DEPM-based spawning biomass of *Emmelichthys nitidus* (Emmelichthyidae) to underpin a developing mid-water trawl fishery in south-eastern Australia

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A R T I C L E   I N F O

A B S T R A C T

Spawning biomass of redbait, *Emmelichthys nitidus* (Emmelichthtyidae), was estimated using the daily egg production method (DEPM) based on egg and adult surveys conducted simultaneously off eastern Tasmania during October 2005 and 2006. Concurrent studies had confirmed that this mid-water, schooling species met all necessary requirements for DEPM-based biomass estimation, including (a) asynchronous oocyte development with release of pelagic eggs in batches; (b) spawned eggs could be assigned ages using a temperature-dependent incubation model; and (c) egg abundances follow the typical exponential decay model. Main spawning areas were identified between north-eastern Bass Strait (38.8°S) and south of the Tasman Peninsula (43.5°S) in 2005 (13220 km^2), and between Cape Barren Is. (40.5°S) and the same southern boundary in 2006 (8695 km^2). Daily egg production (P_0) was estimated by applying two statistical estimation methods to the egg abundance-at-age data, namely the traditional least squares non-linear regression (NLS) and a generalized linear model (GLM). Results indicated that the latter technique provided a better fit, resulting in improved CVs and AIC statistics over the NLS. The GLM-derived average P_0 was estimated at 4.04 eggs/0.05 m^2/day both in 2005 and 2006. Spawning biomass (CV) was ~87000 t (0.37) in 2005 and ~50800 t (0.21) in 2006, with the lower 2006 biomass largely due to a smaller spawning area and higher sex ratio. Estimates are likely to be negatively biased since spawning of *E. nitidus* probably extends as far north as southern New South Wales (35.0°S). In the absence of comparable studies on other emmelichthyids, P_0 and instantaneous egg mortality estimates are compared to those of clupeoid species previously subjected to DEPM, and the method discussed in terms of its suitability to this species in support of a developing mid-water trawl fishery in south-eastern Australia.

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1. Introduction

The daily egg production method (DEPM) has become a robust fishery-independent technique to estimate stock biomass of pelagic, batch-spawning fishes such as clupeids, engraulids and scombrids. Such spawning biomass estimates result from computing total daily egg production at spawning time in the survey area over the daily specific fecundity, i.e. number of eggs per population weight per day. The denominator comprises four adult parameters, namely sex ratio, spawning fraction, batch fecundity and female weight. Both total daily egg production at spawning time and spawning area derive from egg surveys over the presumed region where spawning takes place, while daily specific fecundity is estimated from reproductively active fishes taken concurrently within the same area surveyed for eggs (Lasker, 1985; Alheit, 1993; Priede and Watson, 1993; Lo et al., 1996; Watanabe et al., 1999; Stratoudakis et al., 2006; Cubillos et al., 2007; Bernal et al., 2011).

The DEPM has not previously been used to estimate spawning biomass of a representative of the Emmelichthyidae, a small family containing 15 marine species distributed in tropical to temperate regions of the Indo-Pacific, southern Pacific, eastern Atlantic and Caribbean Sea (Nelson, 2006; Stratoudakis et al., 2006). Of the two species recorded for Australia, *Emmelichthys nitidus*, or "redbait" as it is locally known, constitutes a small (to 36 cm) mid-water schooling species confined to shelf waters ≥30°S (Hoese et al., 2007; Gomon et al., 2008). A mid-water trawl fishery targeting this species along with *Trachurus declivis* developed rapidly off Tasmania in the early 2000s with catches reaching ~8000 t by 2004/05, most destined to feed farmed southern bluefin tuna (Wilson et al., 2010). The rapid expansion of the fishery in south-eastern Australia, coupled with the pressing need to develop a scientifically defensible harvest strategy, led to the development of an integrated study to evaluate the DEPM as a technique to estimate spawning biomass of *E. nitidus*. The study found this species to be a batch spawner with asynchronous oocyte development, with females releasing batches of pelagic eggs (1.00–1.05 mm) approximately once every three days during a brief period between late September and early November, i.e. the austral spring (Ewing and Lyle, 2009; Neira

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et al., 2009). The study also found that eggs could be assigned ages using a temperature-dependent incubation model based on seven distinct developmental stages (Neira et al., 2008). Combining all results, it was concluded that *E. nitidus* fitted the criteria required for the application of the DEPM, and that spawning biomass could therefore be estimated in the same manner to that obtained for pelagic clupeoids (e.g. Somarakis et al.,2002, 2004; Stratoudakis et al., 2006; Cubillos et al., 2007) and non-pelagic teleosts such as *Pagrus auratus* (e.g. Zeldis and Francis, 1998; Jackson et al., 2011).

In this paper we report the first DEPM-based spawning biomass estimates of *E. nitidus* off eastern Tasmania in south-eastern Australia, based on egg and adult parameters derived from mid-water trawls conducted during the peak spawning period of this species in 2005 and 2006. Daily egg abundance-at-age data were employed to compute daily egg production by fitting the traditional least squares non-linear regression model (Lo et al., 1996) and a generalized linear model (Cubillos et al., 2007). Spawning area was calculated from positive stations for each egg survey (Neira et al., 2009) while the four adult parameters derive from reproductive data based on adult redbait collections (Ewing and Lyle, 2009). Average daily egg production and derived biomass estimates are compared for the two models and overall results discussed in relation to the suitability of this egg-based approach to estimate spawning biomass for this species.

