Jack mackerel stock structure in the SPF

C.M. Bulman, E.A. Fulton and A.D.M. Smith
May 2015

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Executive summary

This brief report summarizes information on the stock structure of jack mackerel in the Small Pelagic Fishery (SPF). In particular, questions have been raised by stakeholders about the possibility of a separate stock off the east coast of Tasmania. The information considered includes genetic analyses as well as the spatial distribution of spawning, schooling and eggs.

Evidence from genetic studies is limited but suggests that sub-populations of jack mackerel *Trachurus declivis* may exist in the SPF. A 'sub-population' as defined by Richardson (1982) is a self-sustaining genetic unit of population whereas a 'stock' is the fish available to a fishery.

The study by Richardson (1982) using allozyme electrophoresis found very distinct sub-populations off Western Australia and New Zealand and that two or more overlapping but genetically distinct sub-populations may occur in south–eastern Australia i.e. in the Eastern Zone of the fishery. He concluded that an excess of homozygotes at several of the loci sampled (a Wahlund effect) was most likely caused by the presence of two or more genetically-distinct groups in eastern Australia that had been sampled from the same location. Smolenski et al. (1994), using restriction enzyme analysis of the mitochondrial DNA (mtDNA) on samples from NSW and Tasmania, found limited evidence of reproductive isolation between the two sites but some evidence for genetically distinct schools off eastern Tasmania in different years. At the request of the Expert Panel, both studies were reviewed by Ovenden (2015) who concluded that further research was needed.

Jack mackerel population structure and dynamics has generally been inferred from observations of spawning activity throughout its known range; data from reproductive studies (Stevens et al. 1984, Marshall et al. 1993, Webb 1976), ichthyoplankton surveys of eggs and larvae (Jordan et al. 1995, Neira 2005, Neira et al. 2011, Ward et al. 2015) and observations of surface-schooling behaviour (Maxwell 1979) have all been considered. Spawning occurs from late spring to early summer, firstly off southern NSW and in the GAB and progressing southwards throughout the summer. Distributional patterns of eggs and larval collected during recent ichthyoplankton surveys strongly indicate major spawning sites off southern NSW (in spring) and eastern Bass Strait (in summer). Surveys in the early 1990s also found comparable egg densities off eastern Tasmania (Jordan et al 1995), but more recent surveys have not identified eastern Tasmania as a major spawning area. Jordan et al. (1995) concluded that spawning occurred along the shelf break of the entire east coast of Tasmania in the early 1990s and supported this conclusion by observations that adult (spawning) fish became unavailable to the fishery and were therefore assumed to have moved to the outer shelf (Williams et al. (1987), no spawning fish were caught in inshore fishery samples (Marshall et al. 1993), and high biomasses of jack mackerel occurred off the shelf break on the upper slope in late summer (May and Blaber 1989).

While the overall patterns of spawning and egg distributions in the eastern zone of the SPF could be broadly interpreted as a continuum of spawning distribution, the spatial and temporal separation of the peaks of egg and larval abundances might also be indicative of genetically distinct spawning groups as suggested by one of the genetic studies. However these studies have
been conducted over two decades and the patterns may have changed over this period, with the most recent survey representing the current spawning distribution. A well-designed genetic sampling program aligned with ichthyoplankton (DEPM) surveys and fishery catch sampling would help to clarify these uncertainties.

2 Stock structure studies

2.1 Genetic studies

The Expert Panel on a Declared Commercial Fishing Activity (2014) reviewed the issue of potential localised depletion consequences on stocks of small pelagic fishes in the Small Pelagic Fishery. The issue of stock structure had been reviewed by Bulman et al. (2008) but advancement in genetic techniques in recent years opened up the possibility of re-examination of stock structure. The study by Richardson (1982) on jack mackerel Trachurus declivis suggested that there were very distinct sub-populations in Western Australia and New Zealand and that two or more overlapping but genetically distinct sub-populations may occur in south-eastern Australia. A 'sub-population' was considered by Richardson (1982) as a self-sustaining genetic unit of population whereas a 'stock' was defined as the fish available to a fishery; therefore different stocks may be based on the same sub-population or a mixture of several and that management in the latter circumstance under heavy fishing pressure would be complex.

