

Fisheries

Spawning biomass of Sardine, *Sardinops sagax*, in waters off South Australia in 2025



Ivey, A. R., Grammer, G. L. and Earl, J.

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PO Box 120 Henley Beach SA 5022

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Report to PIRSA Fisheries and Aquaculture



Government
of South Australia

Department of Primary
Industries and Regions



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TABLE OF CONTENTS

EXECUTIVE SUMMARY	1
1. INTRODUCTION	2
1.1. Daily Egg Production Method.....	2
1.2. Rationale, objective and approach	2
2. METHODS.....	3
2.1. Study area and biophysical variables	3
2.2. Mean daily egg production and spawning area	5
2.3. Adult reproductive parameters	8
2.4. Spawning biomass.....	10
2.5. Sensitivity analysis.....	11
2.6. Quality assurance and quality control of data.....	11
3. RESULTS	12
3.1. Distribution and abundance of eggs.....	12
3.2. Biophysical variables	13
3.3. Spawning area.....	17
3.4. Mean daily egg production (P_0).....	18
3.5. Adult parameters	20
3.6. Spawning biomass.....	20
3.7. Sensitivity analysis.....	22
4. DISCUSSION	24
4.1. Egg distribution and environmental factors	24
4.2. Spawning area and mean daily egg production.....	25
4.3. Adult reproductive parameters	26
4.4. Spawning biomass.....	27
REFERENCES	28
APPENDIX 1: ANNUAL AND ALL-YEARS PARAMETERS FOR ESTIMATES OF SPAWNING BIOMASS	32
APPENDIX 2: SARDINE EGG DENSITY AND SEA SURFACE TEMPERATURE, 2018 TO 2025.....	33

LIST OF FIGURES

Figure 1. Map of South Australia showing sites where plankton samples were collected during 2025.....	4
Figure 2. Voronoi nearest neighbour polygons used to estimate the total spawning area in 2025.....	7
Figure 3. Densities of live Sardine eggs at sites sampled off South Australia from February to April 2025.	12
Figure 4. Sea surface temperatures overlaid with densities of live Sardine eggs at sites sampled off South Australia from February to April 2025.....	13
Figure 5. Surface concentration of chlorophyll- <i>a</i> overlaid with densities of live Sardine eggs at sites sampled from February to April 2025.	14
Figure 6. Surface salinity overlaid with densities of live Sardine eggs at sites sampled during February and April 2025.	15
Figure 7. Density of common zooplankton and phytoplankton taxa (displayed in mL.m ⁻²) overlaid with densities of live Sardine eggs at sites sampled from February to April 2025.....	16
Figure 8. Sampling area (open triangles) and spawning area (closed circles) over the history of DEPM surveys in South Australia.....	17
Figure 9. Models fitted to egg densities (eggs.m ⁻²) and egg age (hours) of Sardine cohorts in 2025 (A) and all years combined (1998 to 2025; B). Solid grey horizontal line: mean daily egg density, dashed grey horizontal line: mean total egg density.	19
Figure 10. Estimates of spawning biomass (95% CI) for Sardine in South Australian waters from 1995 to 2025 using the log-linear egg production model and all-years data for all parameters, except for spawning area (<i>A</i>).	21
Figure 11. Sensitivity plots showing effects of variability in adult parameters and egg production on estimates of spawning biomass..	23

LIST OF TABLES

Table 1. Total area surveyed and spawning area (A) estimated in 2025.	17
Table 2. Mean daily egg production (P_0) and instantaneous daily mortality (Z) estimated by fitting the log-linear model and GLM NB1 to all data collected from 1998 to 2025. 18	
Table 3. Mean daily egg production (P_0) and instantaneous daily mortality (Z) estimated by fitting using the log-linear model and GLM NB1 to data solely collected in 2025....	18

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EXECUTIVE SUMMARY

This report provides an estimate of the spawning biomass of Sardine, *Sardinops sagax*, in waters off South Australia during February–April 2025. The estimate of spawning biomass obtained using the Daily Egg Production Method (DEPM) is the key performance indicator for determining the status of the Southern Australia stock of Australian Sardine.

An ichthyoplankton survey was conducted during February–April 2025. The survey area included the sites added in 2023 to the south-east of Kangaroo Island and extended transects in the central Great Australia Bight (GAB), as well as the sites added in 2020. The total survey area was 140,900 km². Live Sardine eggs were collected at 333 of 414 (80.4%) sites. The total spawning area (*A*) in 2025 was 114,640 km².

Mean daily egg production (P_0 , 95% CI) was 88.7 (80.8–97.3) eggs.day⁻¹.m⁻². P_0 was estimated using the linear version of the exponential mortality model and all data combined from 1998 to 2025. Estimates of adult parameters (95% CI) calculated from all data obtained between 1998 and 2024 were: sex ratio (*R*): 0.53 (0.50–0.56); spawning fraction (*S*): 0.111 (0.100–0.122); and relative fecundity (F'): 308.4 (307.2–309.6) eggs.g⁻¹.

Sensitivity analyses showed the effects of inter-annual variability in parameters (i.e. P_0 , *R*, *S* and F') on the estimate of spawning biomass for 2025 and demonstrated the benefits of using adult parameter estimates obtained from historical data to estimate spawning biomass.

The estimate of spawning biomass (95% CI) of Sardine for 2025 was 556,957 t (474,724–639,191), which was above the upper target reference point of 200,000 t set in the harvest strategy for the South Australian Sardine Fishery. On this basis, the Southern Australia stock of Australian Sardine is classified as **Sustainable**. This classification is consistent with the findings of the spawning biomass report for 2024, the stock assessment report for 2023 and the most recent report in the Status of Australian Fish Stocks (2024).

The estimate of spawning biomass of Australian Sardine for 2025 does not account for potential effects of the algal bloom that first occurred in coastal waters off the Fleurieu Peninsula in March 2025 and expanded to Investigator Strait, Gulf St Vincent and Spencer Gulf during April–October 2025 on the Southern Australia stock of Australian Sardine. Notably, (1) extensive and widespread mortalities of finfish, elasmobranchs, cephalopods, and crustaceans have been reported, but not for Australian Sardine, and (2) substantial changes in fisher behaviour, catches and effort have occurred in 2025 (SARDI unpublished data). An assessment of impacts of the algal bloom on South Australia's fish stocks is scheduled for 2025/26 with funding from the South Australian and Australian Governments.

Keywords: Sardine, Spawning Biomass, South Australia, Daily Egg Production Method.

1. INTRODUCTION

1.1. Daily Egg Production Method

The Daily Egg Production Method (DEPM) was developed for stock assessment of the Northern Anchovy (*Engraulis mordax*; Parker 1980, Lasker 1985), and has been applied to more than 20 species of small to medium-sized pelagic fishes (e.g. Stratoudakis *et al.* 2006, Dimmlich *et al.* 2009, Neira *et al.* 2009, Grammer *et al.* 2024a). The method is widely used in coastal fisheries because it is often the most practical option available for assessment of pelagic species (Ward *et al.* 1998).

The DEPM relies on the premise that spawning biomass can be calculated by dividing the mean number of pelagic eggs produced per day throughout the spawning area (i.e. total daily egg production) by the mean number of eggs produced per unit mass of adult fish (i.e. mean daily fecundity, Parker 1980, Lasker 1985). Total daily egg production is the product of mean daily egg production (P_0) and total spawning area (A). Mean daily fecundity is the product of mean sex ratio (by weight, R), mean spawning fraction (proportion of mature females spawning each day/night, S) and mean relative fecundity (number of eggs produced per gram of total female weight (\hat{F}/W), F'). Spawning biomass (SB) is calculated according to the equation:

$$SB = P_0 * A / (R * S * F') \quad \text{Equation 1}$$

The DEPM, as applied to Sardine off South Australia, underwent a comprehensive review in 2021 (Ward *et al.* 2021). The review reanalysed data collected between 1995 and 2019 for South Australian Sardine and identified several ways to increase the precision of estimates of spawning biomass: 1) increase the precision of total daily egg production ($P_0 * A$) by using the estimate of P_0 obtained from all historical data rather than annual estimates of P_0 ; 2) continue to use the log-linear model to estimate P_0 for the southern stock of Australian Sardine; 3) increase the precision of mean daily fecundity ($R * S * F'$) by using the estimates of sex ratio (R), spawning fraction (S) and relative fecundity (F') obtained from all historical data rather than annual estimates of these parameters; and 4) combine batch fecundity (F) and female weight (W) into a single parameter: relative fecundity ($F' = \hat{F}/W$). These recommendations have been implemented since 2022 and are continued for this report to ensure that estimates of spawning biomass are, and continue to be, as accurate and precise as possible.

1.2. Rationale, objective and approach

The DEPM has been used to estimate the spawning biomass of Sardine in South Australian waters since 1995 (e.g. Ward *et al.* 1998, 2011, 2021, Grammer *et al.* 2024a). The estimate of spawning biomass obtained using the DEPM is the key performance indicator for

determining the status of the southern stock of Australian Sardine (PIRSA 2023). The objective of this report is to estimate the spawning biomass of Sardine in waters off South Australia in 2025. Annual estimates of P_0 and A were obtained from an ichthyoplankton survey conducted during February–April 2025. Adult parameters were derived from all adult samples collected off South Australia between 1998 and 2024; an estimate of P_0 was also obtained from all historical data. Sensitivity analyses were undertaken to evaluate the effects of variability in estimates of individual parameters on the uncertainty associated with the estimate of spawning biomass for 2025.

2. METHODS

2.1. Study area and biophysical variables

2.1.1. Study area

An ichthyoplankton survey was conducted from the *RV Ngerin* in shelf and gulf waters off South Australia during 19 February–3 March, 20–28 March, and 7–9 April 2025 (Fig. 1). Plankton samples were collected at 414 sites on 38 transects between Kingston and the Head of Bight (Fig. 1). The 2025 survey included 22 sites added in 2023 to the south-east of Kangaroo Island, extended the transects in the GAB, and included additional sites added in 2020 (Fig. 1). These additional sites were added in response to the expansion of the fishery into this region and recent observations that Sardine eggs had become more common in the area (Ward *et al.* 2020a, Grammer and Ivey 2023; Fig. 1).

An adaptive approach to egg sampling has been applied since 2014 to ensure that each survey covers as much of the spawning area as possible. Adaptive sampling was implemented in response to the incomplete coverage of the spawning area in 2013 (see Grammer *et al.* 2021). Under the protocol, extra samples are taken at sites located outside the area covered by the pre-determined sampling sites (Fig. 1). Decisions about whether (or not) to take extra samples are based on the presence/absence of eggs in samples taken using the Continuous Underway Fish Egg Sampler (CUFES) at sites located on the seaward end of transects. Sampling at additional sites continues until Sardine eggs are not present in the CUFES samples. In 2025, 22 extra sites were sampled on the seaward ends of 16 transects.