2. Materials and methods

2.1. Study area

The study area comprised the continental shelf region from 38.8°S in eastern Bass Strait (north east of Flinders Is.) around southern Tasmania to 43.5°S off the south-west coast (Port Davey) (Fig. 1). The shelf along this region is somewhat narrow, decreasing in width from about 33 nautical miles (nm) at 39.7°S off northern Flinders Is. to 7 nm at 43.2°S off the Tasman Peninsula, before widening to 32 nm at 147°E off southern Tasmania. Oceanographic conditions over the eastern Tasmanian shelf are driven by the southward-flowing East Australian Current (EAC), a major western boundary oceanic feature which forms in the Coral Sea and reaches the south-eastern coast when at its peak intensity during the austral summer. Conditions during October 2005 and 2006 reflected a mixture of three water masses, i.e. warm, saline water to the north derived from the onset of EAC incursion, Tasman Sea water along the inner shelf and cooler subantarctic water to the south (Ridgway, 2007a,b; Neira et al., 2009). Composite sea surface temperature images from the time of the egg and adult surveys showed Tasman Sea water along the inner shelf (12–14 °C) and EAC-derived warmer water along the outer shelf (15–16 °C), with a longitudinal front between these two masses clearly defined along the shelf break both in 2005 and 2006 (see Fig. 2 in Neira et al., 2009). Field-derived average water temperatures off eastern Tasmania (average of medians to 100 m or to maximum depth if <100 m) ranged between 12.2 and 13.6 °C in both 2005 and 2006. In contrast, average temperatures off southern Tasmania in 2006 were lower than those along the eastern shelf, i.e. 11.7–11.9 °C (Neira et al., 2009).

2.2. Adult data

Adult *E. nitidus* were sampled from commercial mid-water trawl catches taken during the 2005 and 2006 spawning seasons (September to October) at depths of 100–140 m along the shelf break off eastern Tasmania (Fig. 1). Catches were obtained mainly at night when the species formed large aggregations, as opposed to daytime when fish tended to be dispersed and difficult to catch. Random samples of 100–200 individuals from selected trawl shots were frozen immediately after capture and thawed in the labora-
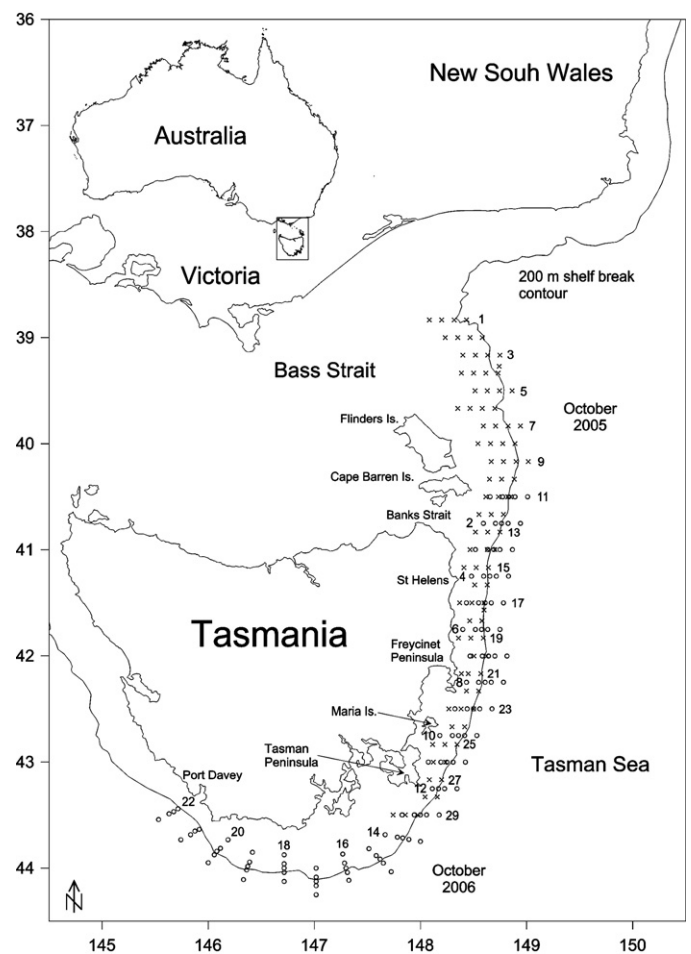

Fig. 1. Map of south-eastern Australia showing stations sampled during egg surveys off north-eastern to south-western Tasmania in October 2005 (crosses) and October 2006 (open circles). For clarity, transects have been numbered on a southerly direction using odd (2005) and even (2006) numbers, respectively.

tory. Each of these was weighted (total weight ±1 g) and sex, gonad weight and maturity stage recorded, and the data employed to estimate average mature female weight (W) and sex ratio (R) by weight. Females deemed as mature comprised those with developing (stage III), hydrated (IV) or running ripe (V) ovaries, based on the macroscopic six-stage criteria of Mendonca et al. (2006) and adapted to *E. nitidus* by Ewing and Lyle (2009).

