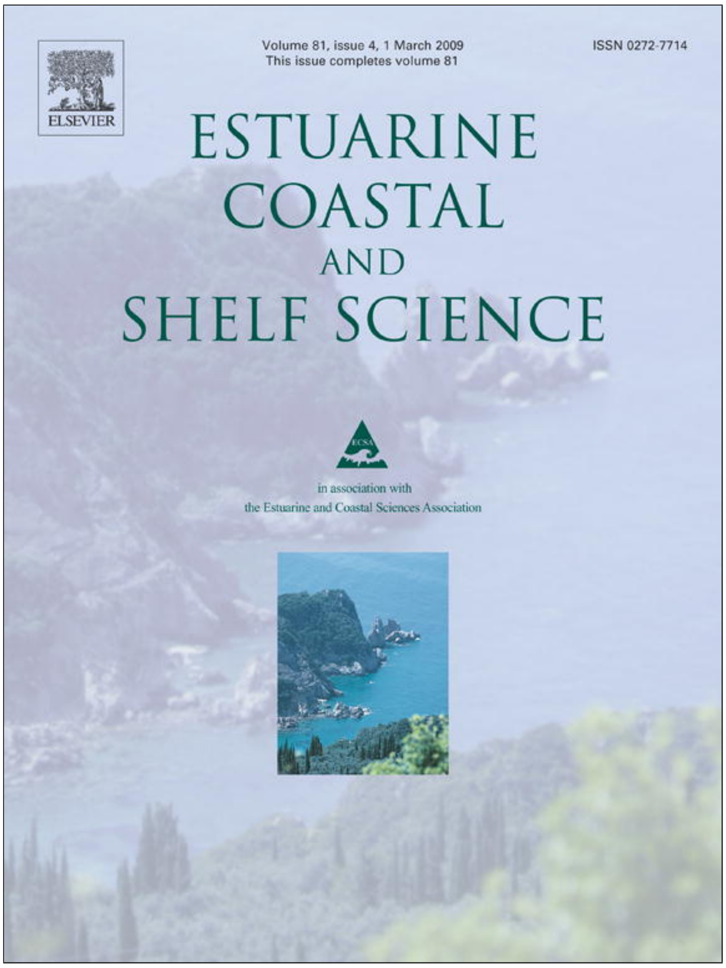
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Shelf spawning habitat of *Emmelichthys nitidus* in south-eastern Australia – Implications and suitability for egg-based biomass estimation

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A B S T R A C T

The spawning habitat of *Emmelichthys nitidus* (Emmelichthyidae) in south-eastern Australia is described from vertical ichthyoplankton samples collected along the shelf region off eastern through to south-western Tasmania during peak spawning in October 2005–06. Surveys covered eastern waters in 2005 (38.8–43.5°S), and both eastern and southern waters in 2006 (40.5°S around to 43.5°S off the south-west). Eggs ($n = 10,393$) and larvae ($n = 378$) occurred along eastern Tasmania in both years but were rare along southern waters south and westwards of 43.5°S in 2006. Peak egg abundances (1950–2640 per m^{-2}) were obtained off north-eastern Tasmania (40.5–41.5°S) between the shelf break and 2.5 nm inshore from the break. Eggs were up to 5-days old, while nearly 95% of larvae were at the early preflexion stage, i.e. close to newly emerged. Average abundances of aged eggs pooled across each survey declined steadily from day-1 to day-5 eggs both in 2005 (97-18) and 2006 (175-34). Moreover, day-1 egg abundances were significantly greater 2.5 nm at either side of the break, including at the break, than in waters ≥5 nm both inshore and offshore from the break. These results, complemented with egg and larval data obtained in shelf waters off New South Wales (NSW; 35.0–37.7°S) in October 2002–03, indicate that the main spawning area of *E. nitidus* in south-eastern Australia lies between 35.5°S off southern NSW and 43.5°S off south-eastern Tasmania, and that spawning activity declines abruptly south and westwards of 43.5°S around to the south-west coast. In addition, quotient analyses of day-1 egg abundances point to a preferred spawning habitat contained predominantly within a 5 nm corridor along the shelf break, where waters are 125–325 m deep and median temperatures 13.5–14.0 °C. Spawning off eastern Tasmania is timed with the productivity outburst typical of the region during the austral spring, and the temperature increase from the mixing between the southwards advancing, warm East Australian Current and cooler subantarctic water over the shelf. Overall, ichthyoplankton data, coupled with reproductive information from adults trawled off Tasmania, indicate that *E. nitidus* constitutes a suitable species for the application of the daily egg production method (DEPM) to estimate spawning biomass. This finding, together with evidence in support of a discrete eastern spawning stock extending from southern NSW to southern Tasmania, strengthens the need for DEPM-based biomass estimates of *E. nitidus* prior to further fishery expansion.

1. Introduction

Most of the 15 known species currently placed in the family Emmelichthyidae support limited commercial fisheries through their geographical range, with catches used predominantly for human consumption, bait and/or fish meal. They are taken by bottom, demersal and mid-water trawling in Europe (Russia, Georgia and Ukraine), South Africa, Australia and New Zealand, either as primary target or by-catch of other offshore trawl fisheries (Heemstra and Randall, 1977; Paul, 1997; Anon, 2001; Heemstra, 2002). Of the two emmelichthyids found in temperate Australia, *Emmelichthys nitidus* have been trawled off eastern and south-western Tasmania since 2002, where captures of around 4000–8000 tonnes p.a. are processed mainly to feed farmed tuna (McLaughlin, 2006; Larcombe and Begg, 2008). This small (to 36 cm TL) mid-water schooling species occurs in shelf waters of temperate Australia ≥30°S, where it is locally known as redbait. It also occurs in New Zealand, South Africa and Chile, including oceanic islands along the same latitudes (Heemstra and Randall, 1977; Last et al., 1983; Gomon et al., 1994; Hoese et al., 2007).

Increasing commercial captures of *Emmelichthys nitidus* off Tasmania led to the implementation of a biological study ultimately

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aimed at evaluating the spawning biomass of this species via the daily egg production method (DEPM). The method combines adult reproductive data with daily egg abundances within a defined spawning area to compute mean spawning biomass within such area. As a well-known fishery-independent technique to estimate stock levels of pelagic fishes such as clupeoids and scombrids (Lasker, 1985; Priede and Watson, 1993; Lo et al., 1996), the DEPM was deemed suitable for *E. nitidus* since several attributes of its reproductive biology, including the release of pelagic eggs in batches (J.M. Lyle, unpublished data), fall within those typically exhibited by DEPM-assessed small pelagic species (Stratoudakis et al., 2006). Before such method could be applied, however, it is critical to define the spawning habitat of the target species as well as having sound information of timing and geographical extent of spawning. In the case of small pelagic fishes, the spatio-temporal characterisation of spawning habitats through the use of hydrography and shelf bathymetry is becoming increasingly important to fishery science, particularly in the context of biomass assessment and subsequent predictions of recruitment success and stock health (e.g. Checkley et al., 1999; van der Lingen et al., 2001, 2005; Castro et al., 2005; Ibaibarriaga et al., 2007; Neira and Keane, 2008).

In this paper we describe the spawning habitat characteristics of *Emmelichthys nitidus* based on eggs and larvae caught primarily during ichthyoplankton surveys carried out along shelf waters of eastern to south-western Tasmania in October 2005 and 2006. Input data for this paper follow from concurrent identification and aging protocols developed for eggs of this species by Neira et al. (2008). Supplementary ichthyoplankton data from southern New South Wales (NSW) in October 2002 and 2003 are employed to examine aspects of the geographical extent of the redbait spawning stock in south-eastern Australia. Cross- and along-shelf egg and larval distributions off Tasmania are examined in terms of environmental conditions, and results discussed in relation to linkages with regional oceanography. Overall results are discussed in terms of the suitability of the DEPM to estimate biomass of this species.

2. Materials and methods

2.1. Study area and surveys

Ichthyoplankton surveys were carried out during October 2005 and 2006, coinciding with the peak spring spawning season of *Emmelichthys nitidus* off eastern Tasmania (J.M. Lyle, unpublished data). Sampling was conducted over the continental shelf region between 38.8°S in eastern Bass Strait (north east of Flinders Is.) and 43.5°S (south of the Tasman Peninsula) in 2005, and from 40.5°S (Cape Barren Is.) around to 43.5°S off the south-west coast (Port Davey) in 2006 (Fig. 1). The continental shelf along this region is relatively narrow, decreasing in width from around 33 nautical miles (nm) at 39.7°S (off the north tip of Flinders Is.) to 7 nm at 43.2°S (off the Tasman Peninsula), before widening to 32 nm at 147°E off southern Tasmania. Two major southward-flowing oceanic currents operate seasonally off Tasmania, namely the western boundary East Australian Current (EAC) and the Zeehan Current (ZC). The EAC forms in the Coral Sea and reaches south-eastern Tasmania during the austral summer when at its maximum intensity, whereas the ZC flows along the west coast and extends eastwards into the south-east during its peak flow in winter. Oceanographic conditions along eastern Tasmanian in October reflect a mixture of warm, saline water to the north derived from the onset of EAC incursion, and cooler subantarctic water to the south following the northward retreat of the warm ZC (Ridgway, 2007a,b).