Five sampling sites on the far eastern transect were excluded from the 2025 sampling design due to their proximity to an Abalone Viral Ganglioneuritis (AVG) outbreak detected in the Southern Zone Abalone Fishery in February 2024 (PIRSA 2024). To mitigate biosecurity risks, decontamination protocols were implemented, whereby all sampling equipment was rinsed in a sodium hypochlorite solution between each transect sampled in the south-east region of the survey.

2.1.2. Water temperature and primary and secondary production

At each sampling site (Fig. 1), a *Sea-Bird* Conductivity-Temperature-Depth (CTD) recorder fitted with a fluorometer was attached to the bottom of the plankton sampling gear (see next section), and lowered to a depth of 70 m, or to 10 m from the seafloor in waters less than 80 m deep. Estimates of water temperature and fluorescence at the surface were extracted from the first 5 m each CTD profile. At sites where water temperature was not available (e.g. in the event of CTD malfunction), the average temperature of the adjacent stations was applied. Fluorescence is an indicator of primary production and gives an un-calibrated measure of chlorophyll-*a* concentration ($\mu\text{g}\cdot\text{L}^{-1}$). Spatial plots of sea surface temperature (SST), salinity and chlorophyll-*a* concentration were prepared using minimum curvature algorithms in ArcGIS Pro[®] (Version 12).

Common taxa of zooplankton and phytoplankton were recorded for each sample and scored as a percentage of the total plankton volume. The total plankton volume was estimated by allowing samples to settle in a measuring cylinder. These data were then converted to areal density ($\text{mL}\cdot\text{m}^{-2}$) for each taxa, using the same method applied to the Sardine egg data. These data were presented on maps generated using ArcGIS Pro[®](Version 17).

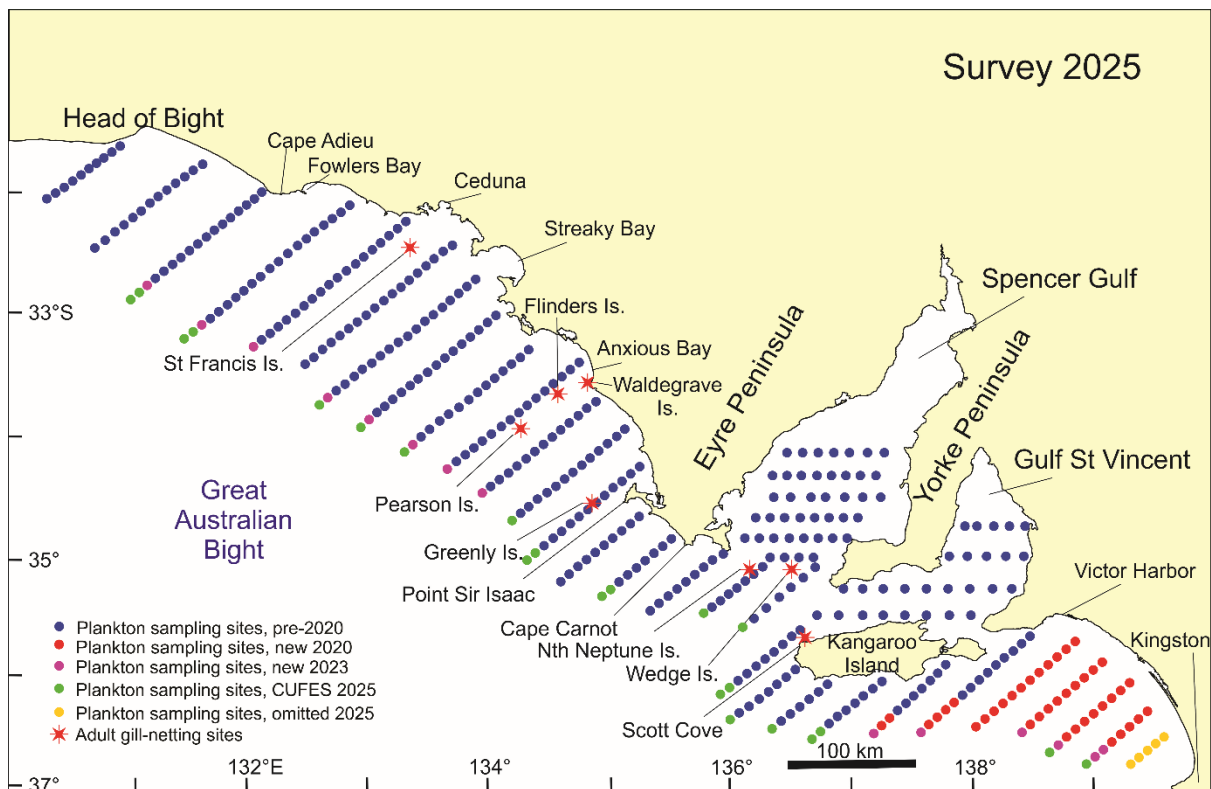


Figure 1. Map of South Australia showing sites where plankton samples were collected during 2025.

2.2. Mean daily egg production and spawning area

2.2.1. Plankton sampling

Plankton samples were collected at each site using paired Californian Vertical Egg Tow (CalVET) plankton nets. Each CalVET net had an internal diameter of 0.3 m, length of 1.8 m, 330 μm mesh and plastic removable cod-ends. The CTD recorder was attached below the cod-ends of the CalVET nets. During each tow, the CalVET nets were deployed to a depth of 70 m, or to 10 m above the seafloor in waters less than 80 m deep. The nets were retrieved vertically at a speed of $\sim 1 \text{ m}\cdot\text{s}^{-1}$. *General Oceanics* 2030 flow-meters and factory calibration coefficients were used to estimate the distance travelled by the net during each tow. Where there was a discrepancy of more than 5% between flow-meters, the relationship between wire length and flow-meter units was used to determine which was correct and that value was used for both nets. Upon retrieval of the nets, the samples from the two cod-ends were rinsed with seawater, combined into a 1 L container, and fixed in 5% buffered formaldehyde and seawater solution.

2.2.2. Laboratory analysis

Sardine eggs and larvae were identified in each plankton sample using published descriptions (Neira *et al.* 1998, White and Fletcher 1998). Eggs were staged based on descriptions in White and Fletcher (1998). Total counts of eggs of each developmental stage in each sample were recorded. Eggs in the first and last stages were excluded from the statistical analyses as they can be under- and over-represented in samples, respectively (Ward *et al.* 2018).

2.2.3. Egg ageing and treatment of zero count egg samples

The development rate of Sardine eggs is dependent on ambient water temperature (Picquelle and Stauffer 1985, Pauly and Pullin 1988). Based on the temperature data from the CTD, egg samples were allocated to one of three temperature bins that covered the range of temperatures encountered during surveys (14–18°C, 18–22°C, and 22–26°C). The temperature bins were comparable to those used by Le Clus and Malan (1995) to describe the developmental rates of Sardine eggs, and consistent with those used in previous DEPM reports (e.g. Grammer *et al.* 2024a) These published development rates were used to assign a mean age to each egg in each sample (Ward *et al.* 2018).

After each egg was assigned an age, the eggs in each sample were grouped into daily cohorts. This was done because a sample usually included eggs spawned on more than one night. The total number of eggs in each daily cohort was calculated by summing the number of eggs of each stage assigned to a spawning day (i.e. day 0, day 1, day 2). The age of a daily cohort

was calculated from the average age of each stage within the daily cohort, weighted by the number of eggs in each stage.

Samples with eggs could contain several possible combinations of daily cohorts depending on water temperature, spawning time (peak around 2:00 am) and sampling time. Zero counts were allocated for daily cohorts where the cohort was expected to be present but was not found within the sample (Ward *et al.* 2018). Samples with no eggs were excluded from the analyses and not considered part of the spawning area.

2.2.4. Egg density

The number of eggs of each day class under one square metre of water (P_t) was estimated at each site according to Equation 2:

$$P_t = \frac{C \cdot D}{V} \quad \text{Equation 2}$$

Where C is the number of eggs of each age in each sample, V is the volume filtered (m^3), and D is the depth (m) to which the net was deployed (Smith and Richardson 1977). Plots of egg distribution and abundance were prepared using ArcGIS Pro® (V17).

2.2.5. Spawning area (A)

The spawning area (A , Lasker 1985, Somarakis *et al.* 2004) was estimated using the Voronoi natural neighbour method (Watson 1981). The survey area was divided into a series of contiguous polygons approximately centred on each site using the *deldir* package in the statistical program R (Fig. 2; R Core Team 2024, Turner 2023). The area represented by each site (km^2) was calculated. A was defined as the total area of the polygons where live Sardine eggs were present in the plankton sample (see Fletcher *et al.* 1998).

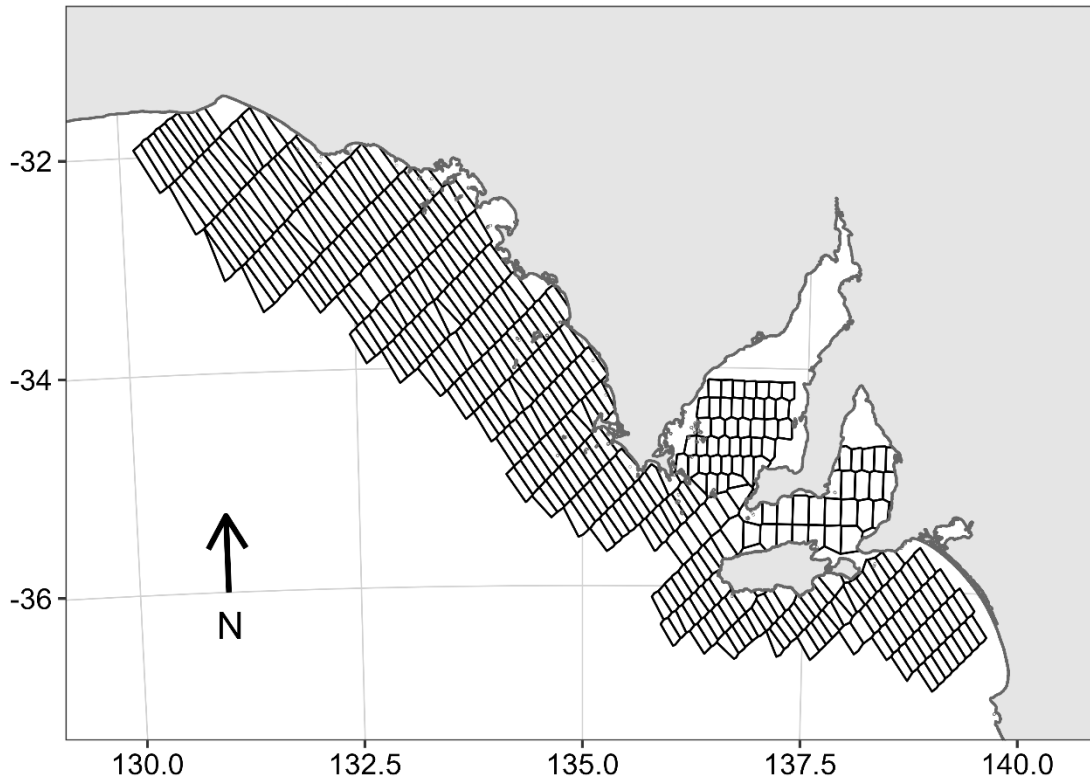


Figure 2. Voronoi nearest neighbour polygons used to estimate the total spawning area in 2025.