In addition randomly selected females from most of the sampled trawl shots were dissected immediately after capture and at least 30 mature females either measured and weighted fresh (±1 g) and their ovaries removed and preserved in FAACC (10% formalin, 5% glacial acetic acid and 1.3% calcium chloride) (2005), or preserved whole (2006) (Ewing and Lyle, 2009). Preserved ovaries were processed to compute spawning fraction (S) and to determine batch fecundity (F). These samples also contributed to the estimation of average female weight (W) but were excluded from sex ratio estimation. Population adult parameters and sample variances were determined using the ratio estimator of Picquelle and Stauffer (1985).

The average mature female weight by year was estimated for each trawl sample and the population average weight of mature females (W) was calculated from the sample means weighted by sample size (Ewing and Lyle, 2009). Population sex ratio (R), i.e. proportion of females in the population by weight, was estimated for each year by employing the whole weights of mature females divided by the total weight of mature males and females in each
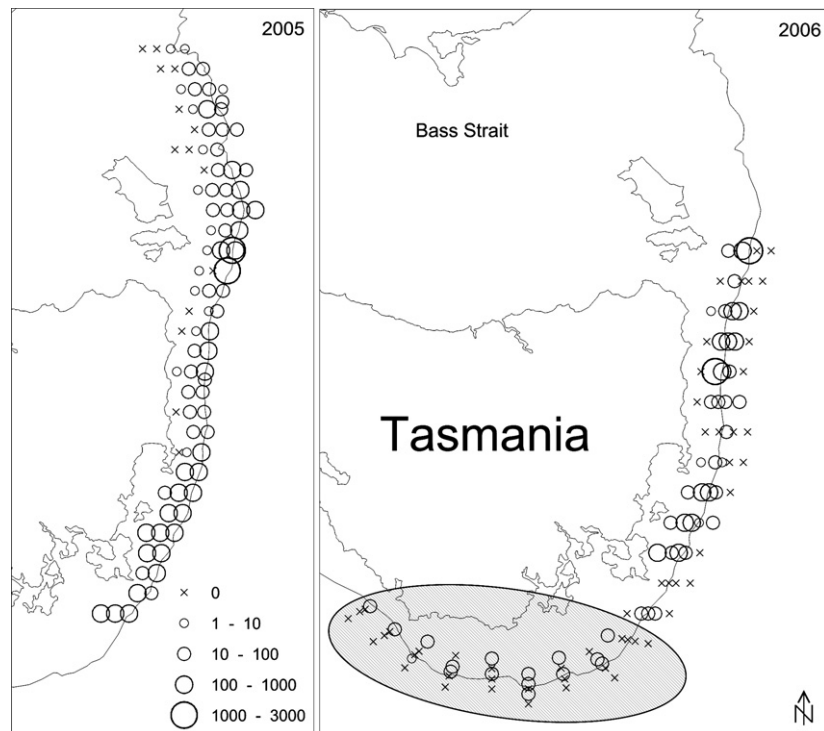
Fig. 2. Distribution of eggs (numbers per m²) of *Emmelichthys nitidus* in shelf waters along eastern Tasmania in October 2005 and October 2006. Circled area off southern Tasmania in 2006 was excluded from the estimation of spawning area (refer to text for details). Negative stations (×) are shown in both plots.

trawl sample, weighted by sample size (Parker, 1985; Cubillos et al., 2007).

Batch fecundity was estimated for fish with hydrated oocytes but no post-ovulatory follicles (POFs), as confirmed by histological examination. Hydrated oocytes were removed from three 100 mg sections taken from the mid region of the ovary, and counts subsequently employed to obtain a mean fecundity estimate using the gravimetric method of Hunter et al. (1985); estimates were rejected if the CV between the three estimates exceeded 10%. The resultant linear model of batch fecundity against ovary-free weight was $F = -2479.1 + 186.43 W_f$, where W_f corresponds to ovary-free weight (Ewing and Lyle, 2009). For each sampled trawl shot, the average mature female weight was converted to ovary-free weight using a linear regression of total weight against ovary-free weight. The batch fecundity relationship was then applied to the ovary free weights to generate average batch fecundity for each shot. The population batch fecundity (F) for each year was calculated from the sample means weighted by sample size.

Population spawning fraction (S) was estimated separately for the 2005 and 2006 spawning seasons by Ewing and Lyle (2009) using standard histological techniques and three criteria based on the presence and/or absence of advanced oocyte and POF stages. In this study we employed estimates derived from females exhibiting hydrated oocytes and/or fresh (<1 day old) POFs, i.e. fish undergoing spawning at the time of capture. This criterion was regarded by Ewing and Lyle (2009) as to best fit *E. nitidus*, with the other two criteria, i.e. early-spawning fish showing migratory nucleus and/or early hydrated oocytes and fresh POFs, and recently spawned fish with fresh POFs but no hydrated oocytes, thought to either overestimate or underestimate spawning fraction.

2.3. Egg surveys

Egg surveys were carried out during 12–17 October 2005 and 10–31 October 2006 to coincide with the peak spring spawning season of *E. nitidus* in eastern Tasmania. The 2005 survey covered

waters from 38.8°S (north-eastern Bass Strait) to 43.5°S (Tasman Peninsula) off eastern Tasmania, corresponding to a distance of approximately 308 nm. The 2006 survey covered from 40.5 to 43.5°S as well as south and westwards from 43.5°S to 43.5°S in south-western Tasmania, equivalent to an approximate distance of 325 nm (Fig. 1). Design rationale of each survey, location of stations as well as sampling and laboratory procedures, are described in Neira et al. (2009). In general, sampling effort in the two years was focused predominantly over the continental shelf, including along the shelf break, with stations located along a series of transects perpendicular to the coastline and 10 nm apart. A total of 9280 and 1113 eggs of *E. nitidus* were collected during the 2005 and 2006 surveys, respectively, with positive stations accounting for 85% of the 91 stations sampled in 2005 and 50% of the 107 stations sampled in 2006 (Neira et al., 2009).

