suggested that some spawning activity occurred prior to April. Densities of *R. sarba* were < 1 larva 100 m$^3$ in all samples (Table 2).

In April, preflexion, flexion and postflexion *Rhabdosargus sarba* occurred mainly over the inner and mid shelf, which is consistent with an inner shelf spawning location for this species (Wallace 1975; Miskiewicz 1986). Some preflexion and postflexion larvae also occurred over the outer shelf. The occurrence of postflexion larvae up to 40 km offshore of Sydney contrasts with the estuarine distribution of juveniles. Postflexion larvae, with some swimming ability, are less likely to have been passively advected away from the inner shelf than the less developed preflexion larvae. The outer shelf may be within the typical distributional range of older larvae.

During night-time sampling in 1994, all developmental stages of *Rhabdosargus sarba* occurred in subsurface samples and were absent in surface samples. *R. sarba* larvae are also in subsurface waters off Sydney during the day (Gray 1998), suggesting that larvae do not undertake daily vertical migrations.

*Pagrus auratus* (snapper) occurred at low densities in January and April (Fig. 4a). Spawning by *P. auratus* occurs throughout the year along the southeastern coast, with a local peak in spawning activity in autumn (Miskiewicz and Neira 1998). Relatively low densities of larvae off Sydney, particularly in January, may reflect limited spawning at this time. Densities of *P. auratus* were < 1 larva 100 m$^3$ in all samples (Table 2).

Preflexion and flexion *Pagrus auratus* mainly occurred in subsurface waters of the inner and midshelf, although preflexion larvae also occurred at the surface and at shallow depths over the outer shelf in April. Spawning occurs in waters of < 50 m depth (Kailola et al. 1993), and so the presence of preflexion
Figure 4. Mean density of preflexion and flexion stage larvae of a) Pagrus auratus, b) Gerres subfasciatus, c) Sardinops sagax and d) Argyrosmus japonicus at sampling locations in January and April, 1994. No postflexion larvae of these species in samples. Circle size is proportional to density of each stage within a month. Circle size is not comparable among stages or months (n = total number of larvae during sampling period).

Densities of both preflexion and flexion Gerres subfasciatus were greatest at shallow depths. Maximum observed density of preflexion larvae was 25 larvae 100 m⁻³, at shallow depth at station A in January (Table 2). Larvae occur at the surface during the day (Gray et al. 1992) and at depth during the night (this study), suggesting diel vertical migration by this species.

Sardinops sagax (pilchard) probably spawns off NSW during most months of the year although the timing of peak activity may vary among years (Miskiewicz 1987). Preflexion larvae were relatively abundant in January, 1994, suggesting significant spawning activity in the Sydney region at this time. S. sagax was largely restricted to the inner shelf in January (Fig. 4c). Larvae were more evenly distributed across the shelf in April, although densities were very low. An inshore larval distribution is consistent with spawning in estuaries and inner shelf waters throughout temperate Australia (Blackburn 1949; Jenkins 1986; Fletcher and Tregonning 1992; Hoedt and Dimmlich 1995). A small number of early stage larvae were found 30-40 km offshore, which is more likely to reflect larval advection than an offshore spawning location (Smith and Suthers 1999).

In January and April, the densities of preflexion and flexion Sardinops sagax were similar at shallow, middle and deep depths, but low at the surface (Fig. 4c). Maximum density of preflexion S. sagax was 40 larvae 100 m⁻³, which occurred within shallow and deep samples at station A in January (Table 2). Flexion stage larvae were absent from samples in April and post-flexion stage larvae were absent from all samples.

The vertical distribution of Sardinops sagax is spatially and temporally variable. Off Sydney, S. sagax has been observed below the surface during the day (Gray 1996) and night (this study). However, in south-western Australia, S. sagax has been observed at the surface during the day but dispersed throughout surface and subsurface waters at night (Fletcher 1999). Hydrology may have influenced these vertical distributions. The water column was stratified during sampling off Sydney, and most larvae occurred just below the thermocline. There was no thermocline during sampling off western Australia.
Similar numbers of preflexion *Argyrosomus japonicus* (mulloway) were caught in January and April, suggesting similar levels of spawning activity at these times (Fig. 4d). The occurrence of larvae in south-eastern Australian coastal waters during January is one month earlier than previous observations, between February and May (Steffe and Ncire 1998). However, juveniles are known to enter local estuaries as early as February (Gray and McDonall 1993), and so the presence of larvae in coastal waters during January is possible. In January and April, densities were highest over the inner and mid-shelf. Larvae of this species also occur in nearshore areas and estuaries of South Africa (Beckley 1990). An inshore larval distribution is consistent with spawning by this species along ocean beaches in temperate and subtropical Australia (Kailola et al. 1993).