2.2.6. Mean daily egg production (P_0) and egg mortality (Z)

The underlying model used to calculate P_0 was the exponential egg mortality model (Equation 3) with a bias correction factor (Equation 4, the 'log-linear model'). The linear version of the exponential egg mortality model is:

$$\ln P_b = \ln(P_{i,t} + 1) - Zt, \quad \text{Equation 3}$$

where $P_{i,t}$ is the density of eggs of age t at site i and Z is the instantaneous rate of egg mortality.

Estimates of P_b obtained using the linear version of the exponential mortality model have a negative bias, therefore a bias correction factor was applied following the equation of Picquelle and Stauffer (1985):

$$P_0 = e^{(\ln P_b + \sigma^2/2)} - 1 \quad \text{Equation 4}$$

where, σ^2 is the variance of the estimate of biased mean daily egg production (P_b).

A generalised linear model (GLM) with a negative binomial error structure (NB1) was also used to estimate P_0 (Equation 5):

$$E[P_0] = g^{-1}(-zt + \varepsilon) \quad \text{Equation 5}$$

where $E[P_0]$ is the expected value of P_0 , g^{-1} is the inverse-link function, zt is the instantaneous rate of daily egg mortality at age t , and ε is the error term. The negative binomial error structure used is considered suitable for over-dispersed data, such as egg density by age (e.g. Ward *et al.* 2011, 2018, 2021). For NB1, variance increased linearly with the mean ($\sigma = \mu^*(1 + \mu + \phi)$), where μ is the model estimate, σ is the model variance and ϕ is the over-dispersion parameter. The GLM used a log-link function (Wood 2006) and was fit using the *glmmTMB* package in R (Brooks *et al.* 2017).

Following the recommendations of Ward *et al.* (2021), the value of P_0 from the log-linear model was used to estimate spawning biomass for Sardine. P_0 was calculated using data collected solely in 2025, as well as with data from all years (combined) between 1998 and 2025. The all-years estimate of P_0 is considered more robust than the individual year estimate of P_0 , because sampling error within a year is greater than inter-annual variability of egg density and egg production (Ward *et al.* 2021).

2.3. Adult reproductive parameters

Adult parameters used to estimate spawning biomass were derived from all adult samples of Sardine collected for DEPM surveys off South Australia between 1998 and 2018 (see Ward *et al.* 2021) and in 2024 (Grammer *et al.* 2024a). No adult samples were collected in 2025.

2.3.1. Sampling methods

From 1998 to 2024, fishery independent samples of mature Sardine were collected from sites located in the eastern Great Australian Bight, southern Spencer Gulf and Investigator Strait using a gillnet (Fig. 1). In the late afternoon, a dual frequency echo sounder (60 and 180 KHz) was used to search areas where schools of adult Sardine were known to aggregate. A gillnet comprised of three panels, each with a different multi-filament nylon mesh size (*Double Diamond*: 210/4 ply meshes 25, 28 and 32 mm; Ward and McLeay 1998) was deployed from the port side of the *RV Ngerin* at protected locations where schools were encountered. Surface and sub-surface lights (150 W) were illuminated near the net after it was set. Net soak times varied from 15 minutes to 3 hours depending on the number of fish caught.

After the net was retrieved, fish were removed and dissected immediately. All Sardine collected were counted and sexed. Mature males and immature fish were frozen. Mature females were fixed in 10% buffered formaldehyde seawater solution.

In 2024, the South Australian Sardine Industry Association (SASIA) collected fishery-dependent samples from selected purse seine net-sets during commercial fishing operations, targeting sets where spawning Sardine were likely to be encountered. Fish sample processing

was consistent with those used for the fishery independent sampling (described above), where fish in each sample were counted and immediately dissected, sexed, and either preserved or frozen. All samples were then sent to SARDI Aquatic Sciences for subsequent processing and analyses.

2.3.2. Female weight (W) and Male weight

Mature females from each sample were removed from the formalin solution and weighed (± 0.01 g). Fixation in formalin has a negligible effect on fish weight (Lasker 1985). The mean weight of mature females in the population was calculated from the average of sample means weighted by proportional sample size:

$$W = \left[\overline{W}_i * \frac{n_i}{N} \right] \quad \text{Equation 5}$$

where, \overline{W}_i is the mean female weight of each sample i ; n is the number of fish in each sample and N is the total number of fish collected in all samples.

Mature males in each sample were thawed and weighed (± 0.01 g).

2.3.3. Sex ratio (R)

The mean sex ratio of mature individuals in the population was calculated from the average of sample means weighted by sample size:

$$R = \left[\overline{R}_i * \frac{n_i}{N} \right] \quad \text{Equation 6}$$

where, n is the number of fish in each sample, N is the total number of fish collected in all samples and \overline{R}_i is the mean sex ratio of each sample calculated from the equation:

$$\overline{R}_i = \frac{F}{(F + M)} \quad \text{Equation 7}$$

where, F and M are the respective total weights of mature females and males in each sample i .

2.3.4. Spawning fraction (S)

Ovaries of females determined mature macroscopically were sectioned and stained with haematoxylin and eosin. Several sections from each ovary were examined to determine the presence/absence of post-ovulatory follicles (POFs). POFs were aged according to the criteria developed by Hunter and Goldberg (1980) and Hunter and Macewicz (1985). The spawning

fraction of each sample was estimated as the mean proportion of females with hydrated oocytes plus day-0 POFs ($d0$) (assumed to be spawning or have spawned on the night of capture), day-1 POFs ($d1$) (assumed to have spawned the previous night) and day-2 POFs ($d2$) (assumed to have spawned two nights prior). The mean spawning fraction of the population was then calculated from the average of sample means weighted by proportional sample size:

$$S = \left[\overline{S}_i * \frac{n_i}{N} \right] \quad \text{Equation 8}$$

where, n is the number of fish in each sample, N is the total number of fish collected in all samples and \overline{S}_i is the mean spawning fraction of each sample calculated from the equation:

$$\overline{S}_i = \frac{[(d0 + d1 + d2POFs) / 3]}{n_i} \quad \text{Equation 9}$$

where, $d0$, $d1$ and $d2$ POFs are the number of mature females with POFs in each sample and n_i is the total number of females within a sample.

2.3.5. Batch fecundity (F)

Batch fecundity (F) was estimated from ovaries containing hydrated oocytes using the methods of Hunter and Macewicz (1985). Fish that showed evidence of commencing spawning (i.e. deflated areas in ovary) or with partially spilled ovaries were excluded from batch estimates. Both ovaries were weighed and the number of hydrated oocytes in three weighed ovarian sub-sections counted. The total batch fecundity for each female was calculated by multiplying the mean number of oocytes per gram of ovary segment by the total weight of the ovaries. Methods to estimate the batch fecundity for mature females without hydrated ovaries (\hat{F}) followed those outlined in Ward et al. (2021).

Relative Fecundity (F') was calculated by using the linear relationship of batch fecundity determined from all-years data (1998–2024) to estimate F and then dividing by the mean weight of all mature females collected (W).

2.4. Spawning biomass

Spawning biomass was calculated using the all-years estimate of P_0 (1998 to 2025) obtained from the log-linear model, spawning area (A) in 2025 and estimates of R , S and F' obtained from adult samples collected between 1998 and 2024.

The reliability of model fits, 95% confidence intervals (CIs) and coefficients of variation (CVs) for P_0 were estimated using bootstrap resampling methods with 10,000 iterations. Coefficients

of variation and CIs for R , S and F' , were calculated from the all-years adult data. A ratio estimator was used calculate the variance for S , R , and F' (Rice 1995). The variance for the spawning biomass estimates were calculated by summing the squared CVs for each parameter and multiplying by the square of the estimate of spawning biomass (Parker 1985). Uncertainty estimates presented for all parameters are 95% CIs. Data analyses were done in the R programming environment (R Core Team 2024).

2.5. Sensitivity analysis

Sensitivity analyses were conducted to assess the effects of variations in the range of values obtained for each parameter in each year between 1998 and 2025 on the estimate of spawning biomass for 2025.

2.6. Quality assurance and quality control of data

All parameters used in the calculation of spawning biomass were computed independently in both the R programming environment and in Microsoft Excel. Physical and biological data were plotted and checked for inconsistencies and outliers. Discrepancies were corrected where necessary by checking against the datasheets recorded in the field and laboratory and re-examining the sample if required. All ichthyoplankton samples and histology slides are retained and archived at SARDI Aquatic Sciences.

3. RESULTS

3.1. Distribution and abundance of eggs

A total of 10,109 live Sardine eggs were collected at 333 of 414 sites (80.4%) on transects between Kingston and Head of Bight from February to April 2025, compared to 8,310 live Sardine eggs from 173 of 405 sites (42.7%) over the same period in 2024 (Fig. 3, Appendices 1 and 2). In 2025, sites with high egg densities were observed across most of survey area, including southern Spencer Gulf, throughout the GAB, south of Kangaroo Island, and in the south-east region. Eggs were also widespread throughout Investigator Strait. Sites where live eggs were not detected were along the northern transects in both Gulfs and the inshore stations near Victor Harbor.