2.4. Spawning area

Dimensions of spawning areas in 2005 and 2006, i.e. positive area in km², were estimated using ArcView GIS 3.2. For each survey a 5 nm diameter circle was drawn around each sampling station, based on the distance between stations across each transect, and each assumed to have the same weighting. A closed polygon was then drawn over the entire surveyed area encompassing positive (i.e. with eggs) as well as negative stations embedded between positive stations, and that area considered as the spawning area (A). All negative stations outside the positive area were omitted from spawning area calculations. Thus, the 2005 spawning area included the entire area surveyed (15650 km²) apart from seven negative stations positioned along the periphery. By contrast, the calculation of the 2006 spawning area did not include the entire area surveyed (21350 km²) but was restricted to the region between the northernmost transect off Cape Barren Island (40.5°S) and the southernmost transect off Tasman Peninsula (43.5°S) off south-eastern Tasmania, where the bulk of the spawning activity was identified to have concentrated (Neira et al., 2009). The rationale behind exclud-

ing southern Tasmania from the area calculation was based on several reasons, including the abrupt decline in egg abundances south and westwards of 43.5°S (Figs. 1 and 2) during the 2006 survey (Neira et al., 2009), and evidence of the existence of discrete eastern and western spawning stocks that separate off southern Tasmania, based largely on reproductive data (Ewing and Lyle, 2009). Furthermore, examination of the highest concentrations of day-1 eggs indicated that the bulk of the spawning activity of *E. nitidus* both in October 2005 and 2006 took place around 40.5–41.5°S in northeastern Tasmania, while the exceptionally few day-1 eggs found just south of 43.5°S in October 2006 ($n = 5$) were more likely to have been advected with the prevailing southward current at the time of sampling (Neira et al., 2009). Consequently, calculation of the 2006 spawning area was based on the eastern survey area (12924 km²) excluding 17 outer negative stations.

2.5. Mean daily egg production

Eggs were separated into seven developmental stages, and each stage assigned an age (days) using the deterministic stage-to-age model described by Neira et al. (2008), i.e. $y = 35.911 \exp[-(0.155t + 0.262i)]i^{2.436}$, which was considered as the most appropriate to describe variability of mean egg ages (y) with temperature (t) and stage (i) for this species.

Eggs abundances at age were assumed to follow the exponential decay model of Picquelle and Stauffer (1985):

$$P_t = P_0 \exp(-Zt) \tag{1}$$

where P_t corresponds to the number of eggs at age t, P_0 the daily egg production by unit area (eggs/0.05 m²/day) at time 0, and Z the daily rate of instantaneous mortality (day⁻¹). The model assumes all eggs to be spawned and instantaneously fertilized at a specific time, and affected by a constant exponential mortality rate, with daily egg abundance-at-age data in each sample to be independent observations from a population with a common P_0 and Z (Stratoudakis et al., 2006). Datasets for the 2005 and 2006 runs comprised egg counts grouped by daily cohorts per station and standardized to area, with egg ages (days) assigned with the temperature-dependent egg incubation model. Computing of egg ages from stages used the median water temperature of each station and local time (hour) of collection. For the purpose of determining daily cohorts, peak spawning hour was assumed to be 21:00 h based on adult reproductive data indicating that spawning was more or less completed by midnight (Ewing and Lyle, 2009). Eggs assigned ages of <4 h old and those with >98% probability of being hatched at the mean station temperature were omitted from P_0 and Z estimations. Exclusion of these extreme cohorts follows current DEPM protocols associated to biases caused by the under-sampling of newly spawned eggs near peak spawning, and/or the reduced probability of encountering small, highly concentrated patches of newly spawned eggs, as well as the high probability of under-sampling eggs close to hatching age (Hunter and Lo, 1997; Somarakis and Tsimenides, 1997; ICES, 2004; Braun et al., 2005; Stratoudakis et al., 2006; Cubillos et al., 2007).

Two statistical procedures were applied to the daily egg abundance-at-age data to estimate P_0, namely the traditional weighted least squares non-linear regression (NLS) technique (Lo et al., 1996), and a generalized linear model (GLM) that employed natural logarithm as a link function and assumed a negative binomial error distribution (Bernal et al., 2001; Cubillos et al., 2007). Functions for the two techniques are available in the library packages STATS and MASS in R (Ihaka and Gentleman, 1996; www.r-project.org). Egg abundance data employed in model runs included all positive stations as well as embedded negative stations within spawning area. Data for each station included each of the seven egg stages (Neira et al., 2008) even if catches were not

recorded for a particular stage(s) at a given station, i.e. all zeros were considered in the analyses (G. Claramunt, Universidad Arturo Prat, Chile, *pers. comm.*). For the GLM, log P_0 and Z correspond to the intercept and slope, respectively. Weighted mean P_0 estimates from both fitting techniques were obtained by multiplying the unweighted values (intercept for NLS and exponential of intercept for GLM) by the ratio of spawning/total survey area for each year. The same applied to the weighted coefficient of variation (CV) of the P_0 estimates. For the two techniques the CVs for Z were calculated by dividing the standard error by the absolute Z value. Log-transformed egg abundances at positive stations (eggs/m² + 1) were plotted against respective ages (days) of daily cohorts for 2005 and 2006.

