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Functionally distinct adult assemblages within a single breeding stock of the sardine, *Sardinops sagax*: management units within a management unit

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Abstract

Distribution of *Sardinops* eggs from seven surveys off southern Western Australia (WA) were assessed to determine if there were separate concentrations of spawning adults. Ten year series (1989–1998) of both age compositions and gonadosomatic indices (GSIs), obtained from routine sampling of commercial catches, were also analysed to aid assessment of stock structure of *Sardinops* from three regions on the southern WA coast. The patterns in the distribution of *Sardinops* eggs provided evidence for the existence of distinct centres of spawning that were joined by intervening areas of less spawning activity. Together with regional differences in mean GSI and independence of age compositions between regions in 5 of the 10 years examined, these results indicate that there is not wide-scale mixing of mature age classes between the three regions. As first vulnerability occurs at time of maturity, these non-mixing assemblages are termed functionally distinct adult assemblages (FDAAs) and may persist due to fitness-related ties to localised areas of higher habitat suitability in a region of the world with an oligotrophic pelagic ecosystem. Alternatively, given that the interrelationships between pre-recruit *Sardinops* across the three regions are poorly understood, it is also possible that behavioural mechanisms, such as natal homing, may be involved in maintaining distinctness of the FDAAs. Regardless of the cause of non-mixing, when fisheries exploit spatially limited but disjunct parts of a single breeding stock, the exploited portions of the stock may in some cases also be considered as distinct for the purposes of management.

Keywords: *Sardinops sagax*; Stock identification; Age composition; Fisheries management units

1. Introduction

Sardinops sagax are a dominant vertebrate resource of the world's eastern current upwelling systems (e.g. Lenanton et al., 1991) and of the Kuroshio Current system; this monotypic genus sometimes dominates the world's annual production of marine fish with annual landings often exceeding 10 million tonnes (e.g. Fréon and Misund, 1999). However, catches in Australia are comparatively small because in this region *Sardinops* live in comparatively oligotrophic waters with neither substantial upwelling systems nor extensive frontal zones (Gaughan et al., 2001a). The largest fishery for *Sardinops* in this broad region has traditionally been in southern Western Australia (WA), with purse seine fisheries for *Sardinops* located

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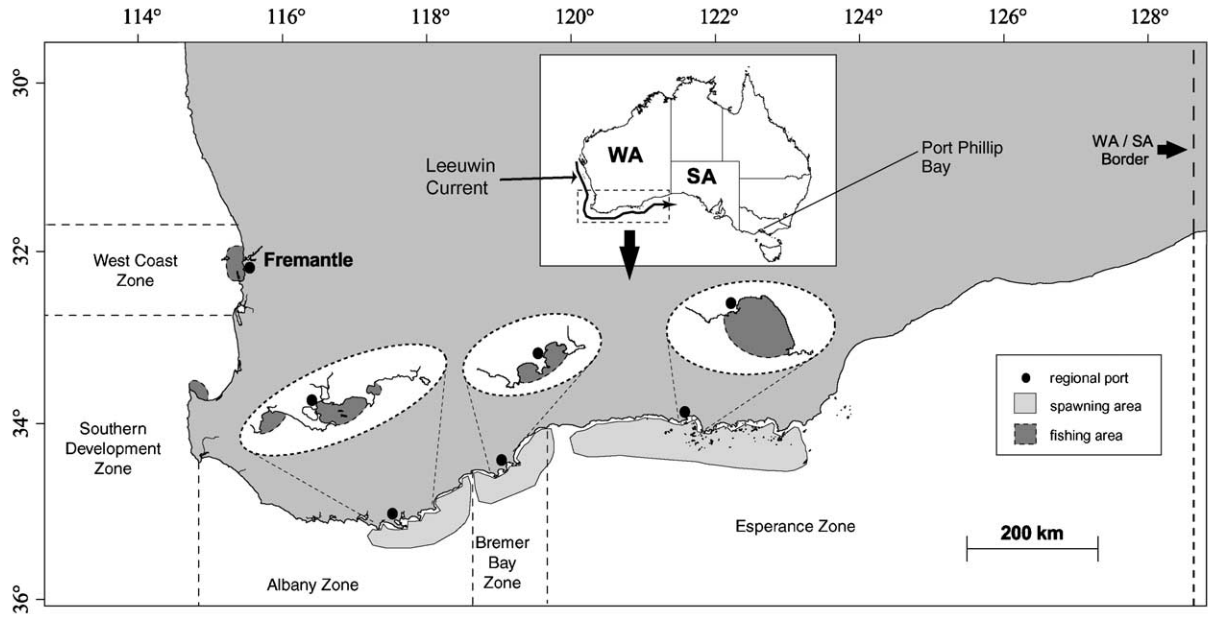