Sampling in 2005 (12–17 October) comprised 29 transects (T) perpendicular to the coastline and 10 nm apart (Table 1; Fig. 1). Up to four stations were located along each transect, and positioned each at the shelf break (200 m contour) and then every 5 nm to the shoreline except along T3, T5, T7 and T9, where stations were also positioned 5 nm offshore from the break. Sampling in 2006 was carried out in two legs, the first covering 12 transects along eastern Tasmania (T1–T12; 10–14 October), and the second covering the remaining 10 transects from the lower south-east to the lower south-west of Tasmania (T13–T22; 30–31 October); transects were also perpendicular to the coastline but 15 nm apart, each containing 4–5 stations (Fig. 1). Sampling effort was concentrated mostly along a 15-nm stretch that followed the shelf break, with stations located 7.5 and 2.5 nm inshore from the break, over the break, and 2.5 and 7.5 nm offshore from the break. The rationale for extending the sampling coverage in 2006 to include southern Tasmania was to sample as much of the southern extent of the spawning area of *E. nitidus* as feasible, based on the presence of spawning females off the south-west region (J.M. Lyle, unpublished data). In all, 201 plankton samples were collected from 198 stations across the two surveys (Table 1).

2.2. Field and laboratory procedures

Plankton samples were taken continuously day and night. Eggs and larvae in 2005 were caught using a bongo sampler consisting of 3 m long, 0.6 m diameter plankton nets of 300 and 500 μm mesh, encased within a custom-built, weighted stainless steel frame to facilitate vertical drops. Samples in 2006 were taken with a modified PAIROVET sampler (bongo version of CalVET sampler; Smith et al., 1985) consisting of 1.5 m long, 0.25 m diameter plankton nets of 300 μm mesh, placed inside a similar but smaller weighted frame.

At each station the sampler was lowered vertically to within ~5 m of the seabed or to a maximum depth of 190 m and immediately brought back on board. Sampling depth was determined using the onboard echosounder, and volume of water filtered (m^{-3}) estimated from counts provided by General Oceanic flowmeters fitted at the mouth of each net. Nets were thoroughly washed immediately after the sampler was on deck, and samples from the codends combined and fixed either in 98% ethanol (2005) or 10% formaldehyde-seawater (2006); redbait eggs fixed in ethanol were subjected to mtDNA analyses to confirm species identifications (refer to Neira et al., 2008 for details).

Vertical data on conductivity, temperature and depth were obtained simultaneously with each plankton sample using a Conductivity–Temperature–Depth (CTD) profiler fitted to the sampler's frame. Temperature data were plotted by depth for the inshore- and offshore-most stations of transects regarded as representative of the areas surveyed in October 2005 (T1, T11, T29) and October 2006 (T1, T13, T22) to determine presence and depth of thermal stratification. Temperatures and salinities at the surface (average of first 10 m) and mid-water (median to 100 m or to maximum depth if <100 m) were calculated for each station; conductivity data from all stations in 2006 were omitted as some values recorded by the profiler were deemed as erroneous. Composite, high resolution sea-surface temperature (SST) images of eastern Tasmania (NOAA AVHRR satellite) were obtained for the survey periods in 2005 and 2006 corresponding to 5-day averages centered on the sampling days (CSIRO Marine & Atmospheric Research, Hobart). Altimetric sealevel and velocity images (not shown) of 15 October 2005 and 2006 were examined to obtain data on prevailing surface currents during the sampling periods (http://www.marine.csiro.au/remotesensing/oceancurrents).

Terminology pertaining to eggs and larvae follows Neira et al. (1998, 2008). All eggs and larvae were removed from samples under a dissecting stereomicroscope, and stored in 70–98% ethanol for analyses. Redbait eggs were identified and sorted by developmental stage (I–VII; Neira et al., 2008), while larvae were separated

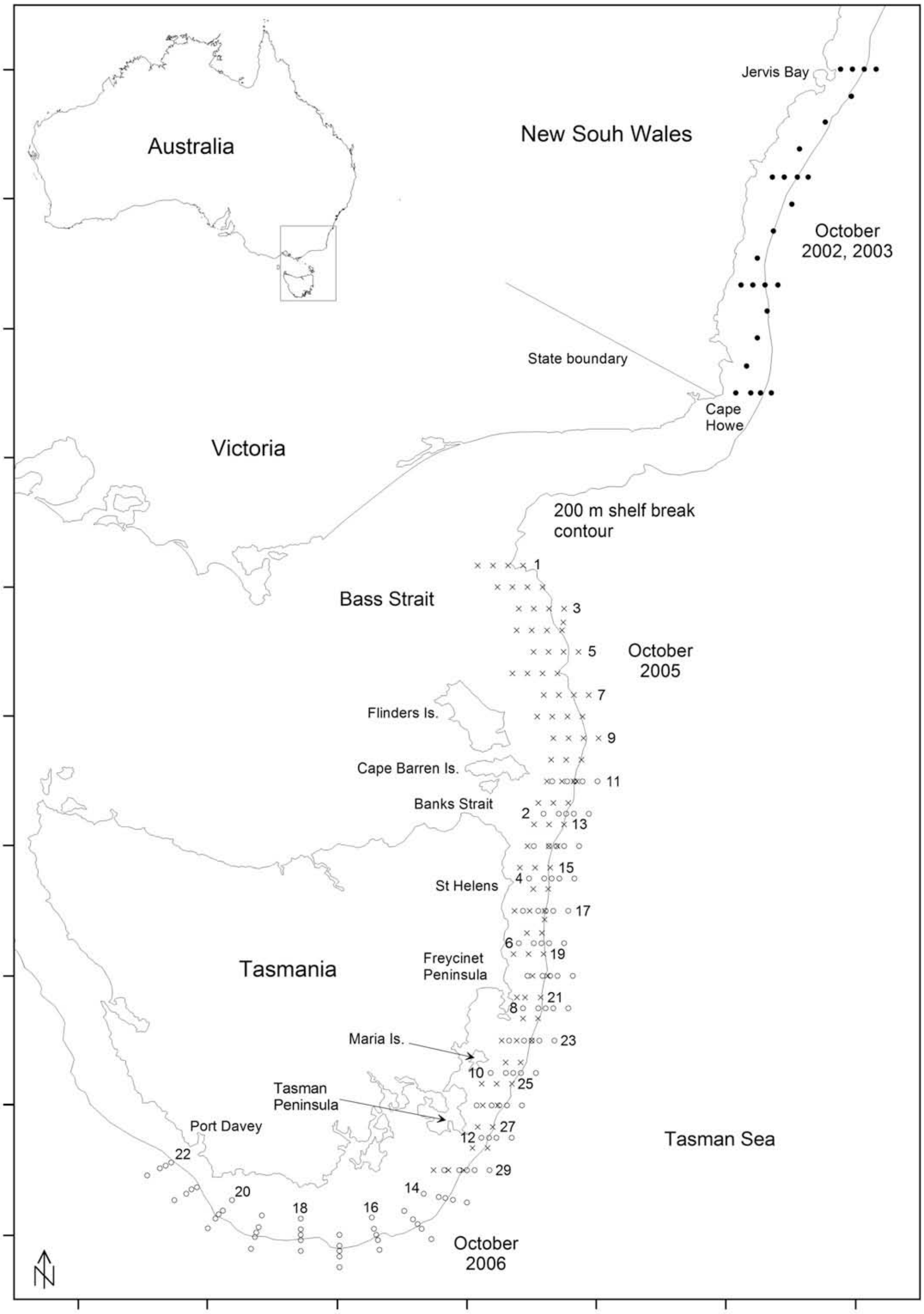

Fig. 1. Map of south-eastern Australia showing source of eggs and larvae of *Emmelichthys nitidus* examined for this study. Symbols denote stations sampled during October 2002 and 2003 along southern New South Wales (dark circles), and October 2005 (crosses) and October 2006 (open circles) around north-eastern to south-western Tasmania. Transects around Tasmania have been numbered on a southerly direction using odd (2005) and even (2006) numbers, respectively.

into preflexion (including yolk-sac larvae), flexion and postflexion stages.

2.3. Supplementary data

Eggs and larvae of *Emmelichthys nitidus* from surveys carried out elsewhere in south-eastern Australia were also examined for this study to provide additional information on temporal and spatial distributions. These included a few larvae from vertically stratified samples collected with an opening–closing BIONESS at specific locations across northern Bass Strait (F.J. Neira, *unpublished data*), and eggs and larvae from shelf waters between 35.0°S (Jervis Bay) and 37.5°S (Cape Howe) in southern NSW in October 2002 and 2003 (Table 1; Fig. 1). Details of the survey design and sampling

Table 1
Survey details and total number (not standardised) of *Emmelichthys nitidus* eggs and larvae caught in shelf waters along north-eastern to south-western Tasmania in October 2005 and 2006; data provided for latter survey have also been provided for the eastern and southern areas – refer to Materials and methods. Details from supplementary surveys of shelf waters along southern New South Wales in October 2002 and 2003 are also provided. Abbreviations: E, eastern; NE, north-eastern; NSW, New South Wales; S, southern; SE, south-eastern; SW, south-western; Tas, Tasmania.