2.6. Spawning biomass model

Spawning biomass (B, tonnes) was estimated using the equation of Parker (1985):

$$B = \frac{P_0 A k}{R F S / W_f} \tag{2}$$

where P_0 is egg production; A the spawning area (km²); k a factor to convert grams to tonnes; R the fraction of mature females by weight (sex ratio); F the batch fecundity (number of oocytes released per mature female per batch); S the spawning fraction (proportion of mature females spawning each day); and W the mean weight of mature females in the population (g). Variance of each biomass estimate, which was subsequently employed to calculate standard deviation (SD), was computed using Parker's (1985) modified equation:

$$\mathrm{Var}(B) = B^2 * \left(\frac{\mathrm{Var}P_0}{P_0^2} + \frac{\mathrm{Var}W}{W^2} + \frac{\mathrm{Var}R}{R^2} + \frac{\mathrm{Var}F}{F^2} \right.$$
$$\left. + \frac{\mathrm{Var}S}{S^2} + 2\{\mathrm{COVS}\} \right)$$

where $COVS$ corresponds to the sum of terms involving the covariance (Cov) of each adult parameter, in this case:

$$\mathrm{COVS} = \left\{ \frac{-\mathrm{Cov}(WR)}{WR} - \frac{\mathrm{Cov}(FW)}{FW} - \frac{\mathrm{Cov}(WS)}{WS} + \frac{\mathrm{Cov}(RF)}{RF} \right.$$
$$\left. + \frac{\mathrm{Cov}(RS)}{RS} + \frac{\mathrm{Cov}(FS)}{FS} \right\}$$

3. Results

3.1. Adult parameters

Parameter estimates and respective CVs of average female weight (W), batch fecundity (F), female sex ratio (R) and spawning fraction (S) of *E. nitidus* are provided in Table 1. Daily specific fecundity was higher in 2006 than in 2005, i.e. 20.6 vs. 14.3 eggs g/day, with mature females sampled that year being both slightly heavier (78.3 vs. 71.7 g) and more fecund (11441 vs. 10894 oocytes). In addition, sex ratio was likewise greater in 2006 (0.44) than 2005 (0.30) while average spawning fraction remained at 0.32 in both years, i.e. approximately once every three days. The CVs for each adult parameter was greater in 2005, linked to the inherent variability between samples as well as the lower number of sample tows carried out that year.

3.2. Egg distributions and spawning areas

Eggs occurred along the entire eastern Tasmanian shelf area surveyed in October 2005 and 2006, but were scarce around the

Table 1
Population average estimates and respective CVs of female sex ratio (R), spawning fraction (S), mature female weight (W; g) and batch fecundity (F) for *Emmelichthys nitidus* from eastern Tasmania during the 2005 and 2006 spawning seasons. Number of trawl samples and total number of fish examined (in brackets) are indicated (data based on Ewing and Lyle (2009)).

Year	Parameter	No. samples (fish)	Population average	CV
2005	R	8 (822)	0.30	0.19
	S	8 (229)	0.315	0.23
	W	8 (507)	71.73	0.19
	F	8 (507)	10894	0.24
2006	R	20 (1934)	0.44	0.05
	S	12 (436)	0.321	0.14
	W	20 (1507)	78.28	0.06
	F	20 (1507)	11441	0.09

southern shelf in October 2006 (Fig. 2). Abundances averaged 133 and 103 eggs/m^2 in 2005 and 2006, respectively, the greatest abundances occurring along shelf break stations at 40.5°S in 2005 (1953 eggs/m^2) and south of 41.2°S in 2006 (2644 eggs/m^2). Spawning areas in 2005 and 2006 were estimated at 13220 km^2 and 8695 km^2, respectively, comprising 84.5% and 67.3% of the respective surveyed areas considered for the purpose of biomass estimation (Fig. 2 and Table 2).

3.3. Daily egg production

Egg abundances plotted against respective estimated ages (days) for 2005 and 2006 followed the typical exponential decay model described for pelagic eggs (Fig. 3). The NLS estimates of P_0, Z and total egg production for 2005 were substantially higher and less precise than those obtained with the GLM technique. By contrast, the three parameter estimates in 2006 were very similar regardless of fitting technique, although the NLS estimates were less precise (Table 2). Considering each fitting technique separately, estimates of the above three parameters were consistently higher in 2005 with the exception of the GLM-based P_0 which was consistent between years, i.e. 4.0 eggs/0.05 m^2/day (Table 2). Model diagnostic plots associated to the GLM runs (not presented here) showed randomly scattered values with a slight negative trend (residuals vs. predicted values), and a linear relationship (SD residuals vs. the-

Table 2
Spawning areas (km^2), average sex ratio (R) and spawning biomass estimates (tonnes) of *Emmelichthys nitidus* for shelf waters of eastern Tasmania in 2005 and 2006. Data for sex ratio (R) comprise average and CVs (in brackets); average batch fecundity (F), spawning fraction (S) and weight (W) in 2005 and 2006 are provided in Table 1. Estimates of weighted mean daily egg production (P_0) and total egg production, as well as spawning biomass and respective CVs (in brackets) for positive spawning areas are provided for the NLS and GLM techniques.