Fig. 1. Purse seine fishing zones in WA for which *S. sagax* constitutes the primary exploited species. The fisheries at Albany and Bremer Bay operate close to port and within 5 km of shore. In the Albany region, fishing also occurs in embayments to the east and west of the town. Fishing at Esperance and Fremantle (not included in this study) extends further offshore (∼15 km) to target locations where *Sardinops* are known to aggregate. A stylised trajectory of the Leeuwin Current, the dominant oceanographic feature of shelf waters in southern WA, is also shown.

off the towns of Albany, Bremer Bay and Esperance (Fig. 1). *S. sagax* in southern WA live to a maximum age of 8 or 9 years (Fletcher and Blight, 1996). Recruitment to the fishery begins at about 2 years of age, with full recruitment at 4–5 years (Fletcher, 1995). Management has primarily operated through individual transferable quotas (ITQs) and total allowable catches (TACs); these are adjusted separately for each south coast management zone on an annual basis. Annual catches for the whole region peaked at 8400 t in 1988, all of which came from Albany in what was the last year prior to the implementation of ITQs for this region (Fig. 2). Since detailed research on the purse seine fisheries commenced in 1988, the combined spawning biomass of *Sardinops* across the south coast was estimated to reach a maximum of about 85 000 t in 1994 (Hall, 2000).

In an allozyme study of *Sardinops* in Australia, Dixon et al. (1993) found evidence for a series of quasi-independent subgroups around the southern coast of Australia. However, the level of variation was sufficiently inconsistent to preclude a clear interpretation of the relationships between these groups, and the results therefore did not permit delineation of genetic stocks. Evidence of low genetic variation among *Sardinops* from southern WA indicated by Dixon et al. (1993) is not surprising given the substantial eastward advection of spawning products, due to the Leeuwin Current (see Fig. 1), between Albany and Bremer Bay, and possibly also to the Esperance region (Fletcher et al., 1994). Furthermore, because there is no recognised nursery area for pilchards off the south coast of WA nor in South Australia (Gaughan et al., 2001b), the fate of fish arising from any one region is unknown over the first 2 years of life. However, following the eastward advection of *Sardinops* larvae within southern WA, and possibly also to South Australia (Gaughan et al., 2001b), there is no recognised oceanographic feature that assists in the westward return of pre-recruits. We therefore assume that the "return migration" must be undertaken solely by swimming. Given the eastward advection of early progeny and the approximate 2-year period between spawning and recruitment to the fishery, there appears

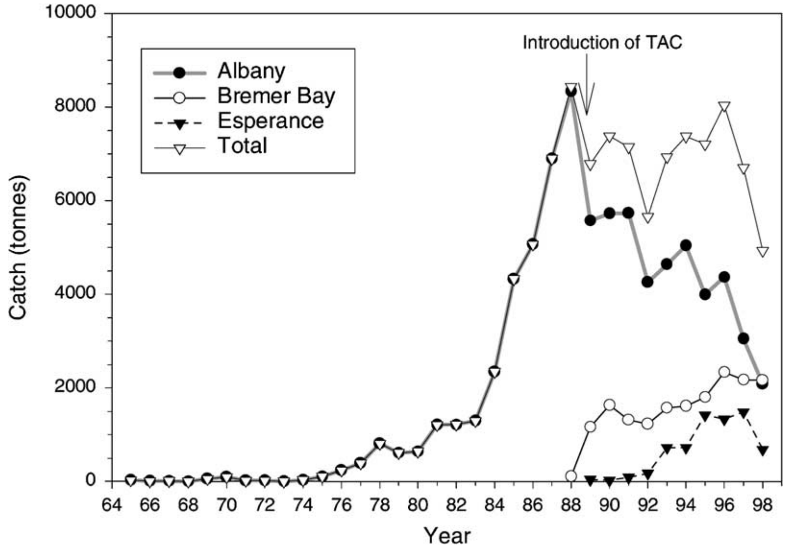

Fig. 2. Annual catches of *S. sagax* from three regions on the south coast of WA.

to be ample time for pre-recruits of different spatial origin to mix both with each other and with mature fish within the different regions. Such a scenario of juvenile dispersal and mixing, and without involvement of an adult spawning–migration, has been described for Icelandic cod off West Greenland and Scotian shelf haddock (Frank, 1992). Because relatively little reproductive exchange between groups is required to maintain genetic homogeneity (e.g. Bembo et al., 1996; Pawson and Jennings, 1996) there is thus wide scope for genetic mixing of *Sardinops* off southern WA over short time scales.