Survey date	Region	Transects (stations)	Samples	Eggs (% positive stations)	Larvae (% positive stations)
12–17 Oct 2005	NE Bass Strait to SE Tas	1–29 (91)	94	9280 (85)	311 (57)
10–31 Oct 2006	E to SW Tas	1–22 (107)	107	1113 (50)	67 (31)
	Eastern Tas	1–13 (64)	64	1069 (59)	53 (39)
	Southern Tas	14–22 (43)	43	44 (37)	14 (19)
Supplementary material					
19–20 Oct 2002	S NSW	7 (25)	23	60 (43)	10 (22)
6–7 Oct 2003	S NSW	7 (25)	15	902 (53)	53 (80)

protocols employed in the latter surveys, as well as water temperature information, are provided in Neira and Keane (2008).

2.4. Treatment of egg and larval data

Total numbers of *Emmelichthys nitidus* eggs and larvae were standardised to abundance per surface area (numbers per m^{-2}) based on water volume filtered and depth of net drop. Each egg was assigned a specific age (days) using the temperature-dependent egg incubation model developed by Neira et al. (2008). The computing of ages by stage employed mid-water temperatures at each station and local time (hour) of collection, with peak spawning time assumed to be 21:00 h based on the fact that spawning activity of *E. nitidus* is complete mostly by midnight (J.M. Lyle, unpublished data).

Statistical analyses were performed using STATISTICA®. Egg and larval abundances, and abundances of day-1 eggs (≤24 h), were plotted using SURFER®. Percentage values are based on abundances unless stated otherwise. Abundances of egg and larvae in 2005 and 2006 are described in terms of shelf region, following the arbitrary classification of each station as shoreward (≥5 nm inshore from

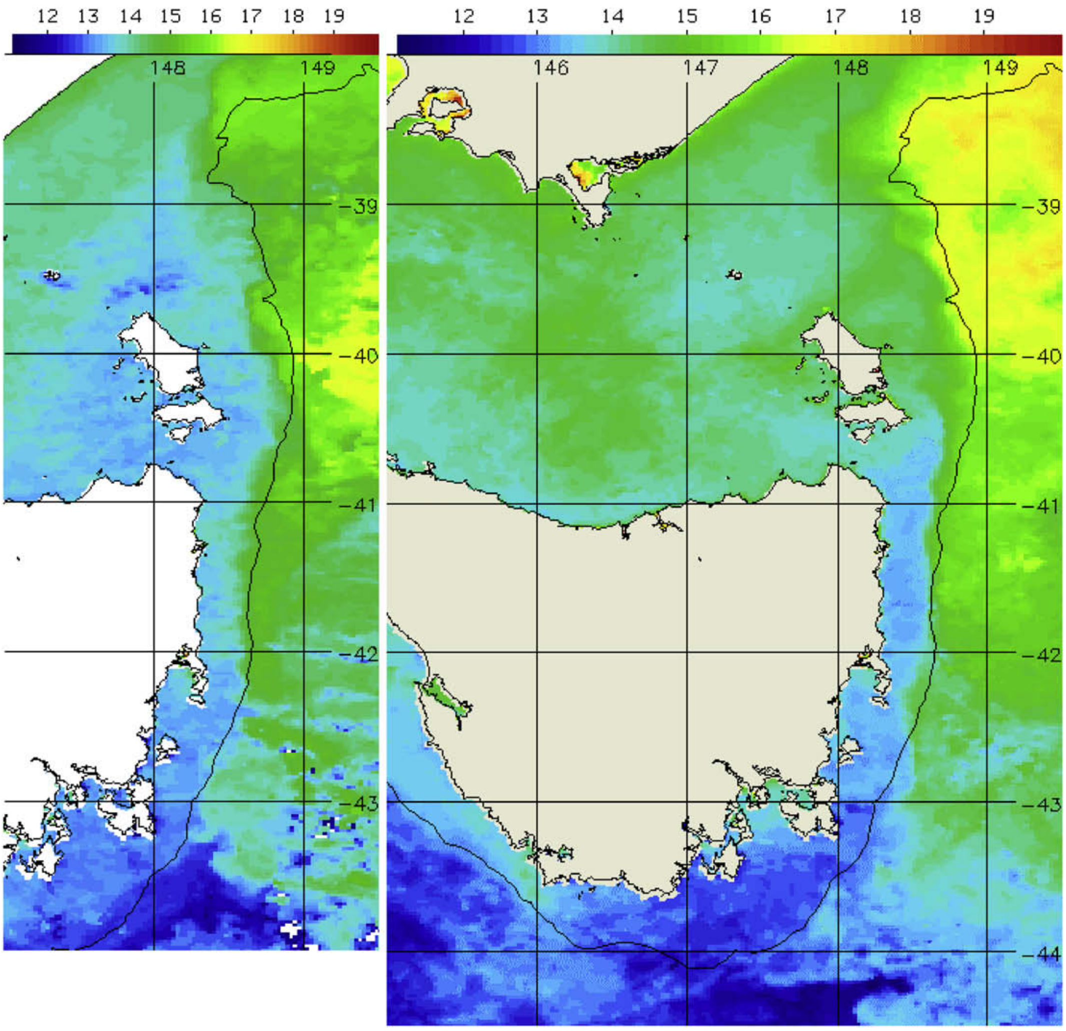

Fig. 2. Sea-surface temperature (SST) images (composite 5-day averages) of eastern Tasmania for the period 6–11 October 2005 (left) and 27 October–1 November 2006 (right), corresponding to the dates of the two surveys. Copyright 2006–2007, CSIRO Marine & Atmospheric Research, Hobart.