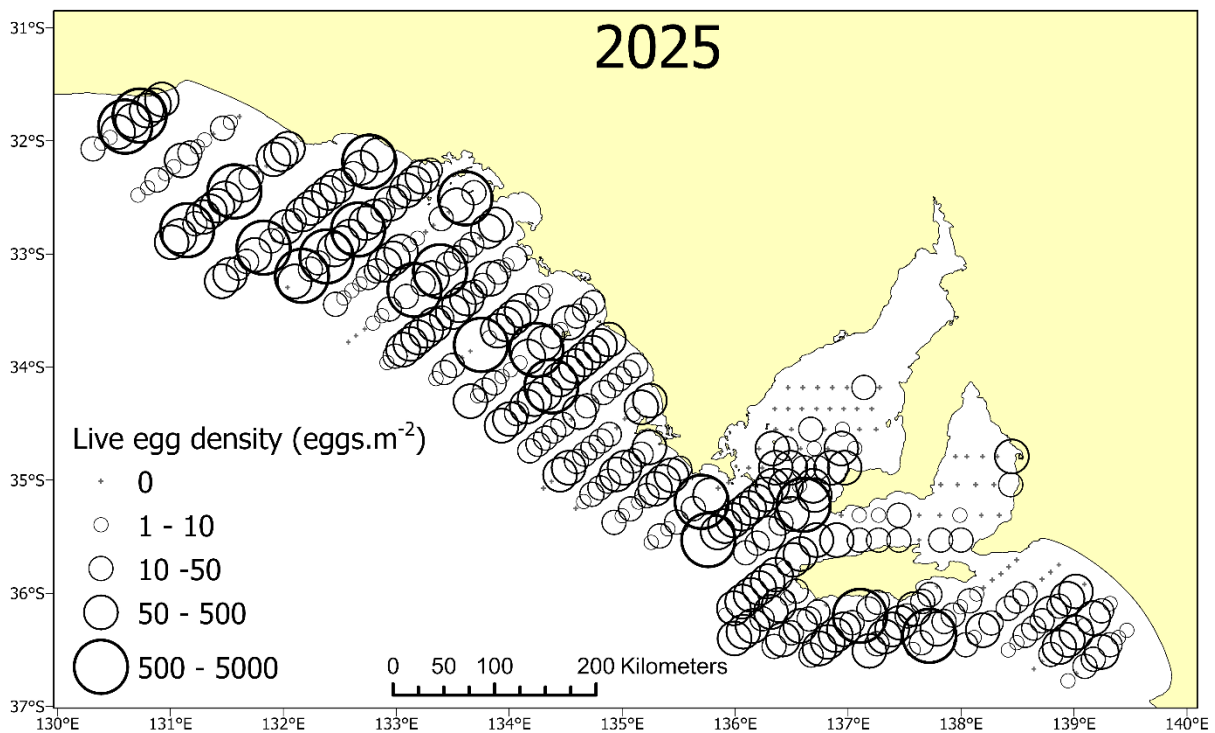


Figure 3. Densities of live Sardine eggs at sites sampled off South Australia from February to April 2025.

3.2. Biophysical variables

3.2.1. Sea surface temperature

Sea surface temperatures (SSTs) in 2025 were broadly warmer than previous years, ranging from 15.6°C in the southeast of the survey to 22.9°C in the central Spencer Gulf and 21.2°C in offshore waters of the GAB (Fig. 4; Appendix 2). The cool, upwelled water often present over the inner shelf region of the eastern GAB and southwest of Kangaroo Island in February to April was absent in 2025 (e.g. 2024; Appendix 2).

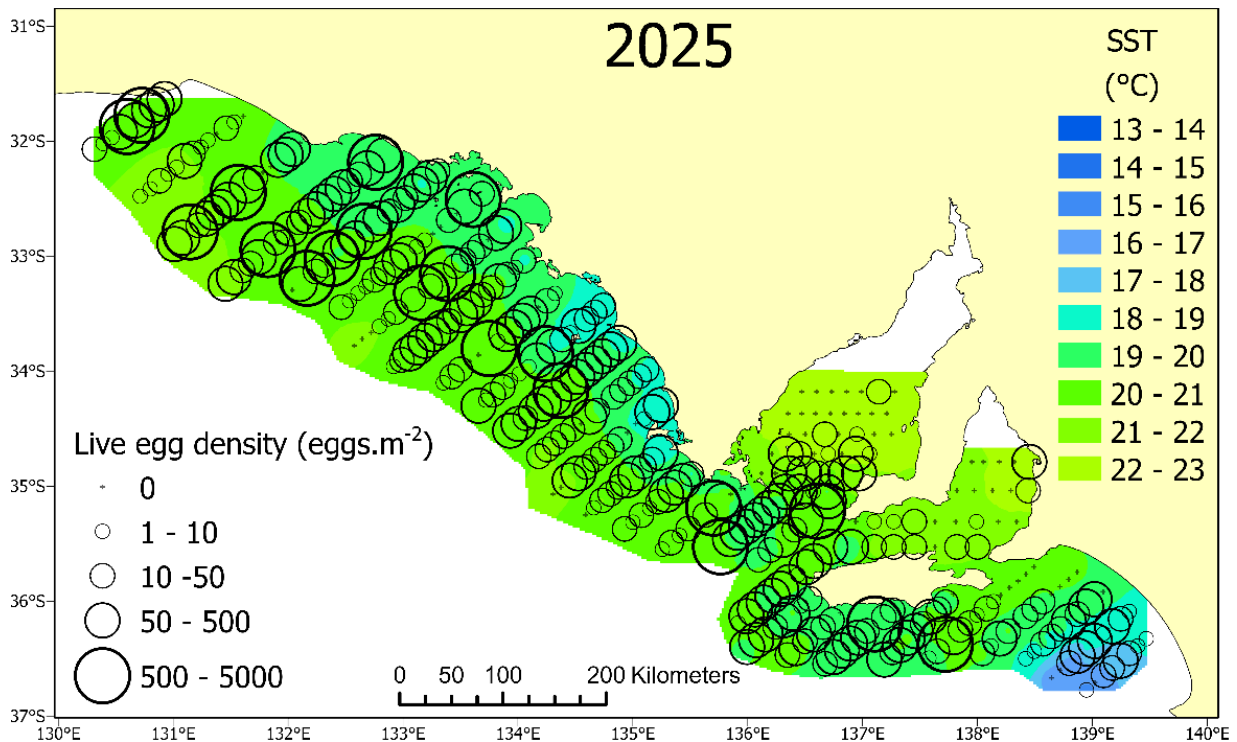


Figure 4. Sea surface temperatures overlaid with densities of live Sardine eggs at sites sampled off South Australia from February to April 2025.

3.2.2. Fluorescence

Surface chlorophyll-*a* concentrations across the survey area ranged between 0 and 1.6 $\mu\text{g.L}^{-1}$ between February and April 2025 (Fig. 5). The highest values were recorded in the south-east of the survey, southern Spencer Gulf and inshore waters towards the Head of Bight. The remaining coastal and shelf waters mainly had chlorophyll-*a* concentrations $<1.0 \mu\text{g.L}^{-1}$.

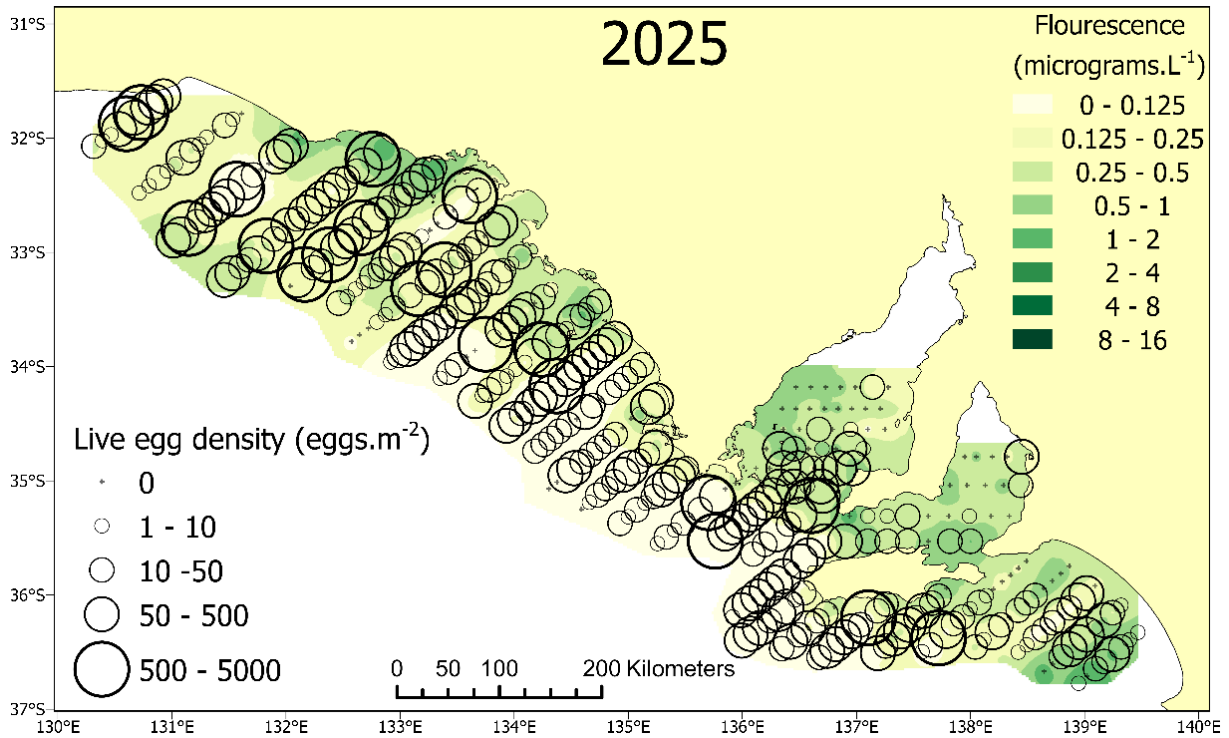


Figure 5. Surface concentration of chlorophyll-*a* overlaid with densities of live Sardine eggs at sites sampled from February to April 2025.

3.2.3. Salinity

Surface salinity at each site ranged from 35.5 to 37.8 ppt between February and April 2025 (Fig. 6). The highest salinities occurred in Spencer Gulf and Gulf St Vincent and the lowest salinities were observed in the south-east region off Kingston and around the south-western coast of Kangaroo Island. Relatively low salinities also occurred along the west coast of the Eyre Peninsula.