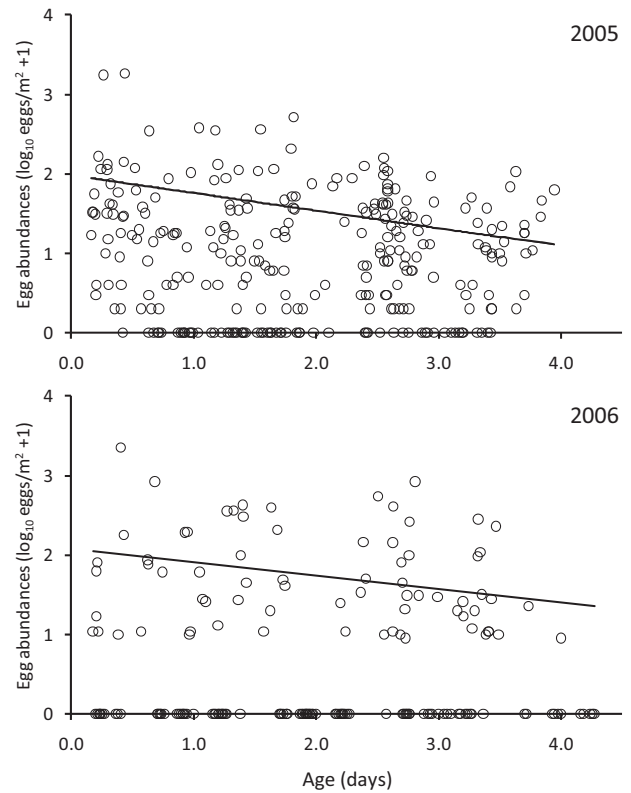| Input data	October 2005	October 2006
DEPM survey area/spawning area (km^2)	15650/13220	12924/8695
Total stations/number of stations included	91/84	64/47
Non-linear least squares (NLS)		
Weighted P_0 (eggs/0.05 m^2/day) (CV)	6.66 (0.32)	3.81 (0.50)
Total egg production (eggs $\times 10^{12}$)	2.08	0.98
Z (day^{-1}) (CV)	1.01 (0.37)	0.36 (0.73)
Akaike Information Criterion (AIC)	3633	2369
Spawning biomass (tonnes) (CV)	143434 (0.47)	47802 (0.51)
Standard deviation	67971	24430
GLM – negative binomial error distribution		
Weighted P_0 (eggs/0.05 m^2/day) (CV)	4.04 (0.14)	4.05 (0.19)
Total egg production (eggs $\times 10^{12}$)	1.26	1.05
Z (day^{-1}) (CV)	0.53 (0.20)	0.39 (0.57)
Dispersion parameter for negative binomial (θ)	0.292	0.088
Akaike Information Criterion (AIC)	2272	1085
Spawning biomass (tonnes) (CV)	86,994 (0.37)	50,782 (0.21)
Standard deviation	32594	10939

Fig. 3. Age-specific egg production of *Emmelichthys nitidus* (log-transformed eggs/m^2 + 1) in shelf waters off eastern Tasmania in October 2005 and October 2006. Curve in each scatterplot corresponds to the superimposed fitted mortality curve derived from GLM assuming a negative binomial error distribution.

oretical quantiles) with some degree of under-dispersion both in 2005 and 2006, indicating less variability in the data than that predicted by the GLM (dispersion parameters and AICs are provided in Table 2).

3.4. Spawning biomass estimates

The 2005 spawning biomass computed using NLS-derived P_0 was 60% greater than that obtained with the GLM, i.e. 143400 vs. 87000 t. By contrast, the 2006 spawning biomass estimates were almost identical in magnitude for both fitting techniques, i.e. 47800 and 50800 t (Table 2). The CVs were substantially lower in both years for the GLM estimates, i.e. 0.21–0.37 compared to 0.47–0.51 obtained for the NLS-based estimates. This result, along with AIC statistics (Table 2), confirmed that the GLM technique provided a better model fit to the data. Spawning biomass per area based on this preferred model was relatively consistent between years, i.e. 5.8–6.6 t/km^2.