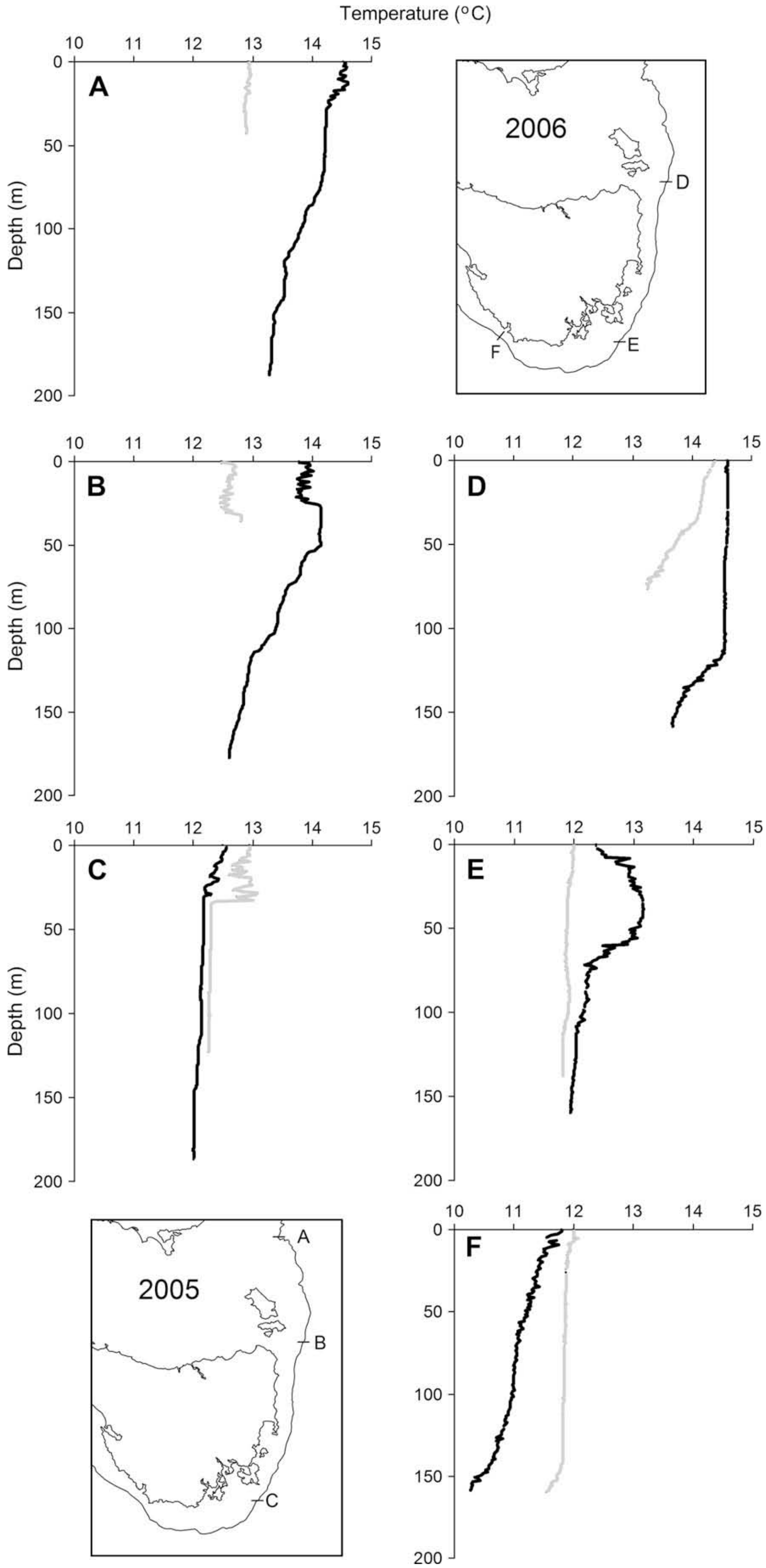

Fig. 3. Vertical temperature profiles (°C) by depth (m) at inshore-most (grey lines) and offshore-most (black lines) stations of selected transects along eastern and southern Tasmania in October 2005 (left) and 2006 (right). Positions of transects in 2005 (A, T1; B, T11; C, T29) and 2006 (D, T1; E, T13; F, T22) are shown in embedded maps; transects B and C are located at the same latitudes of D and E, respectively.

shelf break), shelf break (2.5 nm either side of the break, including at the break) or offshore (≥5 nm offshore from break). Main effects ANOVA (unequal sample size) was performed on the pooled data to determine whether mean egg (all and day-1 eggs) and larval abundances differed significantly by shelf region and survey. Data were log-transformed ($\log_{10}[n+1]$) to account for variance heterogeneity following Cochran's test. When factors were found to be significant, the Bonferroni comparison test was applied to ascertain which levels were different (Quinn and Keough, 2002).

Quotient analyses (Drapeau, 2005; Neira and Keane, 2008) were performed on the abundance of day-1 eggs from the 2005 and 2006 surveys to describe selection of spawning habitat in terms of bathymetric depth (100 m intervals), region of continental shelf (shoreward, shelf break and offshore) and mid-water temperatures (0.5 °C classes). Quotients >1 indicate positive spawning location. Abundances of day-1 eggs by temperature/salinity (mid-water values) were plotted for 2005 to define the specific T/S range within which they occurred in that year.

Preliminary analyses of the spatial distribution of eggs and larvae of *Emmelichthys nitidus* across the two years, coupled with latitudinal differences in water temperatures, indicated the presence of a boundary at 43.5°S corresponding to T29 in 2005 and T13 in 2006 (Fig. 1). Consequently, for the purpose of describing spawning distribution of *E. nitidus*, the area surveyed north of 43.5°S in 2005 (T1–T29) and 2006 (T1–T13) is hereafter referred to as eastern Tasmania whereas the cooler, southern region surveyed in 2006 (T14–T22) is hereafter referred to as southern Tasmania.

3. Results

3.1. Environmental conditions

Composite SST imagery of the eastern shelf shows Tasman Sea water (12–14 °C) along the inner shelf, and the south-flowing East Australian Current (EAC; 15–16 °C) encroaching along the outer shelf, with a longitudinal front between these two masses clearly defined along the shelf break in both 2005 and 2006 (Fig. 2). Vertical temperature profiles from CTD-derived data showed this front being more evident in 2005 than in 2006, particularly along T1 (38.8°S) where surface offshore waters were up to 1.5 °C warmer that those inshore due to the EAC influence (Fig. 3). Furthermore, inshore waters in 2005 were relatively well-mixed throughout most of the survey area except towards the southern end, as indicated by the breakdown in thermal structure detected from the surface to 40 m off T29 (43.5°S) in the lower south-east (Fig. 3C). By contrast, inshore waters at the same latitude in 2006 (T13) were well mixed, while offshore waters exhibited signs of thermal stratification at depths of 20–80 m (Fig. 3E).

Average surface and mid-water temperatures off eastern Tasmania fell within the 12.1–14.5 °C range both in 2005 and 2006, with a maximum latitudinal gradient of 2.3 °C combining data from the two surveys (Table 2). Average offshore mid-water temperatures along southern Tasmania in 2006 were slightly cooler than those off the eastern shelf in both surveys, i.e. 11.7 vs 13.4–13.6 °C. Surface and mid-water salinities off eastern Tasmania during 2005 averaged 35.5 along 38.8°S and 35.0–35.2 along 43.5°S (Table 2). Images of altimetric sealevel and velocities showed a prevailing 0.5 knot (0.25 m s^{-1}) south-bound surface current flowing over the continental shelf along the length of eastern Tasmania both in 2005 and 2006.

3.2. Distribution and abundance of eggs and larvae

A total of 9280 and 1113 eggs of *Emmelichthys nitidus* were caught along shelf waters off Tasmania during October 2005 and 2006, respectively (Table 1). In 2005 eggs were distributed along the entire shelf area but were more abundant off north-eastern Tasmania, particularly off 40.7°S (Fig. 4). In 2006, 96.2% of eggs

Table 2
Temperature (°C) and salinity conditions of shelf waters along north-eastern to south-western Tasmania in October 2005 and 2006. Surface values correspond to 10 m averages; mid-water values correspond to averages of medians to a depth of 100 m, or to maximum depth if <100 m. Maximum (Max.), minimum (Min.) and average (Av.) values provided for the inshore area includes all stations ≥ 5 nm shoreward from the shelf break; offshore include all stations at or offshore of the break. Data for 2006 are provided for the eastern (transects 1–13) and southern (transects 14–22) regions (refer to Materials and methods for details). A dash indicates no data available.

Survey date	Region	Transect (no. stations)	Latitude (°S)		Temperature		Salinity	
					Surface	Mid-water	Surface	Mid-water
2005	Whole	1 (4)	38.8	Av.	13.36	13.40	35.49	35.48
		29 (3)	43.5	Av.	12.60	12.80	35.04	35.15
		1–29 (54)		Max.	13.97	13.51	35.50	35.54
		Inshore		Min.	12.37	12.21	34.69	35.08
				Av.	**13.09**	**12.85**	**35.17**	**35.25**
		1–29 (37)		Max.	15.32	15.05	35.63	35.57
		Offshore		Min.	12.16	11.96	34.85	35.07
				Av.	**13.74**	**13.43**	**35.26**	**35.32**
2006	Whole	1 (5)	40.5	Av.	14.50	14.30	–	–
		13 (5)	43.5	Av.	12.16	12.12	–	–
		22 (4)	43.5	Av.	11.76	11.73	–	–
	Eastern Tasmania	1–13 (64)		Max.	12.89	12.91	–	–
		Inshore		Min.	11.97	11.90	–	–
				Av.	**12.25**	**12.15**	–	–
		1–13 (64)		Max.	14.61	14.62	–	–
		Offshore		Min.	12.34	12.03	–	–
				Av.	**13.66**	**13.62**	–	–
	Southern Tasmania	14–22 (43)		Max.	12.50	12.18	–	–
		Inshore		Min.	11.52	11.46	–	–
				Av.	**12.08**	**11.88**	–	–
		14–22 (43)		Max.	13.04	12.97	–	–
		Offshore		Min.	10.94	10.59	–	–
				Av.	**11.92**	**11.71**	–	–