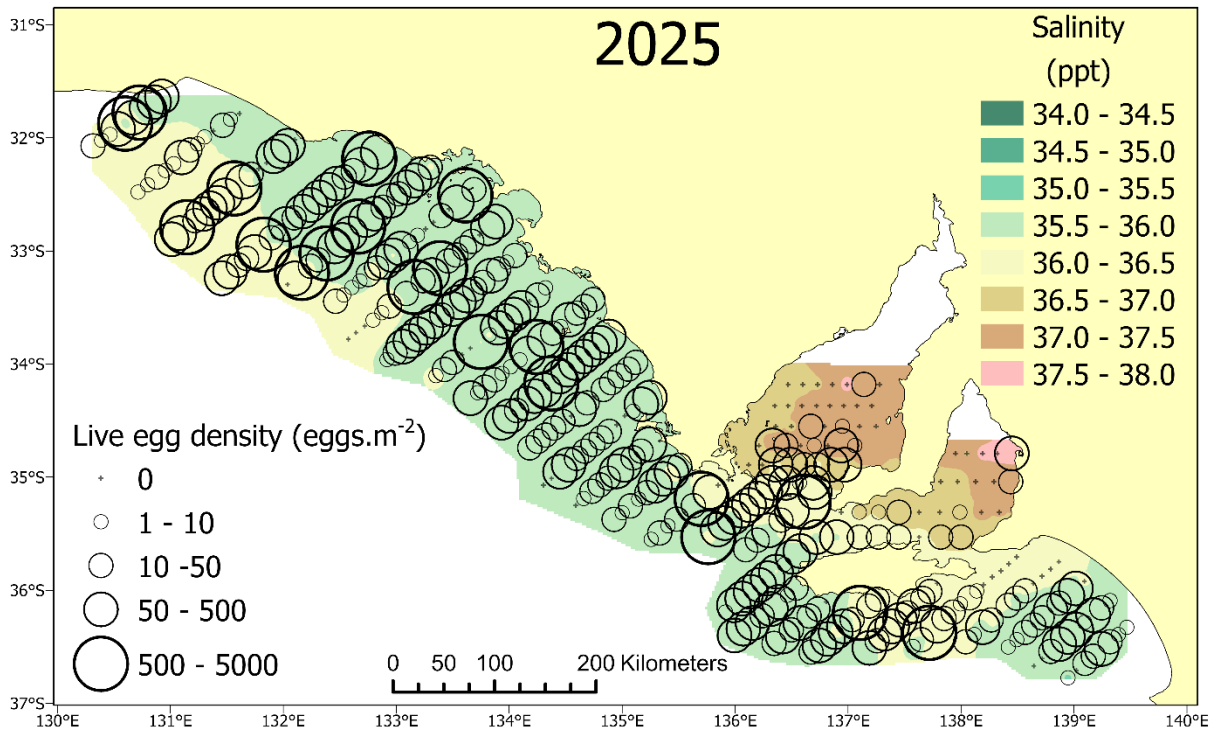


Figure 6. Surface salinity overlaid with densities of live Sardine eggs at sites sampled during February and April 2025.

3.2.4. Distribution and density of common zooplankton and phytoplankton taxa

Common taxa of zooplankton and phytoplankton recorded from the survey area between February and April 2025 were doliolids, larvaceans, copepods, dinoflagellates (*Noctiluca scintillans*), cladocerans and pteropods (Fig. 7). Cladocera were the most abundant zooplankton, followed by copepods and doliolids, all of which were most abundant on the GAB shelf off western Eyre Peninsula, in the mouth of Spencer Gulf, and south of Kangaroo Island. The dinoflagellate *N. scintillans*, and pteropods were most abundant south-east of Kangaroo Island. Unlike previous years (e.g. see Grammer et al. 2024a), salps were almost absent during the 2025 survey.

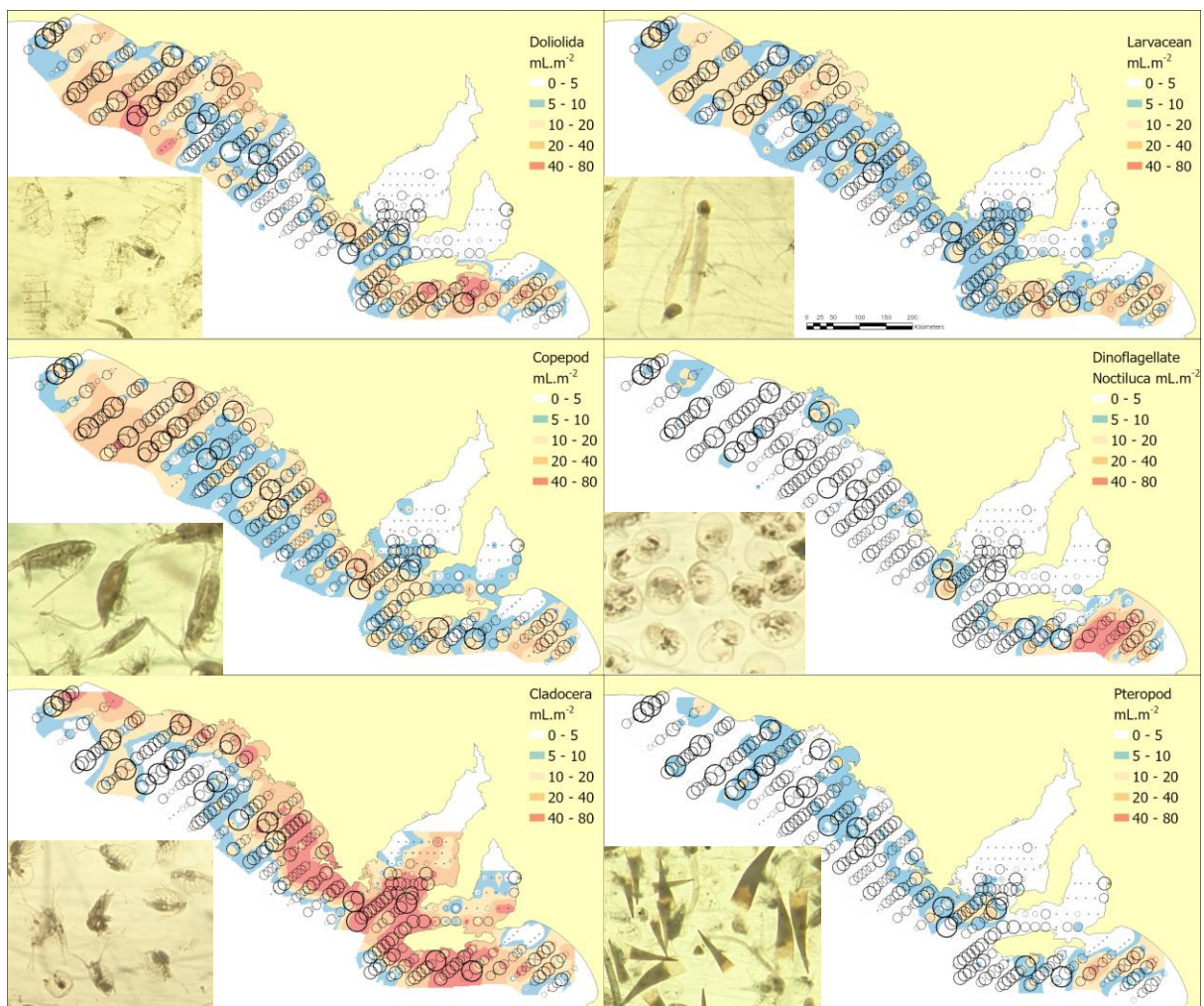


Figure 7. Density of common zooplankton and phytoplankton taxa (displayed in mL.m⁻²) overlaid with densities of live Sardine eggs at sites sampled during February–April 2025.

3.3. Spawning area

The estimated spawning area was 114,640 km² and comprised 81.4% of the total area sampled (140,900 km²; Table 1, Fig. 8). If the additional stations added to the main survey since 2020 were not included, the spawning area would have been 104,357 km², which is the highest estimate on record.

Table 1. Total area surveyed and spawning area (*A*) estimated during February–April 2025.

	Area sampled (km ²)	Spawning area, <i>A</i> (km ²)	Spawning area percentage
Pre-2020 survey	128,158	104,357	81.4%
With new stations	140,900	114,640	81.4%

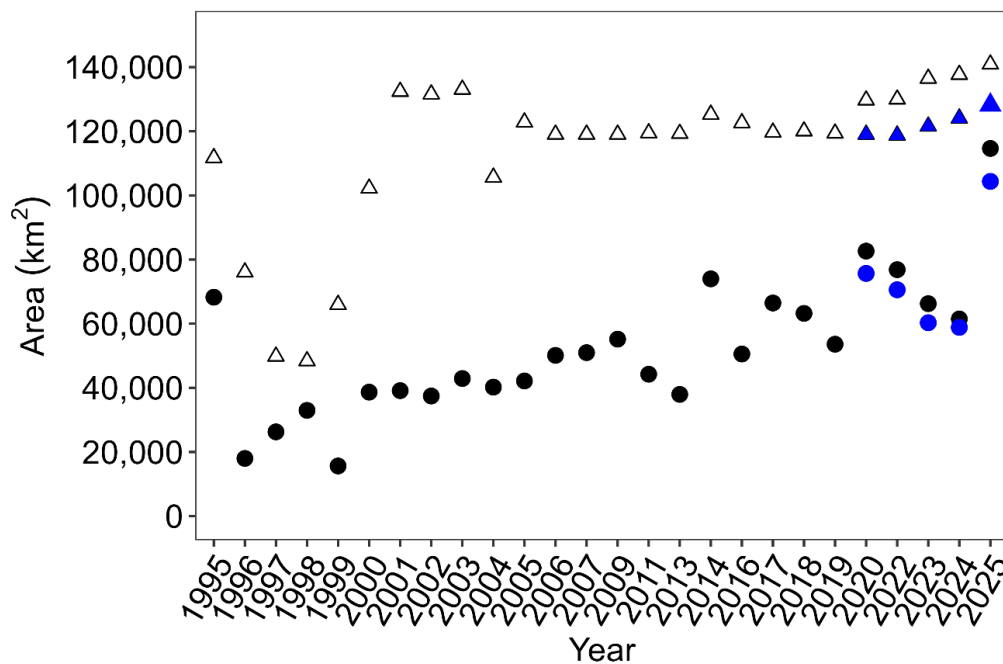


Figure 8. Sampling area (open triangles) and spawning area (closed circles) over the history of DEPM surveys in South Australia. For comparison: blue points exclude additional sites added since 2020.

3.4. Mean daily egg production (P_0)

The estimate of P_0 (95% CI) obtained by fitting the log-linear model (Eq. 3) to all data from 1998 to 2025 was 88.7 (80.8–97.3) eggs·day⁻¹·m⁻² (Table 2; Fig. 9A). The estimate of P_0 obtained by fitting the GLM NB1 (Eq. 5) to all data from 1998 to 2025 was 103.3 (90.8–119.0) eggs·day⁻¹·m⁻² (Table 2; Fig. 9A).

The estimate of P_0 (95% CI) obtained by fitting the log-linear model (Eq. 3) to data solely obtained in 2025 was 101.3 (72.4–139.9) eggs·day⁻¹·m⁻² (Table 3; Fig. 9B). The estimate of P_0 obtained by fitting the GLM NB1 (Eq. 5) to data solely obtained in 2025 was 101.8 (77.9–130.1) eggs·day⁻¹·m⁻² (Table 3; Fig. 9B). Estimates of P_0 (log-linear model) for individual years between 1998 and 2025 have ranged from 39.0 in 2013 to 152.6 in 2024 (Appendix 1).

Table 2. Mean daily egg production (P_0) and instantaneous daily mortality (Z) estimated by fitting the log-linear model and GLM NB1 to all data collected from 1998 to 2025.