Preflexion *Argyrosomus japonicus* larvae occurred at all sampling depths, although surface densities were low. Maximum observed density of *A. japonicus* was 5 larvae 100 m$^{-3}$, at shallow depth at station A in January (Table 2). In April, larvae occurred mainly in middle and deep samples. This distribution may reflect an increasingly demersal habit with increasing size (A. Miskiewicz pers. comm.). This may also explain the rarity of later stage larvae in samples, if later stages typically occurred below the deepest sampling strata. Flexion and postflexion stages of *A. japonicus* were absent from samples in both months.

*Liza argentea* (flat-tail mullet) was more abundant in April than in January, 1994, suggesting an increase in spawning activity between these months (Fig. 5a). *L. argentea* spawn between December and June (Kailola et al. 1993). *L. argentea* larvae occurred over the inner and mid-shelf in January, and also occurred over the outer shelf in April. Maximum observed density of preflexion *L. argentea* was 7 larvae 100 m$^{-3}$, at shallow depth at station A (Table 2). The abundance of preflexion larvae over the inner shelf suggested a nearshore spawning location. Larvae tended to occur further from shore with increasing stage.

Flexion and postflexion *Liza argentea* were most abundant at the surface. Later stage *L. argentea* also occur at the surface during the day (Gray 1993), suggesting that older larvae do not undertake daily vertical migrations.

*Sillago flindersi* (eastern school whiting) was relatively abundant in January and April, 1994, suggesting that the level of spawning activity was similar at these times. The timing of spawning by *S. flindersi* peaks in spring/summer off south-eastern Australia (Kailola et al. 1993). Relatively high densities of later stage larvae in January, 1994, suggest that spawning activity had commenced at least several weeks prior to sampling. Larval of all developmental stages occurred mainly over the inner and mid-shelf regions each month (Fig. 5b). The distribution of preflexion larvae suggested a nearshore spawning location. Maximum observed density of preflexion *S. flindersi* was 82 larvae 100 m$^{-3}$, at shallow depth at station A in January (Table 2).

Each larval stage of *Sillago flindersi* was present at the surface and at all subsurface sampling depths. However, the vertical distribution of larval changed between months. Preflexion larvae were most abundant in shallow samples in January but most abundant at the surface in April. Postflexion larvae occurred in shallow samples and at the surface in January, but in mid and deep samples in April. Preflexion and flexion *S. flindersi* larvae have previously been observed mainly in subsurface waters during the day (Gray 1996). The shift by postflexion larvae from warm, surface water in January to cool, deep water in April suggests that vertical distribution is not strongly influenced by hydrography. Postflexion *S. flindersi* may be patchily distributed throughout the water column.

The carangids, *Pseudocaranx dentex* (silver trevally) and *Trachurus novaezelandiae* (yellowtail scad) were considerably more abundant in January than in April. Larvae of these species have been collected off eastern Australian at most times of the year, although spawning probably peaks in summer (Kailola et al. 1993; Tmski 1998) which is consistent with very high densities of larvae in January. The cross-shelf distributions of preflexion and flexion carangid larvae were similar between species (Fig. 5c). Larvae occurred over the inner and mid-shelf in January, and extended to the outer shelf in April. High densities of preflexion larvae over the inner shelf in January suggested spawning by both species over the inner shelf. The occurrence of larvae over the outer shelf in April resulted from the offshore displacement of larvae by a coastal upwelling event (Smith and Suthers 1999).

Preflexion and flexion carangids occurred in subsurface samples in January, but also occurred at the surface in April. Maximum observed density of preflexion *Pseudocaranx dentex* was 252 larvae 100 m$^{-3}$, at shallow depth at station A in January (Table 2). Maximum observed density of preflexion *Trachurus novaezelandiae* was 1002 larvae 100 m$^{-3}$, at shallow depth at station A in January (Table 2).