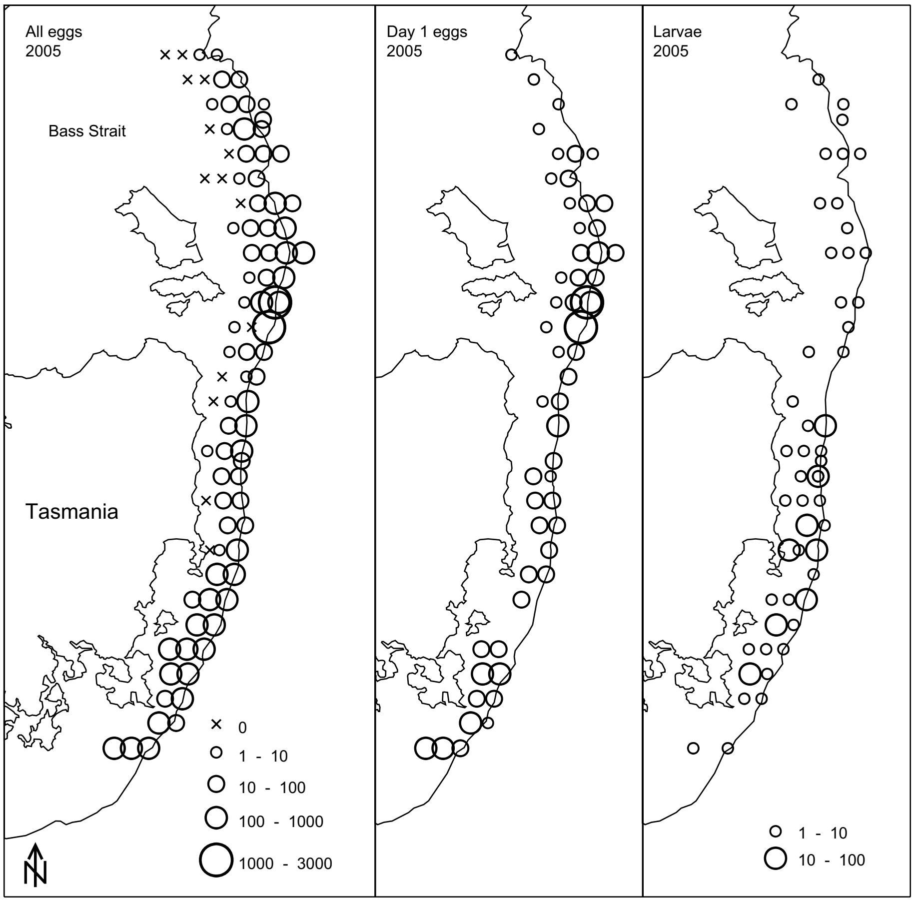

Fig. 4. Distribution of eggs and larvae (numbers per m^{-2}) of *Emmelichthys nitidus* in shelf waters along eastern Tasmania in October 2005. For clarity negative stations (×) are only shown for far left plot; abundance scale for all eggs also applies for day-1 eggs.

originated from eastern Tasmania and the remaining 3.8% from southern Tasmania (Table 1; Fig. 5). Larval *E. nitidus* totalled 311 in 2005 and 67 in 2006. Unlike eggs, nearly 83% of larvae in 2005 came from the southern half of the survey area, i.e. 41.2°S and 43.5°S (Fig. 4), whereas 78% of larvae in 2006 originated from eastern Tasmania (Table 1; Fig. 5).

Egg abundances (numbers per m^{-2}) of *Emmelichthys nitidus* averaged 133 and 103 in 2005 and 2006, respectively (Table 3). Greatest abundances in 2005 (1953) and 2006 (2644) originated from stations located at the shelf break (0 nm) and 2.5 nm shoreward from the break (−2.5 nm) along 40.5°S and south of 41.2°S, respectively (Figs. 4 and 5). Egg abundances varied significantly with shelf region across the two surveys ($F_{2,154}$ = 24.87; $P < 0.0001$), with abundances being significantly higher at stations close to and at the shelf break, i.e. −2.5 nm inshore to 2.5 nm offshore from the break.

Abundances of larval *Emmelichthys nitidus* averaged 7 and 20 in 2005 and 2006, respectively, with maximum abundances in 2005

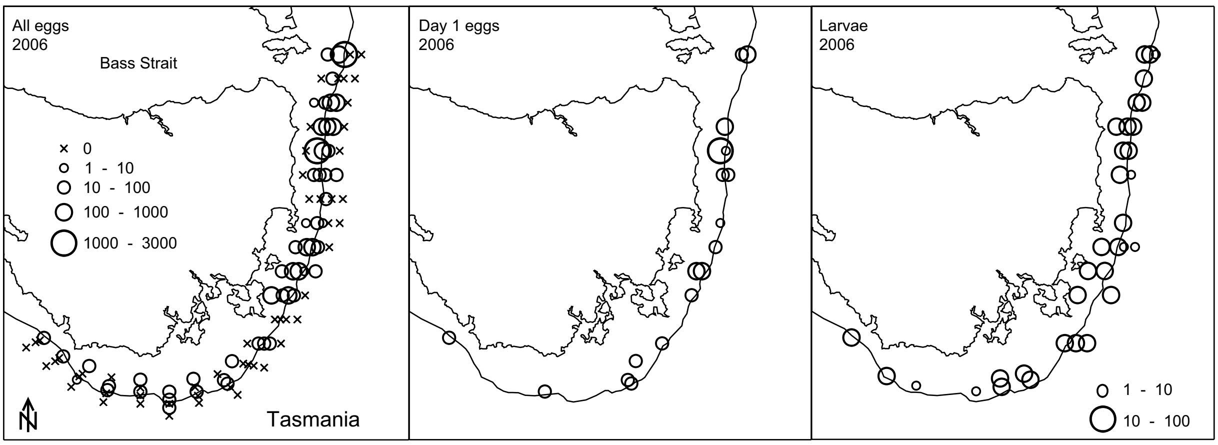

Fig. 5. Distribution of eggs and larvae (numbers per m^{-2}) of *Emmelichthys nitidus* in shelf waters along eastern to south-western Tasmania in October 2006. For clarity negative stations (×) are only shown for far left plot; abundance scale for all eggs also applies for day-1 eggs.

Table 3
Summary statistics of *Emmelichthys nitidus* eggs and larvae caught in shelf waters along north-eastern to south-western Tasmania in October 2005 and 2006. Average abundances (numbers per m^{-2}, 95% C.I.) were calculated with data from positive stations. Greatest abundances of all eggs, aged eggs (days old) and larvae are provided together with latitude (°S) of transect, and seafloor depth and distance of station from shelf break (nm) where these were obtained; negative values indicate shoreward of the shelf break.

Survey date	Descriptor	Eggs						Larvae
		All	Day-1	Day-2	Day-3	Day-4	Day-5	
October 2005	Average abundance (95% C.I.)	133 (59)	97 (82)	59 (29)	31 (8)	24 (9)	34 (36)	7 (3)
	Greatest abundance	1954	1831	512	158	153	81	67
	Latitude (°S)	40.5	40.7	39.8	42.7	42.7	43.5	42.0
	Station depth (m)	276	280	330	120	120	203	122
	Distance from shelf break (nm)	0	0	0	−5	−5	0	−5
October 2006	Average abundance (95% C.I.)	103 (66)	175 (202)	119 (69)	102 (72)	41 (25)	18 (5)	20 (5)
	Greatest abundance	2644	2272	425	838	281	32	62
	Latitude (°S)	41.5	41.5	41.2	40.5	42.5	43.4	41.2
	Station depth (m)	118	118	176	138	400	166	119
	Distance from shelf break (nm)	−2.5	−2.5	0	0	0	−2.5	0

(67) and 2006 (62) originating from stations located between 5 nm shoreward from the shelf break and the break (Table 3). Nearly 95% of the larvae caught in 2005 and 2006 were at the preflexion stage, measuring 2.4–7.2 mm in body length. Unlike eggs, larval abundances did not vary significantly by shelf region, with larvae showing a fairly even cross-shelf distribution (Fig. 6).

Eggs and larvae of *Emmelichthys nitidus* were caught between 35.0°S and 37.5°S in southern NSW in October 2002 and 2003 (Figs. 1 and 7; Table 1). Eggs were more abundant during 2003, with the highest abundance (651) obtained 5 nm inshore from the shelf break in waters 125 m deep (36.7°S). Neither eggs nor larvae were caught at stations sampled to the north of 35.0°S in 2002 or 2003.

3.3. Egg age distributions

Eggs of *Emmelichthys nitidus* obtained in 2005 and 2006 were aged between one-and five-days old. Overall average abundances (numbers per m^{-2}) ranged between 97–175 day-1 eggs and 18–34 day-5 eggs, with abundances during both surveys steadily declining towards late-stage eggs (Table 3). Day-l eggs occurred primarily along the shelf break region between 39.8°S and 41.2°S both in 2005 (Fig. 4) and 2006 (Fig. 5). Furthermore, analysis of the data pooled for both surveys revealed that day-1 eggs were significantly more abundant at stations located along the shelf break region than those either >5 nm shoreward or offshore from the break ($F_{2,154} = 11.91$; $P < 0.0001$). Quotients of day-1 egg abundances pooled across years peaked at stations in waters 225–325 m deep along the shelf break region (Fig. 8).

3.4. Association with environmental variables

Day-1 *Emmelichthys nitidus* eggs caught during 2005 originated from stations with mid-water temperatures of 12.0–15.2 °C and mid-water salinities of 35.0–35.5 (Table 2; Fig. 9). Quotients of day-1 egg abundances by 0.5 °C temperature classes were bi-modal across the two years, comprising a small peak at 12.0–12.5 °C and a major peak at 13.5–14.0 °C (Fig. 8). Eggs and larvae of *E. nitidus* obtained off southern NSW during 2002 and 2003 originated from stations with mid-water temperatures of 14.1–17.0 °C, with the greatest abundance obtained in 14.4 °C (data not shown).