Model fit	P_0 (eggs·day ⁻¹ ·m ⁻²) (95% CI)	Z
Log-linear model	88.7 (80.8–97.3)	0.50 (0.43–0.57)
GLM, Negative Binomial	103.3 (90.8–119.0)	0.32 (0.26–0.37)

Table 3. Mean daily egg production (P_0) and instantaneous daily mortality (Z) estimated by fitting using the log-linear model and GLM NB1 to data solely collected during February–April 2025.

Model fit	P_0 (eggs·day ⁻¹ ·m ⁻²) (95% CI)	Z
Log-linear model	101.3 (72.4–139.9)	0.31 (0.04–0.61)
GLM, Negative Binomial	101.8 (77.9–130.1)	0.15 (0.01–0.33)

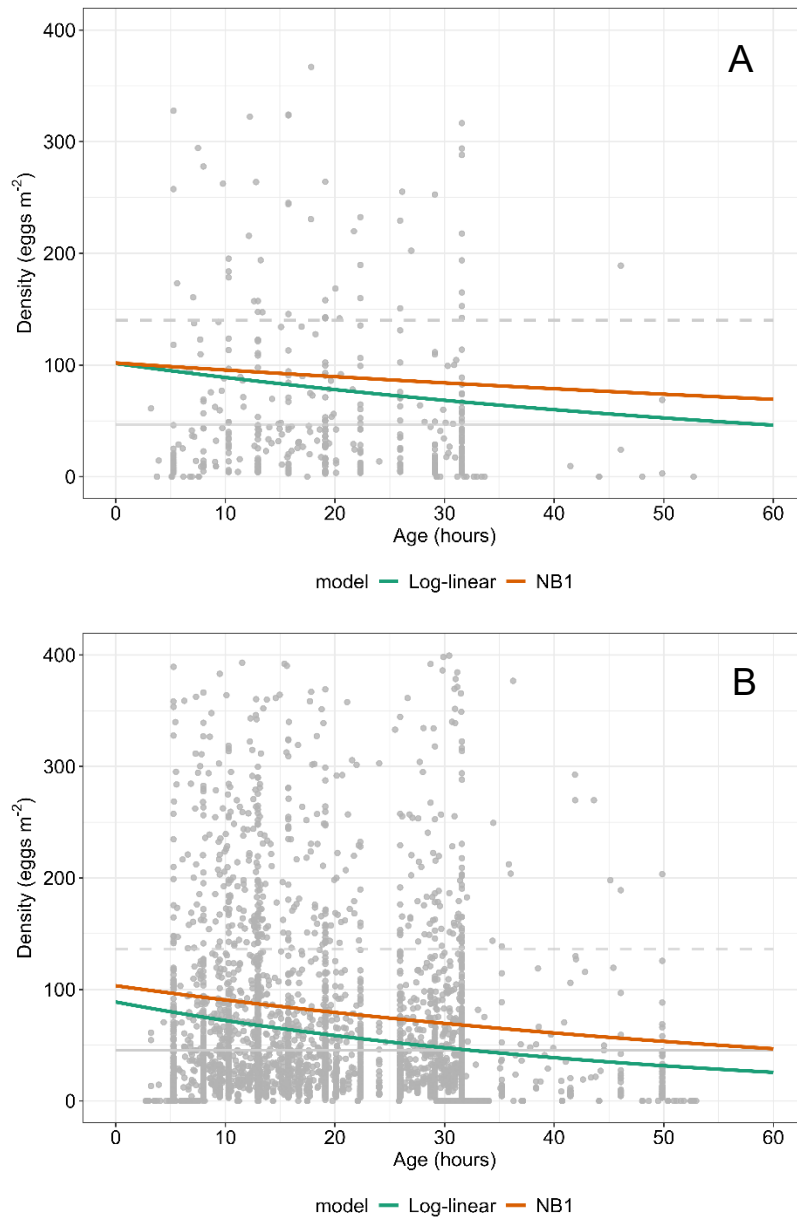


Figure 9. Models fitted to egg densities (eggs. m^{-2}) and egg age (hours) of Sardine cohorts in 2025 (**A**) and all years combined (1998 to 2025; **B**). Solid grey horizontal line: mean daily egg density, dashed grey horizontal line: mean total egg density.

3.5. Adult parameters

3.5.1. Sex ratio

The mean sex ratio by weight (R , 95% CI) calculated from all fish collected between 1998 and 2024 was 0.53 (0.50–0.56) (Grammer et al. 2024a; Table 4). Estimates of R for individual years ranged from 0.36 in 2009 to 0.70 in 2018 (Appendix 1).

3.5.2. Spawning fraction

The spawning fraction (S , 95% CI) calculated from all data collected between 1998 and 2024 was 0.111 (0.100–0.122) (Grammer et al. 2024a; Table 4). Estimates of S for individual years ranged from 0.041 in 2014 to 0.179 in 2001 (Appendix 1).

3.5.3. Mean female weight

The mean weight of mature females (W , 95% CI) estimated from 17,691 fish (271 samples) collected between 1998 and 2024 was 58.3 g (23.1–93.4) (Grammer et al. 2024a; Appendix 1). Estimates of W for individual years ranged between 46.5 g in 1998 and 78.7 g in 2004 (Appendix 1).

Table 4. Parameter estimates used in the calculations of spawning biomass. Estimates of adult parameters (R , S , F') are calculated from all historical data from 1998 to 2024 (Grammer et al. 2024a). CI: confidence interval; CV: coefficients of variation.

Parameter	All years	95% CI	CV	Range (among years)
Egg Production (P_0 , eggs·day ⁻¹ ·m ⁻²)	88.7	80.8–97.3	0.048	39.0–152.6
Sex Ratio (R)	0.53	0.50–0.56	0.028	0.36–0.70
Spawning Fraction (S)	0.111	0.100–0.122	0.050	0.041–0.179
Relative Fecundity (F' , eggs·g ⁻¹)	308.4	307.2–309.6	0.002	298.3–316.2
Spawning Area (A , km ²)	-	-	-	15,637–114,640

3.5.1. Batch fecundity

Between 1998 and 2024, 1,176 females with hydrated oocytes were collected (Grammer et al. 2024a). The fecundity-weight relationship estimated from all batch samples collected between 1998 and 2024 was: Batch Fecundity = $334 \times \text{Gonad Free Female Weight} - 558$ ($R^2 = 0.52$) (Grammer et al. 2024a). Estimates of batch fecundity between 1998 and 2024 ranged between 14,196 and 24,242 oocytes (Appendix 1). Mean gonad free female weight between 1998 and 2024 was 55.5 g and ranged between 43.8 and 75.0 g (Appendix 1). Overall mean batch fecundity (\bar{F} , 95% CI) was 17,967 (3,802–32,131) oocytes (Appendix 1).

3.5.2. Relative Fecundity (Eggs per gram of mature female weight (F'))

The estimate of relative fecundity (F' , 95% CI) calculated from all fish collected between 1998 and 2024 was 308.4 (307.2–309.6) (Grammer et al. 2024a; Table 4). Estimates of F' for individual years ranged from 298.3 eggs·g⁻¹ in 2000 to 316.2 eggs·g⁻¹ in 2011 (Appendix 1).

3.6. Spawning biomass

The estimate of spawning biomass (95% CI) calculated using the estimate of A obtained from the survey conducted in 2025, and the all-years estimates of P_0 (log-linear model), S , R , and F' was 556,957 t (474,724–639,191) (Fig. 10). The estimate of spawning biomass calculated using the value of A without the additional stations added since 2020 was 507,002 t.

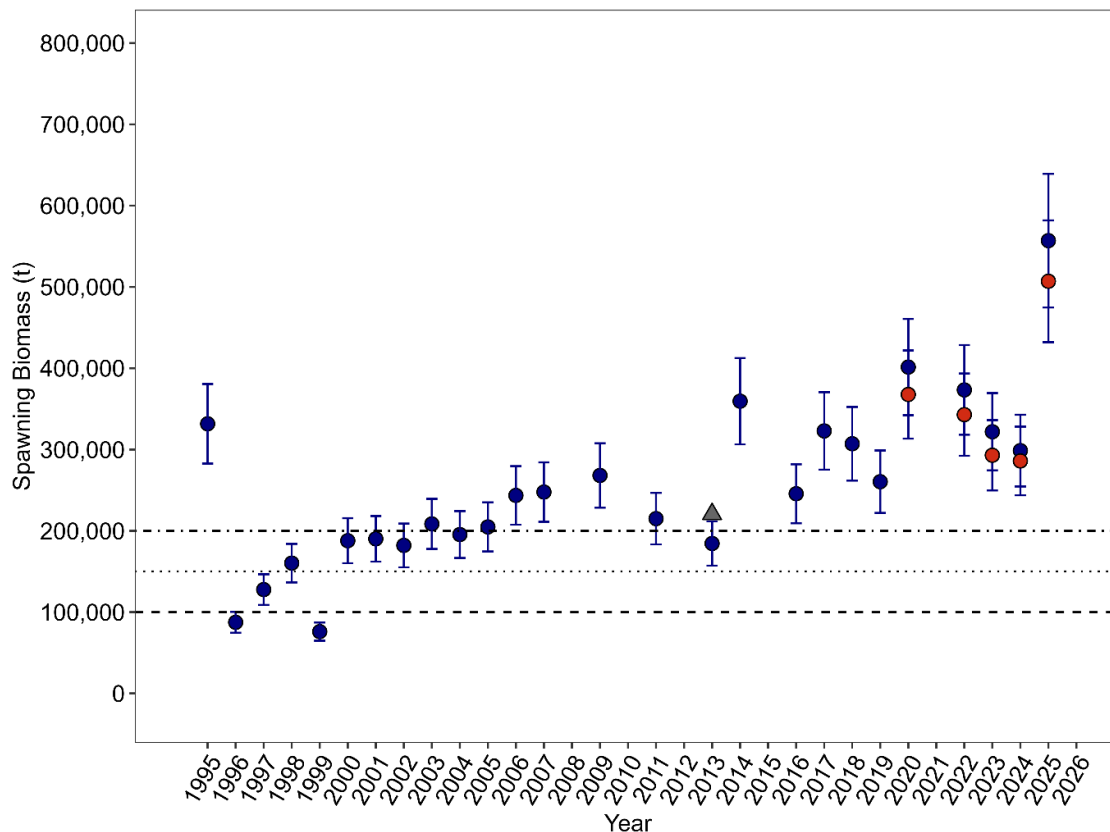


Figure 10. Estimates of spawning biomass (95% CI) for Sardine in South Australian waters from 1995 to 2025 using the log-linear egg production model and all-years data for all parameters, except for spawning area (A). The red circles for 2020 to 2025 are the estimate of spawning biomass obtained using the estimate of A without the additional stations added since 2020. The grey triangle for 2013 (when the survey did not cover the entire spawning area) is the estimate of spawning biomass using the mean A from 2002 to 2011 (45,406 km²). The horizontal lines indicate the 100,000 t (dash), 150,000 t (dotted) and 200,000 t (dash/dot) reference points in the Harvest Strategy (PIRSA 2023).