4. Discussion

4.1. Daily egg production

This study provides the first spawning biomass estimates of *E. nitidus* and constitutes the only available to date for a member of the family Emmelichthyidae worldwide. While the DEPM has traditionally been employed to estimate spawning biomass of small clupeoids and scombrid mackerels (e.g. Alheit, 1993; Watanabe et al., 1999; Cubillos et al., 2007), its successful application during this case study to a non-clupeoid, predominantly mid-water species resulted from strategically planned egg and adult surveys conducted simultaneously during the peak spawning period. In
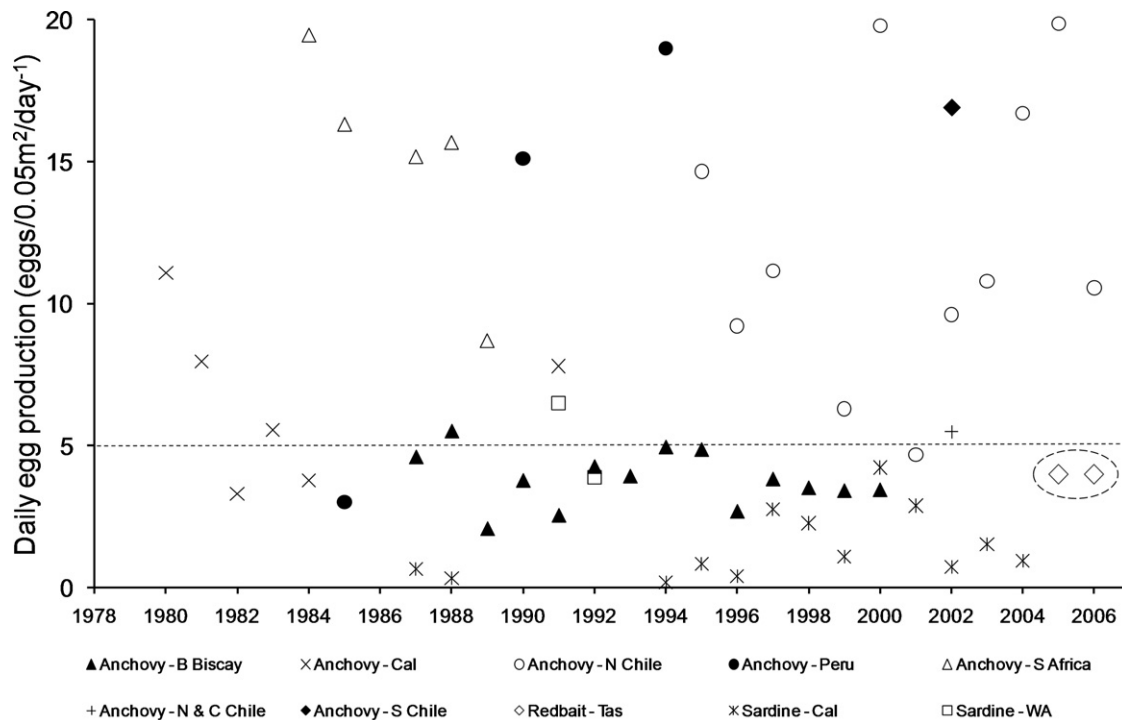
Fig. 4. Comparison of mean daily egg production (P_0; eggs/0.05 m^2/day) across selected pelagic fish taxa from different localities in different years; circled values correspond to P_0 estimates for *E. nitidus* in eastern Tasmania while dashed line at the 5 level is shown for reference. Abbreviations: C, central; Cal, California; N, northern; S, southern; WA, Western Australia.

Sources: anchovy Bay of Biscay – Somarakis et al. (2004; 1987–1990) and ICES (2004; 1990–2000); anchovy California, Peru and South Africa – Somarakis et al. (2004) and references therein; 1991 anchovy California – Cotero-Altamirano and Green-Ruiz (1997); anchovy Northern Chile – Claramunt et al. (2007); 2002 anchovy northern/central and southern Chile – Cubillos et al. (2007); sardine California – Lo et al. (1996; 1987 and 1988) and Lo and Macewicz (2004; 1994–2004); sardine Western Australia – Fletcher et al. (1996).

view of the lack of comparable DEPM-based biomass assessments on other emmelichthyids, results of this study are to some extent contrasted with information available on clupeoids and scombrids, particularly regarding the key parameters needed to compute spawning biomass estimates.

Egg mortality curves obtained for *E. nitidus* followed the typical exponential decay model described for eggs of pelagic clupeoids (Hewitt, 1985; Shelton et al., 1993; Lo et al., 1996; Kim and Lo, 2001; Lo and Macewicz, 2004; Stratoudakis et al., 2006; Cubillos et al., 2007). In terms of average mean daily egg production (P_0), the GLM technique provided a better fit to the daily egg abundance-at-age data than the NLS technique, as evidenced by the improved CVs and AIC statistics. Such findings support the current trend in DEPM application to depart from the traditional NLS approach, with GLMs considered better in describing the decline in egg abundances of daily cohorts in small pelagic fishes (Stratoudakis et al., 2006; Claramunt et al., 2007; Cubillos et al., 2007). Moreover, the GLM accounts for variability of egg production at early ages better than the NLS, resulting in P_0 values with lower associated variances (Claramunt et al., 2007; Cubillos et al., 2007). In addition, the exclusion of *E. nitidus* eggs assigned ages ≤4 h and ≥98% of incubation time resulted in improved goodness of fit for the GLM runs, as evidenced by the dispersion parameters compared to those obtained from runs incorporating all data (results not presented here).

The GLM-based P_0 estimates for *E. nitidus* were essentially the same in both years, i.e. 4.0 eggs/0.05 m^2/day, indicating an overall consistency in spawning effort within the areas surveyed in October 2005 and 2006. However, total egg production (eggs × 10^{12}) was greater in 2005 (1.26) than in 2006 (1.05) reflecting the larger spawning area in the former year. The consistency in P_0 estimates is likely to reflect the similarity in environmental conditions observed over the spawning area in both years, especially the overall nar-

row range of average water temperatures recorded along the shelf break, i.e. 13.4–13.7 °C (Neira et al., 2009).