4. Discussion

4.1. Spawning season

This paper constitutes the first descriptive account of the distribution and abundance of eggs and larvae of *Emmelichthys*

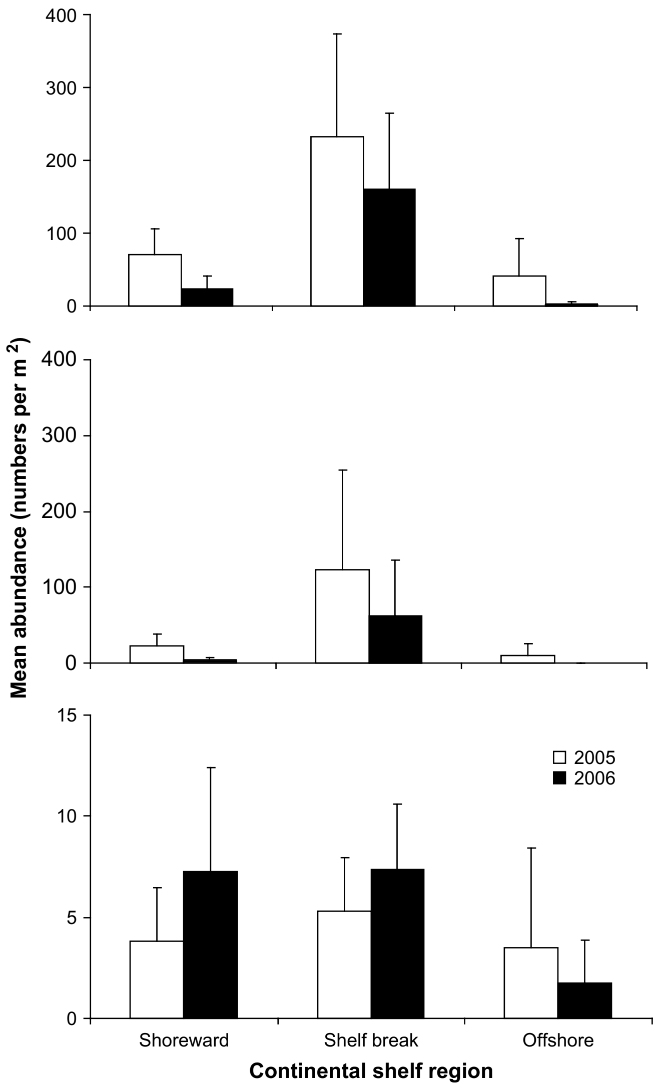

Fig. 6. Mean abundances of eggs (top and middle) and larvae (bottom) (mean numbers per m^{-2} + 95% C.I.) of *Emmelichthys nitidus* across shelf waters of north-eastern to south-western Tasmania in October 2005 and 2006. Data from each sampling station were pooled into one of three regions (*x*-axis), namely shoreward (≥5 nm inshore from shelf break); shelf break (2.5 nm either side of break, including at break); and offshore (≥5 nm offshore from break).

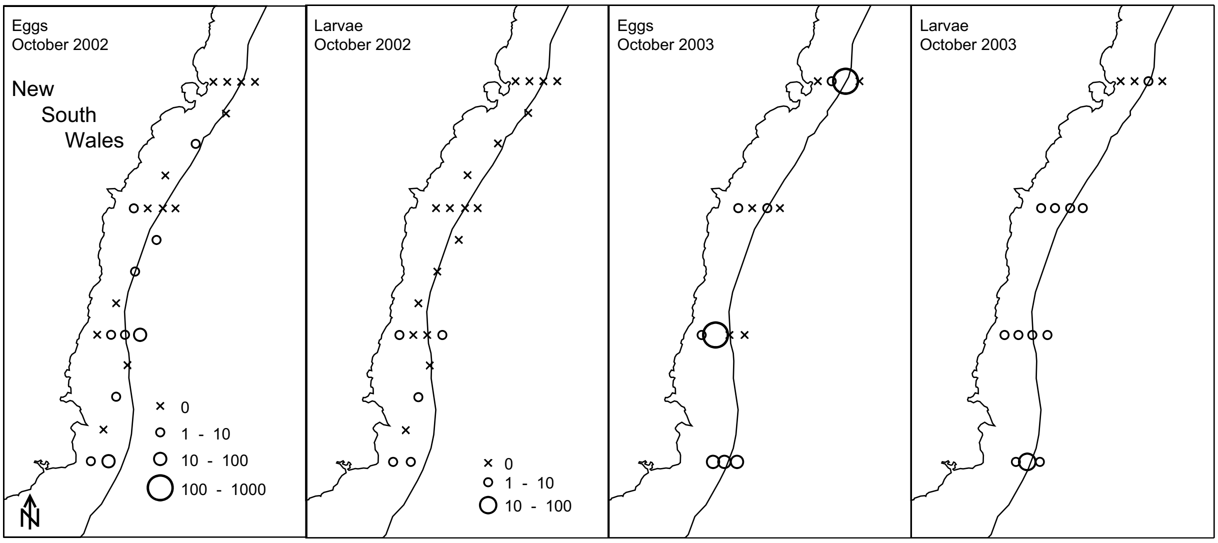

Fig. 7. Distribution of eggs and larvae (numbers per m^{-2}) of *Emmelichthys nitidus* in shelf waters along southern New South Wales during October 2002 and 2003. Abundance scales shown for 2002 eggs and larvae apply also for 2003.

nitidus in temperate Australia. Moreover, as far as we know it also constitutes the first and most comprehensive for a representative of the Emmelichthyidae worldwide, a fact which precludes detailed comparisons with other emmelicththyids in terms of spawning season and habitat.

Ichthyoplankton surveys undertaken during this study indicate that *Emmelichthys nitidus* in south-eastern Australia spawns during October. This finding is consistent with gonad development in fish off Tasmania that indicates spawning occurs mainly between September and November (J.M. Lyle, unpublished data). Furthermore, the timing also matches the presence of *E. nitidus* eggs and larvae off southern NSW as far north as 35.0°S, implying that spawning may occur more or less simultaneously throughout south-eastern Australia during the austral spring. However, it is also possible that some spawning could extend well into February/March, based on records of preflexion *E. nitidus* larvae caught between November and March along waters of northern Bass Strait, and off eastern Tasmania as far south as 42.7°S (Neira et al., 2008).

The temporally discrete spring spawning period of *Emmelichthys nitidus* coincides with the outburst of phytoplankton biomass, and hence abundant larval food, known to occur on average from mid-September to the end of November along eastern Tasmania (Harris et al., 1987). While no chlorophyll or productivity data were obtained during this study, the October SST images coupled with the CTD-derived vertical temperature data showed conditions that were consistent with those typically found during the spring productivity outburst, i.e. the shelf region bathed by warm, high salinity EAC-derived water mixed with cooler, fresh subantarctic water (Harris et al., 1987; Ridgway, 2007a). Furthermore, this nutrient-rich subantarctic water often remains well-mixed to about 300 m until the onset of thermal stratification in late spring/early summer, which denotes the end of the productivity outburst (Harris et al., 1987, 1992). In our surveys, a breakdown in the vertical thermal structure inshore was evident at least as far south as 43.5°S (T29) in 2005, whereas signs of thermal stratification were evident at the same latitude (T13) in 2006. Since egg abundances declined significantly southwards of 43.5°S and around southern Tasmania in 2006, it is likely that the spatial extent of spawning of *E. nitidus* may be linked to some degree to the duration of the spring productivity outburst.

4.2. Extent of spawning area

Data on spatial distribution and abundance of eggs and larvae from this study indicate that *Emmelichthys nitidus* in south-eastern Australia spawns between 35.0°S off central NSW and 43.5°S off the lower south-east coast of Tasmania. This conclusion is based on three main findings from this study, namely (1) eggs and larvae first appeared as far north as 35.0°S in October 2002 and 2003, occurring through to the southern limit of the survey area at 37.5°S; (2) a northern spawning boundary was not detected in the 2005 and 2005 surveys off Tasmania; and (3) there was a sharp decline in spawning activity south and westwards of 43.5°S in 2006, noting that day-1 eggs had occurred at the southern-most sampling location (T29) in 2005.

Based on oceanographic data, and quotient analyses on abundances of day-1 eggs, a likely explanation for a southern spawning area limit in the vicinity of 43.5°S would be a temperature front defined by the interface between EAC-derived water and modified cold, subantarctic water which are known to be present off that region at that time (Harris et al., 1987; Ridgway, 2007a). Such a boundary would thus be consistent with the fact that >96% of eggs in 2006 came from waters of 12.0–14.5 °C compared to the significantly lower egg abundances from waters ≤12.0 °C off southern Tasmania. The observation that the region off 43.5°S may represent the southern limit of *Emmelichthys nitidus* spawning off eastern Tasmania warrants further investigation, particularly since this region is where the western boundary, poleward Zeehan Current (ZC) meets the EAC, forming a well-defined front which is present between June and September (Ridgway, 2007a,b). Moreover, the extent to which this front is linked to the spring productivity outburst off eastern Tasmania remains to be assessed, noting that productivity associated with the ZC off the west coast of Tasmania is markedly lower than off the east coast (Harris et al., 1987).