Richardson (1982) sampled jack mackerel from 22 sites that were grouped into seven geographical areas, 'stocks': central and southern NSW, eastern Victoria, north-eastern and south-eastern Tasmania, western Bass Strait, and south Western Australia (see Fig below). He measured allelic variation in eight polymorphic loci in the nuclear DNA using allozyme electrophoresis and interpreted the distribution of that variation to identify sub-populations. Richardson (1982) found that there was an excess of homozygotes at seven of the loci sampled for which several explanations were discussed but he concluded that the most likely reason was the presence of two or more genetically-distinct groups in eastern Australia. This phenomenon is known as a Wahlund effect (see Appendix A.1 for further explanation). The Western Australia 'stock' was quite distinct from other areas but he found no evidence differentiating the western Bass Strait 'stock' from eastern Australian 'stock'. Richardson (1982) proposed that spatial ranges of adults contract while spawning and expand again later, but interbreeding does not occur between breeding populations. Richardson (1982) concluded that "the critical aspects in the breeding structure of the Australian jack mackerel population that maintain the observed structuring are still unknown and their clarification must await further research."
Smolenski et al. (1994) analysed genetic structure in the eastern Australia population from off Eden, NSW, and southeastern Tasmania using restriction enzyme analysis of the mitochondrial DNA (mtDNA). They found that genetic diversity was low and limited evidence of reproductive isolation between the two sites but that there was some evidence to suggest genetically distinct schools off eastern Tasmania were sampled in different years. The latter lends support to Richardson’s (1982) findings.

Both studies were reviewed by Ovenden (2015) for the Expert Panel, who concluded that the two studies support the existence of sub-populations in eastern Australia which presents “an important risk factor in possible localised depletion.” Ovenden (2015) also pointed out that a similar Wahlund effect has been found in Australian sardine Sardinops sagax by Dixon et al. (1993) and Yardin et al. (1998) despite the rarity of this effect being reported in population genetics studies. Ovenden (2015) asserts that if each sub-population aggregates within a small spatial range during spawning, depletion of that sub-population could have a pronounced effect on its reproductive success and subsequent recruitment. While it is unknown how this could or would affect the overall population, in terms of loss of genetic diversity an allozyme study of Smith et al. (1991 cited in Smolenski 1994) claimed the loss of heterogeneity in orange roughy was due to fishing pressure. Further research is required to determine the existence of sub-populations particularly in the Eastern Zone stock as previously concluded by Jordan et al. (1995) and Bulman et al. (2008).
2.2 Reproductive studies

Other lines of evidence for existence of different ‘stocks’ were reviewed by the Expert Panel (2014) including several hypotheses proposed to account for apparent jack mackerel movements. Maxwell (1979) proposed that jack mackerel migrated southward with the extension of the EAC and the 17°C thermocline. His assumption was based on the observation of surfacing of schools as the water reached 17°C. Webb and Grant (1979) assumed that the CSIRO aerial spotting surveys also suggested a single but migratory stock. However, Jordan et al. (1995) noted that jack mackerel are resident on the east coast of Tasmania throughout the year and might be supplemented by a small migration in summer based upon abundance estimates from the mid-east coast upper slope (Maria Island) during summer by May and Blaber (1989).

Reproductive studies on spawning fish (Stevens et al. 1984, Marshall et al. 1993, Webb 1976) and ichthyoplankton surveys of eggs and larvae (Jordan et al. 1995, Neira 2005, Neira et al. 2011, Ward et al. 2015) suggest that spawning occurs from October in the GAB and NSW through December and January off eastern Bass Strait and Tasmania to mid February contracting to more southern parts of the Tasmanian coast.

While jack mackerel are known to spawn around the whole Tasmanian coast (D. Furlani pers. comm. cited in Jordan et al. 1992), only eastern Tasmanian fish have been studied in detail. Temporal and spatial distributions of eggs and larvae of jack mackerel were determined from collections made off eastern Tasmania during the summers 1988-91 by Jordan et al. (1995). They concluded that spawning occurred all along the shelf break of the east coast and this was further supported by observations of adult fish by:

- Williams et al. (1987) who proposed that fish moved from the shelf to deeper water based on the observation that increasingly larger fish became available to the inshore fishery during autumn post-spawning
- Marshall et al. (1993) who found no spawning fish in the fishery samples from the inshore
- May and Blaber (1989) who found jack mackerel throughout the year but the highest abundance of jack mackerel occurred on the upper slope in summer when the biomass of their main prey, lanternfish Lamponyctodes hectoris also peaked.