Compared to other small pelagic species worldwide, average P_0 levels estimated for *E. nitidus* lie within the range of those reported for species such as *Engraulis encrasicolus* in Bay of Biscay and *Sardinops sagax* from California, i.e. 0.2–5.5 eggs/0.05 m^2 day^{-1}. However, they fall well below values typically recorded for *Engraulis* spp. in California, Chile, Peru and South Africa, i.e. 5.0–20.0 eggs/0.05 m^2/day (Fig. 4; refer to references under figure caption). In terms of daily instantaneous egg mortality rate, Z values obtained from the GLM technique for 2005 (0.53) and 2006 (0.39) fall well within those reported for various clupeoid species, including *Engraulis* spp. and *S. sagax* (Alheit, 1993; Shelton et al., 1993; Kim and Lo, 2001; Somarakis et al., 2004; Cubillos et al., 2007).

4.2. Spawning biomass

Biomass estimates of *E. nitidus* off eastern Tasmania varied substantially between P_0 fitting techniques and years, with those obtained in 2005 (143400 vs. 87000 t) differing by nearly 65% in magnitude compared to those in 2006 (47800 vs. 50800 t). Such conspicuous difference between the NLS and GLM-based biomass outputs in 2005 can be attributed to the influence of the greater NLS-derived P_0, i.e. 6.66 cf. 4.04 eggs/0.05 m^2/day. Furthermore, biomass estimates were consistently less precise using the NLS technique, a fact presumably linked to the greater variability of the NLS-derived P_0 estimate. These findings are consistent with Monte Carlo simulations indicating that nearly 80% of the variance in spawning biomass estimates is linked to the P_0 variance (G. Claramunt, Arturo Prat University, Chile, *pers. comm.*). In any case, the CVs associated with our GLM-based estimates (21–37%)

support the generalization that DEPM-based spawning biomass estimates tend to be rather imprecise though potentially unbiased (Stratoudakis et al., 2006).

Despite the consistency in P_0 and spawning fraction (S) across years, the GLM-based spawning biomass for 2006 (∼50800 t) was about 58% of that in 2005 (∼87000 t), a finding attributable to the combined effects of a higher sex ratio (0.44 cf. 0.30) and a smaller spawning area in 2006 (66% of that in 2005). However, such estimates do not appear to be statistically different if we consider the relatively low precision of the 2005 estimate, i.e. CV = 0.37.

4.3. Fishery implications and future DEPM assessments

Spawning biomass estimates provided in this study are considered negatively biased measures of total stock abundance given that they were derived from areas likely to cover less than half of the actual spawning area of *E. nitidus* in south-eastern Australia. Supporting evidence for a significantly larger spawning area, and hence a larger spawning stock, comes from the presence of eggs and larvae north of the survey area along shelf waters off southern New South Wales (NSW; 35–38°S) in October 2002 and 2003 (Neira et al., 2009), and the fact that no spawning boundary could be identified north of 38.8°S during the 2005 egg survey. By contrast, the effective southern spawning boundary was located just south of the Tasman Peninsula (43.5°S), as indicated by the abrupt decline in eggs and larvae of this species around southern Tasmania (Neira et al., 2009).

Findings of this study indicate that *E. nitidus* is a suitable species for the application of the DEPM. Besides fulfilling essential criteria in terms of adult reproductive biology (Ewing and Lyle, 2009), *E. nitidus* have a temporally discrete spawning period, with spawning occurring along a well-defined area along the continental shelf break. In addition, the pelagic eggs are easily collected and identified, and can be staged and subsequently assigned ages using a temperature-dependent incubation model (Neira et al., 2008). Furthermore, mortality of egg cohorts follows the typical exponential decay curve described for eggs of other small pelagic fishes (Stratoudakis et al., 2006; Cubillos et al., 2007), implying that eggs of different ages are being sampled with similar probabilities of occurrence. At present, the GLM technique appears to be adequate to estimate P_0 since it better handles the variability inherent to DEPM input parameters derived from data-limited situations such as in this case study. However, in future techniques such as general additive models (GAMs) could also be tested to ascertain whether precision in P_0 estimates can be improved (ICES, 2004; Castro et al., 2005; Stratoudakis et al., 2006; Bernal et al., 2011b). Additional ways to improve precision of P_0 estimates should also be investigated, including adaptive sampling, and the use of yolk-sac larvae to better anchor the upper end of the egg mortality curve (Hunter and Lo, 1997).

The current fishery situation for *E. nitidus* off Tasmania is that of a relatively small, low-value and developing mid-water trawl fishery involving very few operators. As such, a critical component of the harvest strategy recently implemented for this fishery is the application of DEPM-based biomass assessments on which to base total allowable catches (AFMA, 2008). Recognising this need, this study has provided a basis for the design and implementation of future DEPM surveys, as well as providing important baseline information about the size of the *E. nitidus* stocks off southeastern Australia. However, of significant importance to the further development of this fishery will be the balance between operational costs and low product value, and the ability of industry to support the high costs of assessment research. Consequently, extensive and regular egg/adult surveys normally justified for large-scale pelagic fisheries are unlikely for this species. Thus even if infrequent, low-sampling intensity surveys are conducted, future

DEPM-based biomass assessments of *E. nitidus* in south-eastern Australia would need to consider a number of logistic issues to increase precision of biomass estimates, including optimising egg survey design and the fact that commercial-scale, mid-water trawling appears to be the only feasible method to sample spawning adults.

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