3.7. Sensitivity analysis

The sensitivity analysis shows the effects of inter-annual variability in parameters (i.e. P_0 , R , S and F') on the estimate of spawning biomass for 2025 (Table 4, Fig. 11, Appendix 1).

The high level of inter-annual variability in the estimates of P_0 reflects the high level of statistical uncertainty associated with annual estimates of this parameter (Fig. 11) (see Ward *et al.* 2021). This range of variability had a strong influence on the estimate of spawning biomass. The estimate of spawning biomass obtained using the P_0 estimated from 2025 survey was marginally higher than the estimate obtained using all-years data (Fig. 11).

The estimates of R obtained in individual years were variable (Fig. 11). The range of historical values (i.e., from 0.36 to 0.70; Table 4) likely reflect the limitations of the adult sampling program rather than the relative abundances of sexes in the population (see Ward *et al.* 2021). The variations in R had a large influence on the estimate of spawning biomass for 2025 (i.e. >400,000 t, Fig. 11).

The estimates of spawning fraction (S) obtained in individual years were also highly variable (i.e. ranging from 0.041 to 0.179) (Fig. 11, Appendix 1). Inter-annual variations in S are more likely to reflect the limitations of the adult sampling program than differences in the spawning rates occurring in the population (see Ward *et al.* 2021). Inter-annual variability in S had the strongest influence of all the parameters on the estimate of spawning biomass (i.e. 185,000 to 800,000 t, Fig. 11), which demonstrates the benefits of using all-years data to estimate this parameter.

The estimate of relative fecundity (F') was similar among years (Fig. 11, Appendix 1) and inter-annual variation in this combined parameter had a relatively minor effect on spawning biomass (i.e. 300,000 to 317,000 t, Fig. 11). Inter-annual variations in W and F were large (Appendix 1) and are known to have a strong influence on the estimate of spawning biomass (see Ward *et al.* 2021). Estimating F' as a single parameter, as done in the original formulation of the DEPM (Parker 1980), from all historical data greatly increases the precision of estimates of spawning biomass for Sardine (Ward *et al.* 2021).

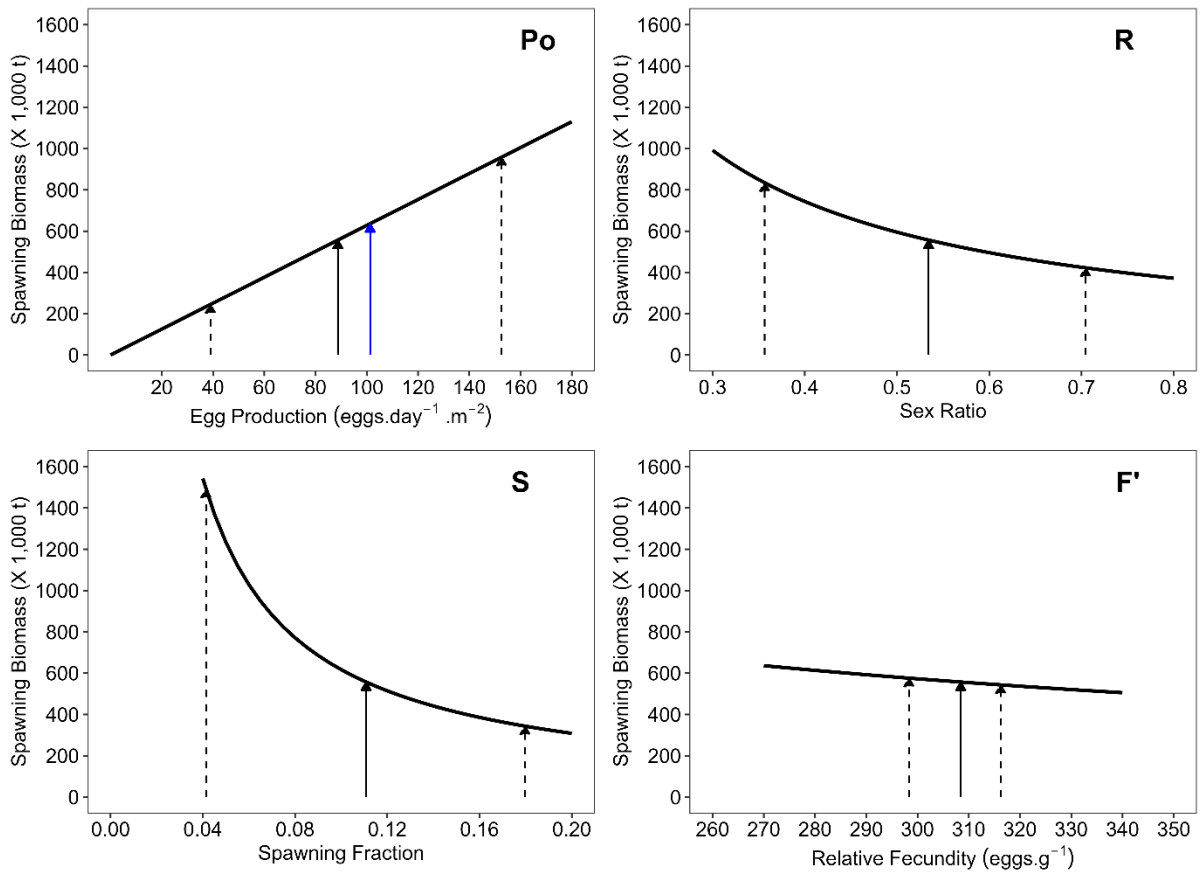


Figure 11. Sensitivity plots showing effects of variability in adult parameters and egg production on estimates of spawning biomass. Solid black arrows: parameter estimates for all years combined; Dashed arrows: range of values recorded between 1998 and 2025; blue arrow: P_0 estimates using only data collected during February–April 2025.

4. DISCUSSION

4.1. Egg distribution and environmental factors

The distribution of live Sardine eggs off South Australia during the February–April 2025 survey was broader than in any other survey since 1998. Live Sardine eggs were recorded across almost the entire survey area, including all continental shelf transects from Kingston in the south-east to Head of the Bight, as well as Investigator Strait and southern Spencer Gulf. The areas where live eggs were not detected were the northern transects in both Gulfs and the inshore stations on two transects near Victor Harbor. The widespread occurrence of Sardine eggs in the new sampling sites added since 2020 continue to provide evidence that the expansion of the survey area was warranted and should be maintained in future years. Consideration should be given to expanding the survey in the future if an estimate of spawning biomass for the entire southern stock of Australian Sardine is required.

Plankton samples collected during the February–April 2025 survey contained a total of 10,109 live Sardine eggs, which is the highest number recorded in any survey off South Australia. The second-highest total was recorded in 2024, when 8,310 live eggs were collected. In 2025, live eggs were found at 333 of 414 stations (80.4%), which represents the highest number and percentage of positive stations on record. Prior to 2025, the highest percentage of positive stations was in 1998, when 109 of 164 stations (66.5%) contained live eggs. However, the 1998 survey area was smaller than recent survey design. The 2020 survey had the next highest percentage of positive stations with 241 of 379 stations (63.6%) containing live eggs.

During the summer of 2024/25, a persistent moderate marine heatwave affected South Australian waters, with all regions averaging 1–2°C warmer compared to usual conditions over that period (Hobday *et al.* in-review). The warmer conditions during the 2025 survey contrast with the summer of 2023/24, when a widespread upwelling event occurred in the eastern GAB along western Eyre Peninsula, south-west of Kangaroo Island and along the Bonney Coast brought cooler temperatures to the inner and mid-shelf waters in these areas (Grammer *et al.* 2024a). There was an absence or low densities of live Sardine eggs in these areas of cooler water during the 2024 survey, suggesting that conditions were less favorable for spawning and potentially contributed to Sardine aggregating within the remaining favourable habitat to spawn in 2024 (e.g. in the Head of the Bight, southern Spencer Gulf and south of Kangaroo Island; see Grammer *et al.* 2024a).

The seasonal upwelling usually observed in the GAB during the survey period was less pronounced in 2025 compared to other years, and this trend was evident in the SSTs observed during the survey. The chlorophyll-*a* concentrations often associated with cool, upwelled water were also low during the survey compared to previous years and the salinity of surface water

during February–April 2025 was ~0.5 ppt higher across the entire survey than during 2024 (e.g. Grammer and Ivey 2022, 2023, Grammer *et al.* 2024a).

The widespread distribution and abundance of live Sardine eggs observed in the February–April 2025 survey may also reflect changes in the zooplankton assemblage. Live eggs were predominantly found in areas with high copepod and Cladocera abundance; both are important prey for adult Sardine (Van der Lingen 2002). In contrast, the 2023 and 2024 surveys reported reduced Sardine egg presence in areas dominated by salps (Grammer and Ivey 2023; Grammer *et al.* 2024a); salps were almost entirely absent from the ichthyoplankton samples in 2025. Salp blooms have previously been associated with cooler, upwelled waters in South Australia and the north-west Pacific (Grammer and Ivey 2023; Ishak *et al.* 2022); these conditions were absent during the 2025 survey. Similarly, *Noctiluca* blooms, common in previous years, were restricted to the south-east of the survey area in 2025, while cladocerans and doliolids were widespread and abundant. These changes in zooplankton composition align with patterns observed during warm phases in other systems, where increased doliolid abundance and reduced salp presence have been reported (Ohman and Venrick 2013; Galbraith *et al.* 2016; Martin *et al.* 2017; Pinchuk *et al.* 2021).

4.2. Spawning area and mean daily egg production

The spawning area during February–April 2025 was estimated to be 114,640 km², which is the largest on record for Sardine off South Australia. Excluding the additional sites that have been added to the survey since 2020 reduced the spawning area to 104,357 km², which is still larger than the previous maximum of 82,627 km². Spawning area is strongly correlated with Sardine abundance (Magel and Smith 1990, Gaughan *et al.* 2004), and spawning area is a good proxy for the abundance of adult Sardine off South Australia (Ward *et al.* 2021). The large spawning area observed in this study provides strong evidence that Sardines were widespread and abundant off South Australia during February–April 2025.

Using both historical and current data combined to estimate all DEPM parameters except spawning area, means that fluctuations in estimates of spawning biomass are driven almost entirely by changes in the measure of spawning area. Adaptive sampling to improve the ability to collect plankton samples from the entire spawning area, particularly on the seaward end of transects, has been regularly applied since 2014 (Ward *et al.* 2013, 2014) and was continued in 2025, when 22 additional sites were added due to the presence of live eggs in the CUFES. Future surveys must cover as much of the spawning area as possible and should continue to involve the adaptive approach to sampling.