Jordan et al. (1995) also concluded that jack mackerel are adapted to local patterns of oceanographic variability which result in interannual variability in onshore-offshore movements of eggs and larvae, and mortality rates but have no effect on the distribution of spawning locations.

2.2.1 Egg surveys

Jordan et al. (1995) found high egg densities on the shelf break and along the entire coast line although in one year high egg densities were also found on the inner shelf as a result of a La Nina event. The highest concentrations (<200 eggs per 100 m³) appeared to be off Bicheno/St Helens and also off Triabunna/Eaglehawk Neck (Fig 4 of Jordan et al. 1995 in Appendix A.1.): the highest larval concentrations (<500 larvae per 100 m³) were in similar locations (Fig 5 of Jordan et al. 1995 in Appendix A.1.). N.B. These numbers need to be multiplied by depth (up to 100m) to obtain a number in m² comparable with the following surveys and which would suggest high abundances along the entire Tasmanian east coast. Ichthyoplankton surveys in eastern Australia in 2002 and
2003 by Neira (2011) found T. declivis off southern regions of NSW in October with the greatest numbers off Jervis Bay in 2002 (1000 eggs per m$^3$) (see figures in Appendix A.1). Egg densities off other areas including Tasmania (see figures 4 & 5 of Neira (2011)) were lower (<200 eggs per m$^3$). Neira et al. (2011) concluded that spawning is progressive starting in spring in northern regions and moving progressively south to Tasmania in mid-summer and therefore the area sampled in October 2002 was not representative of the whole spawning area.

A recent survey on the spawning stock of jack mackerel in eastern Australia (Ward et al. 2015) found that eggs were concentrated around eastern Bass Strait and Flinders Island (50-500 eggs per m$^3$) and off St Helens (see Fig 4 of Ward et al. 2015 in Appendix A.1). While there is difference in scale categories used in the figures of all the studies, these results appear to correlate well with the earlier studies within the same region and time. However, this survey would have missed earlier spring spawning events if any such as occurred off NSW in October 2002.

Whether there is a distinction between spawning groups between western Bass Strait and eastern Australia is unknown: Richardson (1982) found no distinction in fish sampled from these areas and Neira et al. (1999) suggested that the eggs and larvae they collected from western Bass Strait were unlikely to have been spawned on east Tasmania due to the opposing direction of winds and currents through Bass Strait.

The evidence from all these surveys suggests spawning in the Eastern Zone moves progressively south starting in NSW (and in GAB) in spring, into eastern Bass Strait and Tasmania in summer and contracting to the most southern regions of eastern Tasmania by late summer. The most recent survey pattern suggested a broad distributional range centred in eastern Bass Strait area, but if all surveys are considered together, the spatial and temporal separation of the ‘peaks’ of egg and larval abundances that have occurred could indicate several spawning groups distributed throughout the whole range.

Whether these studies represent the spawning sites of specific sub-populations is unknown but genetic testing of eggs sampled from these areas could provide some much needed evidence. Ovenden (2015) suggested that a re-analysis of the original data using new statistical techniques may be result in a clearer picture (see section 3.7.2.3) but that re-sampling from both spawning grounds (i.e. using eggs and larvae from DEPM surveys) and from fished populations (i.e. sub-adults and adults)(see section 3.7.2.4) would provide the most definitive answers.

3 Conclusion

There is reasonable evidence from the genetic studies, in particular that of Richardson (1982), to suspect that sub-populations of jack mackerel may exist in the Eastern Zone of the SPF (and therefore quite likely across the Western Zone as well). Richardson (1982) found an excess of homozygotes at seven of the loci sampled (a Wahlund effect) and concluded that the most likely reason was the presence of two or more genetically-distinct groups in eastern Australia. It is also clear that the fish sampled from southern Western Australia were genetically distinct. Smolenski et al. (1994) using restriction enzyme analysis of the mitochondrial DNA (mtDNA) on samples from NSW and Tasmania, found limited evidence of reproductive isolation between the two sites but some evidence of genetically distinct schools off eastern Tasmania in different years.
The distribution of eggs and larvae collected during the several ichthyoplankton surveys strongly indicate major spawning sites off eastern Bass Strait and southern NSW with smaller aggregations at more southerly locations off eastern Tasmania. Whether these locations are the sites of sub-populations or are just the extremities of the broad distributional range is unknown.