Analysis of the stable isotope ratios of oxygen and carbon obtained from whole sagittal otoliths of adult *Sardinops* (>2 years old) has indicated that the exploited assemblages in the Albany, Bremer Bay and Esperance regions are non-mixing (Edmonds and Fletcher, 1997). Differences in oxygen isotope ratios, in particular, indicate that the Esperance *Sardinops* are distinct from those at Bremer Bay and Albany. These differences reflect the consistent eastward decrease in mean water temperature between Albany (18.3 °C) and Esperance (17.6 °C), noting that oxygen isotopes are deposited in equilibrium with temperature (e.g. Devereux, 1967). Even though Albany and Bremer Bay are geographically close (150 km apart), and a temperature-based difference in otolith chemistry might not be expected over such scales, *Sardinops* in these two regions still exhibited significant differences in the carbon isotope ratios (Edmonds and Fletcher, 1997).

A spatial discontinuity in the distribution of *Sardinops* eggs between Albany and Bremer Bay during winter (July 1991), and the occurrence of eggs only at the former region during summer (December 1991), had previously led Fletcher et al. (1994) to suggest that the adult assemblages at these two regions, later shown to be spatially separate (i.e. using the otolith isotopic ratios), could function separately as adult populations. In consideration of this and the possibility of substantial mixing of pre-recruit stages, our hypothesis is therefore that *Sardinops* off the south coast of WA consists of three functionally distinct adult assemblages (FDAAs) that are, however, directly linked by early life-history stages and thus contribute to a common pool of recruits. *Sardinops* fisheries in southern WA have been managed for several years with respect to this concept of stock structure. The alternative hypothesis of some members of the WA purse seine fishing industry is that *Sardinops* mix extensively across the three south coast management zones.

The aim of this paper is to examine aspects of the reproductive biology and age composition of *Sardinops* in southern WA in order to further explore the FDAA hypothesis in an holistic manner, as recently recommended by Begg and Waldman (1999). Distribution of *Sardinops* eggs in years subsequent to those presented by Fletcher et al. (1994) are examined for evidence of regional population concentrations (e.g. Begg et al., 1999), which may indicate reproductive separateness. Annual spawning patterns and age compositions over a 10-year period from 1989 to 1998 are also compared between Albany and Bremer Bay, with comparisons for Esperance from 1992 to 1998. Such characteristics compliment the information from other techniques that have been previously used and, as with life-history parameters, can assist in delineating genetically similar assemblages for which certain age classes remain largely separate (Begg and Waldman, 1999; Begg et al., 1999).

2. Material and methods

2.1. Egg distributions

Seven surveys of *Sardinops* eggs in southern WA were undertaken between July 1992 and 1995; these were initially planned with the specific objective of assessing stock structure, but some were subsequently also used to estimate egg production as part of daily egg production method (DEPM) estimates of spawning biomass (Fletcher et al., 1996). The surveys focussed on the south coast from Albany to Esperance. Eggs were collected using 500 and later 300 μm mesh bongo nets and surveys attempted to cover all of the continental shelf. Because *Sardinops* eggs in southern WA hatch in about 2 days and can be subjected to considerable alongshore advection (Fletcher et al., 1994), plots of only Day 1 (<24 h old) egg densities for these surveys were examined to determine if there was evidence of spatially separate concentrations of spawning *Sardinops*.

To clarify interpretation of egg concentrations, sampling stations between Albany and Esperance were assigned to alongshore strata, or blocks, consistent with those of Fletcher et al. (1994). Adherence to previously delineated strata allowed the grouping of plankton samples to be undertaken objectively. Each stratum represented about 40 km of coast and contained 2–27 sampling stations.