4.3. Preferred spawning habitat

The spatial distribution of eggs and larvae indicates that *Emmelichthys nitidus* spawns primarily along a narrow 2.5 nm corridor either side of the continental shelf break, where seafloor depths are mostly 125–325 m. This observation is based on the significantly higher average egg abundances, including day-1 eggs,

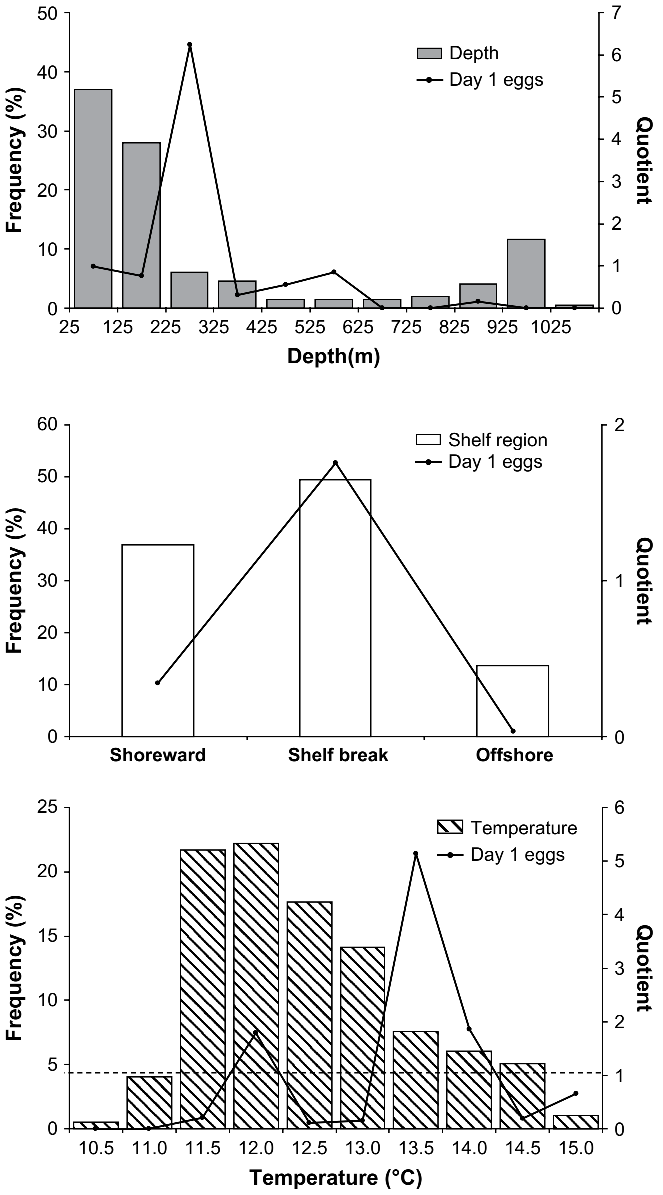

Fig. 8. Abundance quotients of day-1 eggs of *Emmelichthys nitidus* (numbers per m^{-2}) by depth of station, shelf region and mean temperature, based on data from shelf waters of north-eastern to south-western Tasmania in October 2005 and 2006. Data from each station in middle plot were pooled into one of three regions, namely shoreward (≥5 nm inshore from shelf break), shelf break (2.5 nm either side of break, including at break), and offshore (≥5 nm offshore from break). Bars along *x*-axis in plots correspond to percentage frequencies of sampling occurrences of depth intervals, shelf regions and temperatures, and include all stations across the two years. Temperature corresponds to mid-water values at each station. Positive temperature selection (quotient values > 1) is indicated by broken line in bottom plot.

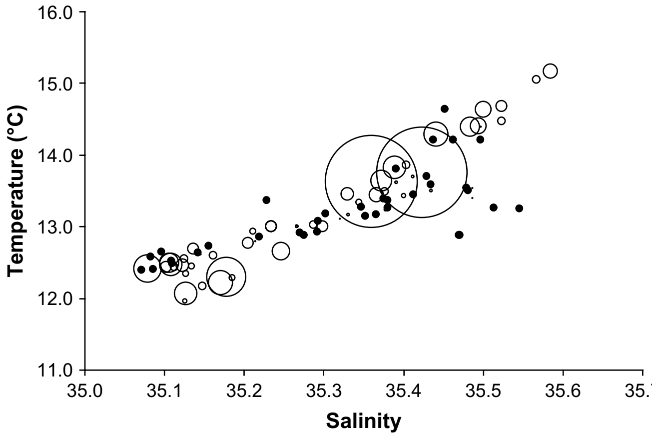

Fig. 9. Abundances of day-1 eggs of *Emmelichthys nitidus* obtained at different combinations of temperatures (°C) and salinities (mid-water values at each station) along eastern Tasmania in October 2005. Bubbles sizes are proportional to abundances (eggs per m^2); black dots correspond to stations with zero day-1 egg catches.

from stations close to and at the shelf break compared to catches from stations ≥5 nm either side of the break. The finding of the shelf break as preferred spawning region also matches echosounder-based observations of *E. nitidus* aggregations at depths of around 140 m in the latter region during spawning time (J.M. Lyle, personal observation). In this context, it is perhaps relevant that the shelf break region off eastern Tasmania has also been described as a key summer spawning area for the carangid *Trachurus declivis* (Jordan et al., 1995).

Most *Emmelichthys nitidus* larvae caught during 2005 and 2006 were at the preflexion stage, i.e. close to newly hatched. Unlike eggs, however, larvae were more evenly dispersed across the shelf, with abundances showing no significant differences among shoreward, shelf break and offshore areas. This finding implies the existence of dispersal mechanisms (e.g. wind-driven surface currents) that may affect late-stage eggs (≥4-days old) as well as young larvae to a greater extent than early-stage eggs. Such dispersal scenario, moreover, would make sense if spawning occurs deep in the water column (e.g. shelf break), with eggs becoming increasingly buoyant with development and hence gradually subjected to advection. While no evidence of egg transport could be detected with the available data, the fact that >80% of the larvae in 2005 came from the southern half of the survey area, i.e. further south of where the greatest abundances of eggs were obtained, suggests some level of southwards advection consistent with the prevailing south-bound surface flow present over the shelf region at that time. Since a similar south-bound shelf flow was present along the shelf in October 2006, it is likewise plausible that a proportion of the *E. nitidus* larvae caught along the northern half of the survey area at that time may have originated from eggs spawned and hatched further north and subsequently advected southwards.

4.4. Spawning stocks

Data from this study, combined with previous larval records (Neira et al., 2008) and recent adult reproductive information (J.M. Lyle, unpublished data), point to two scenarios which call for further investigation to support current stock management strategies in place for *Emmelichthys nitidus* in south-eastern Australia. These are (a) discrete eastern and western stocks that split off the lower south-east Tasmanian coast; or (b) one continuous stock distributed along the outer continental shelf from at least western Tasmania around southern Tasmania and up to central NSW. Our finding of simultaneous spawning between southern NSW and the lower south-east coast of Tasmania, coupled with the abrupt decline in egg and larval abundances off southern Tasmania, suggests the presence of a discrete eastern spawning stock of *E. nitidus*, i.e. a two-stock scenario model.

Additional evidence supporting a discrete eastern stock lays in the fact that reproductively active females trawled from the east coast differed substantially from those from the lower south-west coast of Tasmania in terms of size structure, and size at maturity (J.M. Lyle, unpublished data). Even under a two-stock scenario, it is feasible that some low-intensity shelf spawning activity may take place off southern Tasmania as our 2006 ichthyoplankton data seem to suggest. In the case of a single-stock scenario, on the other hand, spawning activity off southern Tasmania could be delayed until the onset of suitable habitat requirements, e.g. higher temperatures resulting from the southwards EAC inflow into the region during summer (Ridgway, 2007a). However, given the abrupt decline in eggs south and westwards of 43.5°S, coupled with the discrete spring spawning season based on reproductive data from adults caught in eastern and south-western Tasmania (J.M. Lyle, unpublished data), this scenario seems unlikely.

5. Conclusions

This study has demonstrated that spawning of *Emmelichthys nitidus* in south-eastern Australia takes place along a narrow, well-defined area of the continental shelf break between 35.0°S and 43.5°S, and that spawning activity occurs throughout October, i.e. the austral spring. These findings, coupled with adult reproductive data obtained concurrently with that of this study, indicate that *E. nitidus* constitutes a suitable species for the application of the daily egg production method (DEPM) to estimate spawning biomass (ICES, 2004; Stratoudakis et al., 2006). Firstly, *E. nitidus* are batch spawners with asynchronous oocyte development and indeterminate fecundity (J.M. Lyle, unpublished data). Secondly, the pelagic eggs (1.00–1.05 mm) are easily collected, identified and staged, and can be assigned ages using an existing temperature-dependent incubation model (Neira et al., 2008). Thirdly, the size of the spawning area can be estimated based on the relatively well-defined spatial distribution of eggs, noting, however, that the areas surveyed during this study covered little more than half of the likely spawning area. Lastly, egg abundances were found to decline with age, implying that mean daily egg production could be estimated by fitting exponential mortality models as with other multiple spawning fishes from non-clupeoid families (Stratoudakis et al., 2006; Cubillos et al., 2007). Our conclusion on the suitability of *E. nitidus* for DEPM-based biomass estimation represents a key step in the quest for scientifically defensible catch limits early in the development of a localised industrial-scale fishery that is likely to expand throughout temperate Australia.