A well-designed genetic sampling program aligned with ichthyoplankton (DEPM) surveys and fishery catch sampling would have a high chance of determining the stock structure of jack mackerel in the eastern zone of the SPF (and across zones), enabling appropriate and precautionary management of the stocks into the future (Stephenson, 1999).

4 References


Fisheries Research and Development Corporation Project No 1994/024. (SARDI: Adelaide, SA.)
5 Appendices

A.1 Figures of egg distribution from Neira (2011).

Figure 4. Distribution of pelagic eggs of jack mackerel (Trachurus decliventis) along shelf waters of southern NSW during October 2002 and October 2003 (data combined for the two surveys).
Figure 5. Distribution of pelagic eggs of jack mackerel (Trachurus declivis) along shelf waters of southern NSW through to central eastern Tasmania during February 2003 and February 2004 (data combined for the two surveys).
Fig. 4. *Trachurus declivis* egg concentrations (no. per 100 m²) during the summers of (A) 1988–89, (B) 1989–90 and (C) 1990–91. Note additional offshore stations sampled during CR 89-2 and CR 89-3. X indicates station not sampled.

Source: Jordan et al. 1995.
Fig. 6. *Trachurus declivis* larval concentrations (no. per 100 m³) during the summers of (A) 1988–89, (B) 1989–90 and (C) 1990–91. Note additional offshore stations sampled during CR 89-2 and CR 89-3. X indicates station not sampled.

Source: Jordan et al. 1995
4. Results

4.1 Environmental Variables

4.1.1 Sea surface temperature

Sea surface temperatures (SSTs) ranged from 14.3 to 25.8°C (Figure 4) during January 2014. The highest temperatures were recorded in the north and the lowest in the south.

Figure 4. Sea surface temperature (SST) with egg densities of Jack Mackerel and 50 m depth contours.
A.2 Other useful information

**Wahlund Effect**

The Wahlund effect is the reduction in the overall heterozygosity of a population as a result of subpopulation structures. Essentially, if two or more subpopulations have independent allele frequencies then the overall heterozygosity is reduced, irrespective of whether those subpopulations are in Hardy-Weinberg equilibrium. The most common cause is a geographical barrier to gene flow between the subpopulations, followed by independent genetic drift in each subpopulation.

The simplest example is where you have a population, P, with the allele frequencies of A and a given by p and q, respectively (where \( p + q = 1 \)). Suppose this population is split into two subpopulations, P1 and P2, and that all the dominant A alleles are in subpopulation P1 and all the recessive a alleles are in subpopulation P2 (this is a feasible consequence of genetic drift). This means there are no heterozygotes, even though the subpopulations are in Hardy-Weinberg equilibrium.

To make a slight generalisation of the above example, let \( p_1 \) and \( p_2 \) represent the allele frequencies of A in P1 and P2 (and likewise let \( q_1 \) and \( q_2 \) represent the frequencies of a). Suppose the allele frequencies in the two subpopulations P1 and P2 are unequal (i.e. \( p_1 \neq p_2 \) and \( q_1 \neq q_2 \)) and suppose that each subpopulation is in Hardy-Weinberg equilibrium, so that the genotype frequencies in each subpopulation are \( p_1^2, 2p_1q_1 \) and \( q_1^2 \) (where the sum of these is 1). Then the heterozygosity of the overall population is given by the mean of the two:

\[
\frac{(2p_1q_1) + (2p_2q_2)}{2}
\]

which cancels out to give \( p_1q_1 + p_2q_2 \), or \( p_1(1 - p_1) + p_2(1 - p_2) \), which is always smaller than \( 2pq(1 - p) = 2pq \) unless \( p_1 = p_2 \).

*Source: http://genetics-notes.wikispaces.com/Wahlund+effect*

**Expert Panel (2014).**

Ovenden (unpublished), reviewed genetic studies on the SPF target species and supported Richardson’s (1982) suggestion that overlapping, but genetically distinct, populations of jack mackerel probably occur as a result of spawning site fidelity. Maxwell (1979) proposed that jack mackerel migrated southward with the 17°C thermocline as the EAC extended, based on observations that jack mackerel schools surfaced when the SST was 17°C. Jordan et al. (1995), however, asserted that a resident population occurs in eastern Tasmania which might be supplemented by a small southerly migration. They thought resident schools surfaced as the thermocline advanced rather than a migrating school. Following the thermocline. This hypothesis tends to support the original conclusion of distinct populations on the east coast of Tasmania but also highlights an association of jack mackerel with SST.