2.2. Sample collection and processing

Samples of *Sardinops* were obtained monthly from the commercial fleets at Albany, Bremer Bay and Esperance (Table 1). The fish landed at each port are caught only within that same region (Fig. 1); purse seining for *Sardinops* at all of these regions occurs relatively close to shore, typically at depths less than 50 m. The proportions of the stocks vulnerable to fishing at any one time have not been determined. However, although the distribution of *Sardinops* in each region extends beyond the fishing areas, both offshore and alongshore (see Fig. 1), it is likely that seasonal patterns in landings reflect stock availability and thus that the samples obtained from commercial

Table 1
Numbers of samples (and number of months sampled) of *S. sagax* from commercial catches, plus numbers ≥2 years old aged and numbers of female GSI measured at each of the three regions of southern WA between 1989 and 1998

Year	Albany			Bremer Bay			Esperance		
	Number of samples (months)	Number of aged	Number of GSI	Number of samples (months)	Number of aged	Number of GSI	Number of samples (months)	Number of aged	Number of GSI
1989	243 (12)	1249	920	60 (11)	534	189	25 (5)	537	65
1990	189 (12)	1539	1101	77 (12)	619	449	3 (3)	13	14
1991	160 (12)	1874	1431	64 (12)	625	602	22 (9)	143	166
1992	106 (12)	702	1035	55 (12)	536	525	24 (8)	134	230
1993	89 (12)	1448	879	79 (12)	1344	766	44 (9)	747	414
1994	95 (12)	973	957	62 (12)	686	440	45 (12)	406	327
1995	120 (12)	1384	1204	102 (12)	1085	995	62 (11)	553	574
1996	115 (12)	1046	1042	102 (12)	1048	951	42 (11)	266	315
1997	124 (12)	1042	1139	120 (12)	1075	1133	54 (11)	477	526
1998	105 (10)	1427	1064	59 (10)	746	523	50 (7)	486	678

catches are representative of the stock in each area. The presence of post-ovulatory follicles in *Sardinops* caught by commercial fishing during peak spawning periods (Fletcher et al., 1996) indicated that females involved in recent (<1–3 days) spawning activity were vulnerable to the fishery. Thus, although spawning *Sardinops* have not traditionally been caught in southern WA and are therefore probably less vulnerable to purse seining, there appears to be only a short delay before they become "fully" vulnerable again. This indicates that any offshore movements associated with the spawning season are unlikely to constitute an important source of bias in samples collected from commercial fishing.

In some months few or no samples were obtained, while in other months 10–15 samples, each of $\geq$25 fish, were obtained from each region (i.e. 250–400 individuals per region each month). Cost–benefit analysis indicated that this number of samples was sufficient to adequately represent the commercial catch in each month. The total number of samples collected at each region each year varied from low (i.e. less than 30) to in excess of 100 (Table 1), with each usually coming from a single catch from a single school. Given the assumption that the samples were representative of the stock, Esperance data for 1989 and 1990 were removed from the analysis because they were each based on catches obtained in fewer than 6 months of the year (Table 1) and thus considered unreliable.

The fork length, weight, sex and gonad weight was measured for 25 randomly selected individuals from each sample. The sagittal otoliths were removed from the first 5–20 fish in each sample and later used to assign ages using the otolith weight/age relationship for *Sardinops* in southern WA developed by Fletcher (1991, 1995). The regional proportion at each age was then determined for each month.

2.3. Gonadosomatic indices (GSIs)

The weight and gonad weight of female *Sardinops* were used to calculate GSIs, which were considered proxy indicators of spawning activity. The annual number of GSI estimates for each region typically exceeded 300 (Table 1). ANOVA was used to model the effects of region, month and year, with age considered a covariate. Monthly GSI data are typically skewed, and the profile likelihood function for a Box–Cox transformation model (Box and Cox, 1964) suggested a fourth-root transformation as optimal for normalising the response. Since GSI data arose from samples of commercial catch, the design was unbalanced and some months from particular regions contained little data. Data from adjacent months were pooled to reduce this lack of balance (i.e. January and February pooled, March and April pooled, etc.).