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References

Anonymous, 2001. FAO Yearbook of Fishery Statistics – Capture Production 1999. FAO Fishery Information, Data and Statistics Unit, Rome.

Castro, L.R., Fréon, P., van der Lingen, C.D., Uriarte, A., 2005. Report of the Small Pelagic Fishes and Climate Change Programme Meeting on Small Pelagic Fish Spawning Habitat Dynamics and the Daily Egg Production Method (DEPM). Report 22. Global Ocean Ecosystem Dynamics (GLOBEC), Plymouth Marine Laboratory, United Kingdom, 107 pp.

Checkley Jr., D.M., Ortner, P.B., Werner, F.E., Settle, L.E., Cummings, S.R., 1999. Spawning habitat of the Atlantic menhaden in Onslow Bay, North Carolina. Fisheries Oceanography 8, 22–36.

Cubillos, L.A., Ruiz, P., Claramunt, G., Gacitua, S., Nunez, S., Castro, L.R., Riquelme, K., Alarcon, C., Oyarzun, C., Sepulveda, A., 2007. Spawning, daily egg production, and spawning stock biomass estimation for common sardine (*Strangomera bentincki*) and anchovy (*Engraulis ringens*) off central southern Chile in 2002. Fisheries Research 86, 228–240.

Drapeau, L., 2005. Introduction to the use of quotient curves for characterizing spawning habitat of small, pelagic fish. In: van der Lingen, C.D., Castro, L., Drapeau, L., Checkley Jr., D. (Eds.), Report of a Global Ocean Ecosystem Dynamics – Small Pelagic Fishes and Climate Change Programme (GLOBEC-SPACC) Workshop on Characterizing and Comparing the Spawning Habitats of Small Pelagic Fish. Global Ocean Ecosystem Dynamics (GLOBEC), pp. 5–6. Report 21.

Gomon, M.F., Glover, C.J.M., Kuiter, R.H., 1994. The Fishes of Australia's South Coast. State Print, Adelaide, 992 pp.

Harris, G.P., Griffiths, F.B., Clementson, L.A., 1992. Climate and the fisheries off Tasmania – interactions of physics, food chains and fish. South African Journal of Marine Science 12, 585–597.

Harris, G., Nilsson, C., Clementson, L., Thomas, D., 1987. The water masses of the east coast of Tasmania: seasonal and interannual variability and the influence on phytoplankton biomass and productivity. Australian Journal of Marine and Freshwater Research 38, 569–590.

Heemstra, P.C., 2002. Emmelichthyidae. In: Carpenter, K.E. (Ed.), The Living Marine Resources of the Western Central Atlantic. FAO Species Identification Guide for Fishery Purposes, vol. 3. FAO, Rome, pp. 1475–1478. part 2.

Heemstra, P.C., Randall, J.E., 1977. A revision of the Emmelichthyidae (Pisces: Perciformes). Australian Journal of Marine and Freshwater Research 28, 361–396.

Hoese, D.F., Bray, D.J., Allen, G.R., Paxton, J.R., Wells, A., Beesley, P.L., 2007. Parts 1–3: Fishes. Zoological Catalogue of Australia, vol. 35. Zoological Catalogue of Australia Series, CSIRO Publishing /Australian Biological Resources Study (ABRS), Canberra, 2248 pp.

Ibaibarriaga, L., Irigoien, X., Santos, M., Motos, L., Fives, J.M., Franco, C., Lago De Lanzos, A., Acevedo, S., Bernal, M., Bez, N., Eltink, G., Farinha, A., Hammer, C., Iversen, S.A., Milligan, S.P., Reid, D.G., 2007. Egg and larval distributions of seven fish species in north-east Atlantic waters. Fisheries Oceanography 16, 284–293.

ICES, 2004. The DEPM estimation of spawning-stock biomass for sardine and anchovy. ICES Cooperative Research Report 268 91pp.

Jordan, A.R., Pullen, G., Marshall, J.A., Williams, H., 1995. The temporal and spatial patterns of spawning in jack mackerel, *Trachurus declivis* (Pisces: Carangidae), during 1988–1991 in eastern Tasmanian waters. Marine and Freshwater Research 46, 831–842.

Lasker, R., 1985. An Egg Production Method for Estimating Spawning Biomass of Pelagic Fish: Application to the Northern Anchovy, *Engraulis Mordax*. National Oceanic and Atmospheric Administration (NOAA) National Marine Fisheries Service (NMFS), United States Department of Commerce, Technical Report 36, 99 pp.

Larcombe, J., Begg, G. (Eds.), 2008. Fishery Status Reports 2007: Status of Fish Stocks Managed by the Australian Government. Bureau of Rural Sciences, Canberra, 294 pp.

Last, P.R., Scott, E.O.G., Talbot, F.H., 1983. Fishes of Tasmania. Tasmanian Fisheries Development Authority, Hobart, Tasmania, 563 pp.

van der Lingen, C.D., Castro, L., Drapeau, L., Checkley Jr., D. (Eds.), 2005. Report of a Global Ocean Ecosystem Dynamics – Small Pelagic Fishes and Climate Change Programme (GLOBEC-SPACC) Workshop on Characterizing and Comparing the Spawning Habitats of Small Pelagic Fish. Global Ocean Ecosystem Dynamics (GLOBEC), Plymouth Marine Laboratory, United Kingdom, Report 21, 33 pp.

van der Lingen, C.D., Hutchings, L., Merkle, D., van der Westhusien, J.J., Nelson, J., 2001. Comparative spawning habitats of anchovy (i) and sardine (*Sardinops sagax*) in the southern Benguela upwelling ecosystem. In: Krause, G.H. (Ed.), Spatial Processes and Management of Marine Populations. University of Alaska Sea Grant, Anchorage, Alaska, pp. 185–209. AK-SG-01-02.

Lo, N.C.H., Ruiz, Y.A.G., Cervantes, M.J., Moser, H.G., Lynn, R.J., 1996. Egg Production and Spawning Biomass of Pacific Sardine (*Sardinops Sagax*) in 1994, Determined by the Daily Egg Production Method. Report 37. California Cooperative Oceanic Fisheries Investigations (CalCOFI), La Jolla, California, pp. 160–174.

McLaughlin, K., 2006. Fishery Status Reports 2005: Status of Fish Stocks Managed by the Australian Government. Bureau of Rural Sciences, Canberra, 268 pp.

Neira, F.J., Keane, J.P., 2008. Ichthyoplankton-based spawning dynamics of blue mackerel (*Scomber australasicus*) in south-eastern Australia: links to the East Australian current. Fisheries Oceanography 17, 281–298.

Neira, F.J., Keane, J.P., Lyle, J.M., Tracey, S.R., 2008. Development of eggs and larvae of *Emmelichthys nitidus* (Percoidei: Emmelichthyidae) in south-eastern Australia, including a temperature-dependent egg incubation model. Estuarine Coastal and Shelf Science 79, 35–44.

Neira, F.J., Miskiewicz, A.G., Trnski, T., 1998. Larvae of Temperate Australian Fishes – Laboratory Guide for Larval Fish Identification. University of Western Australia Press, Nedlands, 474 pp.

Paul, L.J., 1997. A summary of biology and commercial landings, and stock assessment of rubyfish, *Plagiogeneion rubiginosum* (Hutton, 1875) (Percoidei: Emmelichthyidae). New Zealand Fisheries Research Document 97/27, 22 pp.

Priede, I.G., Watson, J.J., 1993. An evaluation of the daily egg production method for estimating biomass of Atlantic mackerel (*Scomber scombrus*). Bulletin of Marine Science 53, 891–911.

Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge, 537 pp.
Ridgway, K.R., 2007a. Seasonal circulation around Tasmania: an interface between eastern and western boundary dynamics. Journal of Geophysical Research 112, C10016, doi:10.1029/ 2006JC003898.
Ridgway, K.R., 2007b. Long-term trend and decadal variability of the southward penetration of the East Australian current. L13613. Geophysical Research Letters 34, doi:10.1029/2007 GL030393.
Smith, P.E., Flerx, W., Hewitt, R.P., 1985. The CalCOFI Vertical Egg Tow (CalVET) net. Technical Report 36. In: Lasker, R. (Ed.), An Egg Production Method for Estimating Spawning Biomass of Pelagic Fish: Application to the Northern Anchovy, *Engraulis mordax*. National Oceanic and Atmospheric Administration (NOAA) National Marine Fisheries Service (NMFS), pp. 27–32.
Stratoudakis, Y., Bernal, M., Ganias, K., Uriarte, A., 2006. The daily egg production method: recent advances, current applications and future challenges. Fish and Fisheries 7, 35–57.