Whenever hypothesis to correct, jack mackerel off eastern Tasmania were found to move from shelf to deeper water to spawn during the summer probably to avoid the more variable surface conditions of the EAC (Jordan et al. 1995). This migration to deeper water, leaving the smaller non-spawning fish on the shelf, rendered them less susceptible to capture. A peak in landings indicated that adults returned to the shelf in autumn (Jordan et al. 1995). Coincidentally, deeper ‘jack mackerel’ took advantage of the ‘bloom’ of mesopelagic fish that occurs on the upper slope at this time which follow the primary productivity blooms in the early summer (Blaber and Bulman 1987, May and Blaber 1989). These observations again suggest an ‘association’ of jack mackerel with oceanographic conditions that are favourable to them when they are spawning or feeding and which would dictate their behaviour and movement, and consequently, their susceptibility to capture.
5.1.1 Stock structure

Genetics

There are two genetics-based studies into jack mackerel in Australian waters. The first study by Richardson (1982) used allozymes to determine that the Western Australian (western GAB) jack mackerel were distinct from the New Zealand populations but the eastern populations were less clearly defined. In the south-eastern samples, five enzymes exhibited an excess of homozygotes presumed to be a result of two or more overlapping but genetically distinct populations.

The second study by Smolenksi et al. (1994) used 6– and 4–base restriction enzyme analyses to investigate the southeastern Australian jack mackerel populations, by comparing fish from off Eden, NSW to those of south-east Tasmania. They found that there was limited evidence using the 6–base analyses based on the occurrence of a rare haplotype in the Tasmanian samples but that overall, the analyses were not significant. The 4–base analysis also showed no separation between locations however there was evidence of genetically distinct schools off Tasmania between years, i.e. the 1990 Tasmanian sample appeared to be genetically distinct from all other samples. The results supported the assumption that jack mackerel maintain school fidelity but that in years when their major prey Nyctiphanes australis is low in abundance, they disperse into deeper water to find food, thus the school disintegrates. Smolenksi et al. (1994) suggested that increased mortality from variable hydrographic conditions and greater exposure to predation on eggs and larvae during and post-spawning, could result in a reduction in effective population size and consequently in mtDNA diversity.

The two studies support the view that there are genetically distinct populations of jack mackerel; one in the GAB and one in eastern Australia.

Morphometrics

Lindholm and Maxwell (1982) used principal component analysis of morphometric measurements and meristic counts from jack mackerel from the GAB, NSW and Tasmania to determine significant separation between the GAB and the NSW samples. The Tasmanian fish overlapped with NSW fish suggesting no differences between the fish (contrary to their conclusions, and partially with GAB. The fish from GAB were generally smaller so allometric growth differences might account for the morphological differences however the sizes did overlap therefore there is not strong evidence.

Parasite indicators

There are no studies of parasite indicators in Australian fish. However, Maxwell (1982) studied cymothoid isopod C. imbricatus infestations in jack mackerel collected from southeastern Australia, from Eden to off Bruny Island, (southeast Tasmania). The linear relationships between size of parasite and hosts suggested that juvenile jack mackerel were infected while schooling in shallow inshore waters, and the low overall infestation rate and lack of small isopods in adult fish suggests that further infestation by adults from adults does not occur.

Size structure

Stevens & Hausfeld (1982) found that fish larger than 30 cm (FL) were absent from samples south of 39°S (i.e. from Flinders Island and southwards) but there were fewer fish between 10–25 cm in samples north of 39°S. Contrary to these findings, larger fish were caught in the Tasmanian purse seine fishery from 1984 to 1994. Pullen and Lyle (1994) found that the mean monthly size of jack mackerel for each season of the purse
seine fishery from 1984 to 1994 was usually >30 cm until the 1990s. Furthermore, pelagic fish (21–37 cm) were caught up to 360 m deep over the slope off Maria Island (east Tasmania) (Blaber and Bulman 1987).