Larvae of both carangids displayed an ontogenetic shift in distribution although trends differed between species (Fig. 5d). Larvae of *Trachurus novaezelandiae* occurred further offshore with increasing stage. Larvae of *Pseudocaranx dentex* were
Figure 2. Mean density of Pseudocromileptus lecsoni and position of larval stage at intervals of time (s).
more abundant at the surface with increasing stage. During the day, the average size of *Pseudocaranx dentex* larvae is greater in subsurface waters (Gray 1993), which suggests diel vertical migration by this species. However, differences in observations between studies may also reflect differences in hydrography (i.e. lack of water column stratification during sampling by Gray). The shift in cross-shelf distribution between January and April during coastal upwelling indicates that carangid larvae are indeed subject to hydrodynamic influences.

Conclusions

Approximately 90% of larvae of each species occurred at stations A, B or C (i.e. within 17 km of the Sydney coast) during January and April, 1994 (Fig. 6). The highest densities of each species generally occurred at 'shallow' or 'middle' sampling depths, which corresponded to water within the mixed layer or upper thermocline (Fig. 2). No species was most abundant at the surface. These results highlight the importance of the nearshore mixed layer to many commercially significant fish larvae off south-eastern Australia.

![Figure 6. Mean (± standard deviation) percentage of larvae of each species at sampling stations in January and April, 1994.](image)

The vast majority of individuals of all species observed in this study were at a preflexion stage of development. This is not unexpected and is likely to reflect the combined effects of high larval mortality and increasing net avoidance with increasing larval size. In some species, lower catchability of older larvae may also result from a movement away from the marine, pelagic environment towards the end of the larval phase. For example, older *Argyrosomus japonicus* larvae are believed to adopt a benthic habit prior to settlement in estuaries (A. Miskiewicz pers. comm.). Many coastal species have a coastal or estuarine juvenile phase and marine larvae must eventually migrate towards the coast. Postflexion larvae, nearing settlement, could have been present < 2 km from the coast, inshore of station A during this study. This relatively shallow region was not accessible to the sampling gear employed by this study.

Limitations on sampling location imposed by the use of a particular gear type confound many plankton studies, and contribute to an incomplete understanding of the life history of many fish species. In particular, no sampling of the extreme nearshore zone (i.e. m's from shore) or absolute bottom (< 1 m from bottom) is reported for the south-eastern Australian coast. Such regions have been sampled elsewhere by use of light-traps or diver-operated nets and often host settlement stage larvae (e.g. Hickford and Shiel 1999). Off south-eastern Australia, these regions may host late-stage larvae of numerous commercial species, especially sparids, that are highly abundant as juveniles within coastal waters but relatively infrequently observed as larvae.

All species encountered during this study are coastally distributed as juveniles and adults (Kailola et al. 1993), and the nearshore distribution of most larvae suggests that the life cycle of each species is typically completed close to the coast. However, observations of some larvae over the outer shelf and slope during this study provide an insight into the extent of distributional variability that larvae may experience. Larvae of five species (*Sardinops sagax*, *Hyperlophus vittatus*, *Pseudocaranx dentex*, *Trachurus novaenelandiae*, *Sillago flindersii*) were found > 30 km offshore in January. Larvae of nine species (*Sardinops sagax*, *Engraulis australis*, *Pogonias awatitis*, *Rhabdosargus sarba*, *Pseudocaranx dentex*, *Trachurus novaenelandiae*, *Liza argentea*, *Argyrosomus japonicus*, *Sillago flindersii*) were found > 30 km offshore in April. The increased incidence of larvae in offshore waters in April, compared with January, is unlikely to have arisen by chance, considering the lower abundances of larvae in April. Passive larval advection during coastal upwelling in April is the most likely cause of these offshore distributions. The frequency of such offshore excursions by coastal-spawned larvae is unknown. Anomalous episodes of offshore advection may contribute to spatial and temporal variability of coastal recruitment by these species. Similarly, downwelling events may enhance the coastal recruitment of surface-oriented larvae.
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