2.4. Age composition

Relative age distribution and numbers of fish caught (total catch/mean weight) in each month were used to generate annual catch-at-age data for each region. The time series of catch-at-age data were compared using a multivariate regression tree (MRT, De'ath, 1999), which are a natural extension of univariate classification and regression trees to accept a multivariate response. The explanatory variables used in the MRT were derived variables describing the shape of the region–year distributions, namely the average, median, variance, skewness and kurtosis. While this method can produce a classification tree that could ultimately separate every region by year distribution, cross-validation by single-case deletion (due to the low number of region–year combinations) was used to examine the relative predictive error so as to produce a tree with the optimum number of levels, or terminal nodes. An optimal size tree was chosen on the basis that it had the smallest number of terminal nodes with a concomitant relative predictive error within 1 S.E. of the tree-size with the smallest relative predictive error (Breiman et al., 1984). The Manhattan metric (sum of absolute differences) was used to define dissimilarity between group centroids.

3. Results

3.1. Egg distribution

Along the south coast of WA there was an almost continuous distribution of *Sardinops* eggs between Albany and Esperance during each July from 1992 to 1994 (Fig. 3). However, the abundance of eggs was uneven along the coast, with regions of high concentrations interspersed with regions of low concentrations. Notwithstanding the gaps in the distribution of