**Reproduction and spawning**

Jack mackerel, like most *Trachurus* species, are serial spawners although neither the spawning frequency nor the number of batches spawned per season has been determined (Marshall et al. 1993). Annual fecundity has also proven indeterminable. Marshall et al. (1993) found that the mean age of maturity based on the more commonly accepted stage at which vitellogenesis occurs, stage 3, was 31.45 cm FL. This value is larger than the 24–24.9 cm TL of Webb and Grant (1976) who based maturity on macroscopic stage 2. Eggs are pelagic and spherical, and of between 1.1–1.3 mm diameter (Neira et al. 1998).

Jack mackerel are known to spawn around the whole coast of Tasmania (D. Furlani pers. comm. cited in Jordan et al. 1992) and in the GAB (Stevens et al. 1984). These separate spawning locations represent what is thought to be distinct stocks (Richardson 1982). In the GAB, jack mackerel spawn in summer (Shuntov 1969). During ichthyoplankton surveys of southeastern Australian waters in summer 1997 and winter 1998, Neira et al. (1999) caught jack mackerel larvae almost exclusively during the summer and most abundantly in western Bass Strait. They suggested that these larvae belonged to a South Australian–GAB population because it was highly unlikely that larvae spawned off east Tasmania could be transported against prevailing currents and winds to the region. Whether there is a distinction between NSW and Tasmanian stocks is unclear. Maxwell (1979) presumed that jack mackerel migrated south from NSW in summer following the 17 °C isotherm. However, Jordan et al. (1995) noted that there is resident winter population of jack mackerel on the east coast of Tasmanian and that it might only be boosted by a spring migration from the north.

Maxwell (1979) suggested that jack mackerel in NSW waters spawn earlier than in Tasmania, from October through to January. Off eastern Tasmania, jack mackerel spawn between mid-December and mid-February (Marshall et al. 1993, Jordan 1994, Jordan et al. 1995, Neira et al. 1998). Jordan et al. (1995) investigated spawning over 3 years off eastern Tasmania, and found little difference in timing between years despite interannual variability in oceanographic conditions. Spawning occurred on the shelf break with some spread inshore in certain years when a strong intrusion of EAC surface waters appeared to heavily influence distribution. Larvae of jack mackerel have been caught in coastal waters of eastern Tasmania from December to April (Marshall and Jordan 1992 cited in Neira et al. 1998), and in eastern Bass Strait in February (Neira 2005).
Ichthyoplankton surveys in eastern Australia (Neira et al. 2007) found *Trachurus* spp. eggs and larvae distributed from southern Queensland down the east coast in October 2002 and 2003, February and July 2004, and off east Tasmania in February 2003 (Fig 14 but see Figs 9.1–9.4 in Neira et al. 2007 for complete data). Eggs of species of *Trachurus* are visually indistinguishable but given the known ranges of jack mackerel and yellowtail scad (Kailola et al. 1993), the eggs found off southeast Victoria and northeast Tasmania likely to be jack mackerel and eggs and larvae collected off southeast Queensland and NSW were presumed to be yellowtail scad (Neira et al. 2007). Larger larvae can be differentiated, however, and preliminary DNA analysis of the early preflexion larvae collected during these surveys indicate that jack mackerel and yellowtail scad (Kailola et al. 1993), the eggs found off southeast Victoria and northeast Tasmania likely to be jack mackerel and eggs and larvae collected off southeast Queensland and NSW were presumed to be yellowtail scad (Neira et al. 2007). Larger larvae can be differentiated, however, and preliminary DNA analysis of the early preflexion larvae collected during these surveys indicate that jack mackerel occur in the southern region of the survey area, that they mix with yellowtail scad e off central NSW and only yellowtail scad occur in the northern regions (Neira et al. 2007). Analyses of *Trachurus* sp. egg abundances, average SST and salinities from the top 10 m indicated two groupings of high egg abundance: one group associated with an average temperature of 17 °C reflecting high jack mackerel larval abundance and another group associated with average temp of 19.5–20.5 °C reflecting high yellowtail scad larval abundance (F. Neira [TAFI] 2007, pers. comm.).

*Trachurus* eggs and larvae were also found off South Australia during 2003, 2004 & 2005 and a few in the western GAB in 2006 (Neira et al. 2007). However, the numbers were far fewer despite the fact that previous studies have found reproducitively active jack mackerel. Neira et al. (2007) concluded that the low numbers were because the surveys did not coincide with peak spawning season, which was previously determined to be September-January by Stevens et al. (1984).