Inter-annual variability in estimates of P_0 is low compared to statistical uncertainty (imprecision) for Sardine off South Australia (Ward *et al.* 2021). The estimate for P_0 in 2025

was $101.3 \text{ eggs} \cdot \text{day}^{-1} \cdot \text{m}^{-2}$ (log-linear model). The estimate of P_0 obtained by adding the 2025 data to all historical data (1998–2024) of $88.7 \text{ eggs} \cdot \text{day}^{-1} \cdot \text{m}^{-2}$ was more precise (SD = 4.3) than the estimate obtained using data from 2025 only (SD = 17.4). Using historical data to estimate P_0 prevents large inter-annual fluctuations in estimates of spawning biomass driven by variations in the annual estimates of this parameter caused by statistical uncertainty.

The estimate of P_0 for 2025 was 14% higher than the estimate of P_0 derived from all years between 1998 and 2025. Comparatively, the estimate of P_0 for 2024 was 76% higher than the estimate of P_0 derived from all years between 1998 and 2024. The high estimate of P_0 for 2024 indicates that some aggregation of spawning Sardine may have occurred during the 2024 survey, perhaps in response to limitations on suitable spawning habitat caused by environmental factors (i.e. strong upwelling), thus increasing the density of adult Sardines in areas of suitable habitat (see Ward *et al.* 2021). This was evident in the patchiness of the egg distribution across the survey area in 2024 (see Grammer *et al.* 2024a). In South Australia, spawning habitat for Sardine has been characterised by mid-range SST (i.e. 19–20°C) and surface salinities (36.1–36.6 PSU) with intermediate phytoplankton biomass (chlorophyll-*a*: 0.4–0.9 $\mu\text{g} \cdot \text{L}^{-1}$) and the deep chlorophyll maxima between 60 to 90 m (Doubell *et al.* 2015). Due to the exceptional upwelling in 2024, large portions of the survey area had conditions that were outside of these ranges (Grammer *et al.* 2024a). Warmer conditions were widespread during the 2025 survey. It is critical that P_0 continue to be monitored annually to identify any changes in the parameter over time, thereby reducing the risk of over- or under-estimating spawning biomass (Ward *et al.* 2021). In future applications of the DEPM for Sardine off South Australia, P_0 should continue to be estimated using data obtained in all years since 1998.

4.3. Adult reproductive parameters

Samples of adult Sardine were not collected in 2025. The estimates of adult reproductive parameters used to estimate spawning biomass in 2025 were derived from data obtained in all years from 1998 to 2018, and from 2024 (Grammer *et al.* 2024a). Estimates of adult parameters from samples obtained in 2024 were within the range of the annual estimates from previous years. Re-analysis of all adult samples of Sardine collected off South Australia since 1998, including 2024, produced values that were similar to the all-years values for each parameter reported in Ward *et al.* (2021) (Grammer *et al.* 2024a). This indicates that both individual parameters and mean daily fecundity have been relatively stable among years, especially when inter-annual variability is evaluated within the context of potential sources of statistical uncertainty (i.e. precision and bias; Ward *et al.* 2021). Large variations of the estimates of adult parameters among years are likely indicative of the limitations of adult sampling, rather than actual differences among years in the reproductive patterns of the population (Ward *et al.* 2021). Therefore, in the foreseeable future, adult parameters used to

calculate the spawning biomass of Sardine off South Australia should continue to be estimated from data obtained in all adult surveys since 1998.

Detecting changes in the adult population of Sardine over time due to environmental conditions (e.g. intensity/duration of upwelling) or density dependent effects is important (see Ward *et al.* 2021). The dedicated adult sampling program conducted in 2024 strengthened our understanding of key adult reproductive parameters, which was largely consistent with the historical data. Samples collected from commercial catches in 2024, with their associated histological preparations of ovaries, were valuable additions to the adult reproductive dataset. This program should continue to be repeated every 5 years to determine if changes to adult parameters have occurred.

4.4. Spawning biomass

The estimate of spawning biomass for 2025 of 556,957 t (474,724–639,191) is above the upper target reference point of 200,000 t in the harvest strategy for the South Australian Sardine Fishery (PIRSA 2023). On this basis, the southern stock of Australian Sardine is classified as **Sustainable**. This classification is consistent with recent assessments provided in the spawning biomass report for 2024 (Grammer *et al.* 2024a), the stock assessment report for 2023 (Grammer *et al.* 2024b) and the most recent report on the Status of Australian Fish Stocks (Roelofs *et al.* 2024).

The DEPM used to estimate the spawning biomass of Sardine off South Australia in 2025 integrated data from adult sampling between 1998 and 2024, and Sardine egg density and distribution data from the ichthyoplankton survey conducted between February and April 2025. The estimate of spawning biomass for 2025 does not account for potential effects of the harmful algal bloom that first occurred in coastal waters off the Fleurieu Peninsula in March 2025, and subsequently expanded to Investigator Strait, Gulf St Vincent and Spencer Gulf during April–October 2025. Notably, (1) extensive and widespread mortalities of finfish, elasmobranchs, cephalopods, and crustaceans have been reported, but not for Australian Sardine, and (2) substantial changes in fisher behaviour, catches and effort have occurred in 2025 (SARDI unpublished data). However, all ichthyoplankton sampling in the area affected by the algal bloom for the 2025 DEPM occurred prior to the onset of the bloom in mid-March. The timing, spatial extent, and reported fishery impacts of the algal bloom to date, suggest that only a small portion of the Southern Australia stock of Australian Sardine spawning area (e.g., southern Gulf St Vincent and Investigator Strait) may have been affected. An assessment of impacts of the harmful algal bloom on South Australia's fish stocks is ongoing in 2025/26 with funding from the South Australian and Australian Governments.

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APPENDIX 1: ANNUAL AND ALL-YEARS PARAMETERS FOR ESTIMATES OF SPAWNING BIOMASS

Annual and all-years parameters used to calculate estimates of Spawning Biomass. Total A : total area sampled (km²), A : spawning area (km²); P_0 : mean daily egg production (egg·m⁻²·day⁻¹); S : spawning fraction; R : sex ratio; W : mean female weight (g); \hat{F} : batch fecundity (oocytes·batch⁻¹); F' : Fecundity / Female Weight. Errors around the estimates are standard deviation (SD). N : number of samples; n : number of individuals. F' was calculated using the all-years \hat{F} relationship with W from that year. Data sources for table: Ward et al. (2021), Grammer et al. (2024).

Time	Total A	A	P_0	P_0 SD	N. P_0	S	S SD	N.S	n.S	R	R SD	N.R	n.R	W	W SD	N.W	n.W	\hat{F}	\hat{F} SD	N. \hat{F}	n. \hat{F}	F'	F' SD
All Years	-	-	88.7	4.3	7654	0.111	0.006	251	17210	0.53	0.02	226	30713	58.3	17.9	271	17691	17967	7227	271	17691	308.4	0.6
1998	48379	32980	99.0	30.8	164	0.139	0.015	12	530	-	-	-	-	46.5	11.2	11	461	14196	5365	11	461	305.0	3.9
1999	65956	15637	50.0	14.9	213	0.179	0.020	16	715	-	-	-	-	52.4	13.0	17	738	15879	5692	17	738	303.3	3.1
2000	102198	38658	52.9	12.7	290	0.158	0.012	15	1012	0.52	0.05	15	2179	49.2	12.2	16	1032	14664	5484	16	1032	298.3	2.6
2001	132382	39131	59.7	15.6	316	0.179	0.014	10	743	0.56	0.04	10	1397	50.7	9.1	11	1002	15765	5138	11	1002	310.7	2.7
2002	131574	37462	97.4	29.1	319	0.077	0.014	23	1631	0.60	0.04	23	2932	61.8	19.5	22	1836	19289	7749	22	1836	312.1	1.8
2003	133058	42905	113.5	27.4	320	0.103	0.009	8	435	0.48	0.03	8	986	52.4	8.5	8	435	16348	4796	8	435	312.1	3.9
2004	105621	40219	145.3	41.3	284	0.166	0.016	10	412	0.52	0.03	10	879	78.7	16.2	10	413	24242	7673	10	413	308.0	3.7
2005	122831	42142	59.5	14.3	334	0.100	0.019	33	2223	0.51	0.04	33	4827	73.9	16.0	33	2228	22642	7435	33	2228	306.5	1.6
2006	119038	50121	102.4	26.5	341	0.095	0.018	20	1332	0.59	0.04	20	2445	63.1	21.8	21	1335	19362	8285	21	1335	306.8	2.2
2007	119036	50972	104.9	27.1	341	0.130	0.019	20	1084	0.54	0.06	20	2244	71.1	16.8	21	1084	21940	7342	21	1084	308.8	2.3
2009	119031	55179	66.3	14.1	340	0.156	0.022	19	1537	0.36	0.03	9	2425	59.9	13.3	19	1536	18059	6251	19	1536	301.6	2.0
2011	119449	44245	51.5	15.4	340	0.044	0.006	14	1169	0.65	0.05	13	1798	46.8	12.3	15	1171	14793	5570	15	1171	316.2	2.5
2013	119297	37953	39.0	8.7	340	0.072	0.017	9	703	0.69	0.02	9	1089	51.3	12.3	9	721	15995	5836	9	721	312.1	3.2
2014	125249	73981	92.7	20.0	355	0.041	0.006	16	886	0.57	0.02	16	1574	47.9	13.9	16	861	15046	6065	16	861	314.3	3.0
2016	122598	50551	47.7	9.9	350	0.088	0.013	9	656	0.65	0.03	9	1088	49.7	17.3	9	679	15561	6863	9	679	312.8	3.4
2017	119661	66453	136.3	25.8	343	0.120	0.019	8	504	0.53	0.04	8	1030	59.6	12.3	9	511	18518	6321	9	511	310.9	3.7
2018	120043	63215	112.4	24.6	343	0.054	0.009	9	714	0.70	0.04	9	1026	46.5	7.2	9	718	14610	4500	9	718	314.1	3.1
2019	119369	53600	68.1	16.3	339	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2020	129700	82627	94.0	18.4	379	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2022	129982	76842	97.6	19.0	381	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2023	136471	66248	93.8	26.1	403	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2024	137679	61471	152.6	33.2	405	0.162	0.022	14	924	0.37	0.06	14	2794	55.6	16.3	15	930	17178	6800	15	930	309.0	2.7
2025	140900	114640	101.3	17.4	414	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

APPENDIX 2: SARDINE EGG DENSITY AND SEA SURFACE TEMPERATURE, 2018 TO 2025