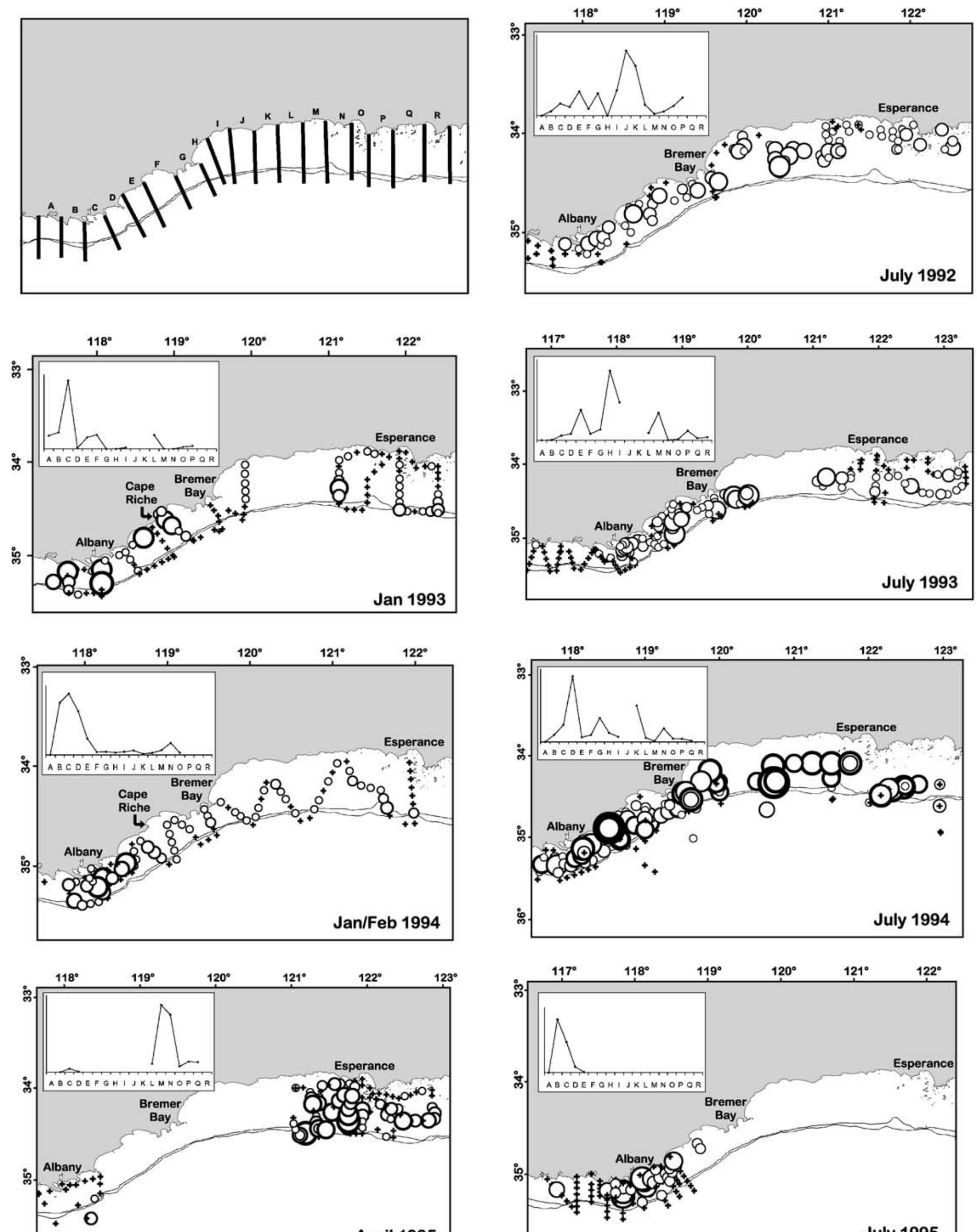

Fig. 3. Expanding-symbol plot of the distribution of Day 1 (<24 h old) *S. sagax* eggs between Albany and Esperance off southern WA from individual surveys between July 1992, 1993 and 1995. For each survey, the mean concentration of eggs in strata corresponding to approximately 40 km of coastline as in the upper left panel are also shown. Crosses represent stations with zero Day 1 eggs. The edge of the continental shelf is shown by the 100 and 200 m depth contours.

Table 2
Results of ANOVA (sequential sums of squares) on GSIs (fourth-root transformed) of female *S. sagax* from three regions in southern WA between 1989 and 1998

Effect	d.f.	SS	MS	F-value	Level of significance
Age	1	33.120	33.120	935.265	<0.0000
Month (pooled)	5	338.563	67.712	1912.164	<0.0000
Region	2	54.446	27.223	768.770	<0.0000
Year	9	66.960	7.440	210.102	<0.0000
Month × region	10	51.127	5.113	144.379	<0.0000
Month × year	45	63.770	1.417	40.019	<0.0000
Region × year	18	23.525	1.307	36.908	<0.0000
Month × region × year	79	30.200	0.3823	10.795	<0.0000
Residual	20303	718.959	0.0354		

samples in some surveys, multiple peaks were evident in each survey except that in July 1995 which focussed on the Albany region. Demarcations in mean egg concentrations at block D in January 1993 and block E or F near Cape Riche during winter (Fig. 3) indicate a level of separation between spawning centres at Albany and Bremer Bay. Although a similarly consistent demarcation between Esperance and Bremer Bay was not evident, peaks were nonetheless present concurrently in each of these regions in July 1993 and 1994. The April 1995 survey was undertaken when it became apparent from examination of GSI data that

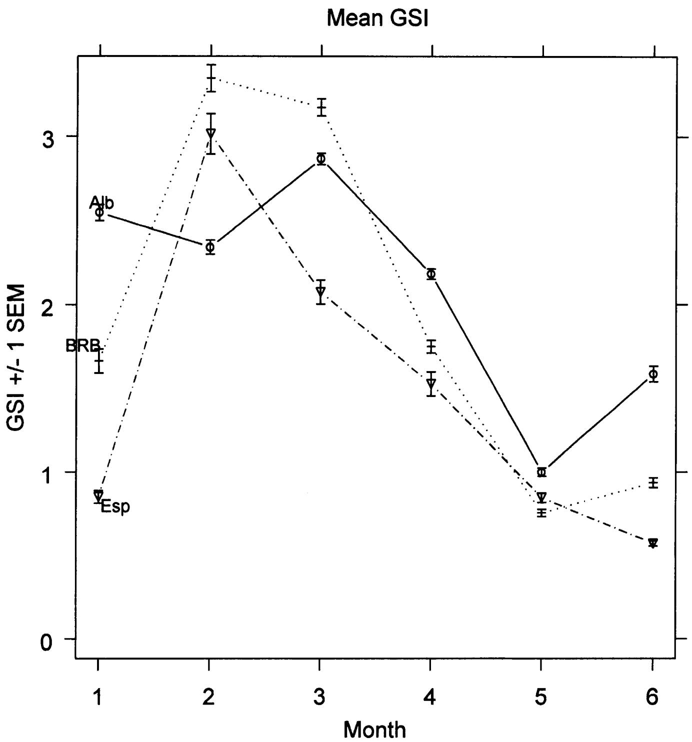

Fig. 4. Monthly (pooled; 1: January–February, 2: March–April, etc.) GSI of *S. sagax* at three zones on the southern coast of WA. The mean (±S.E.) were derived from data pooled across the years 1989–1998 for Albany (Alb) and Bremer Bay (BRB) and from 1991 to 1998 for Esperance (Esp).

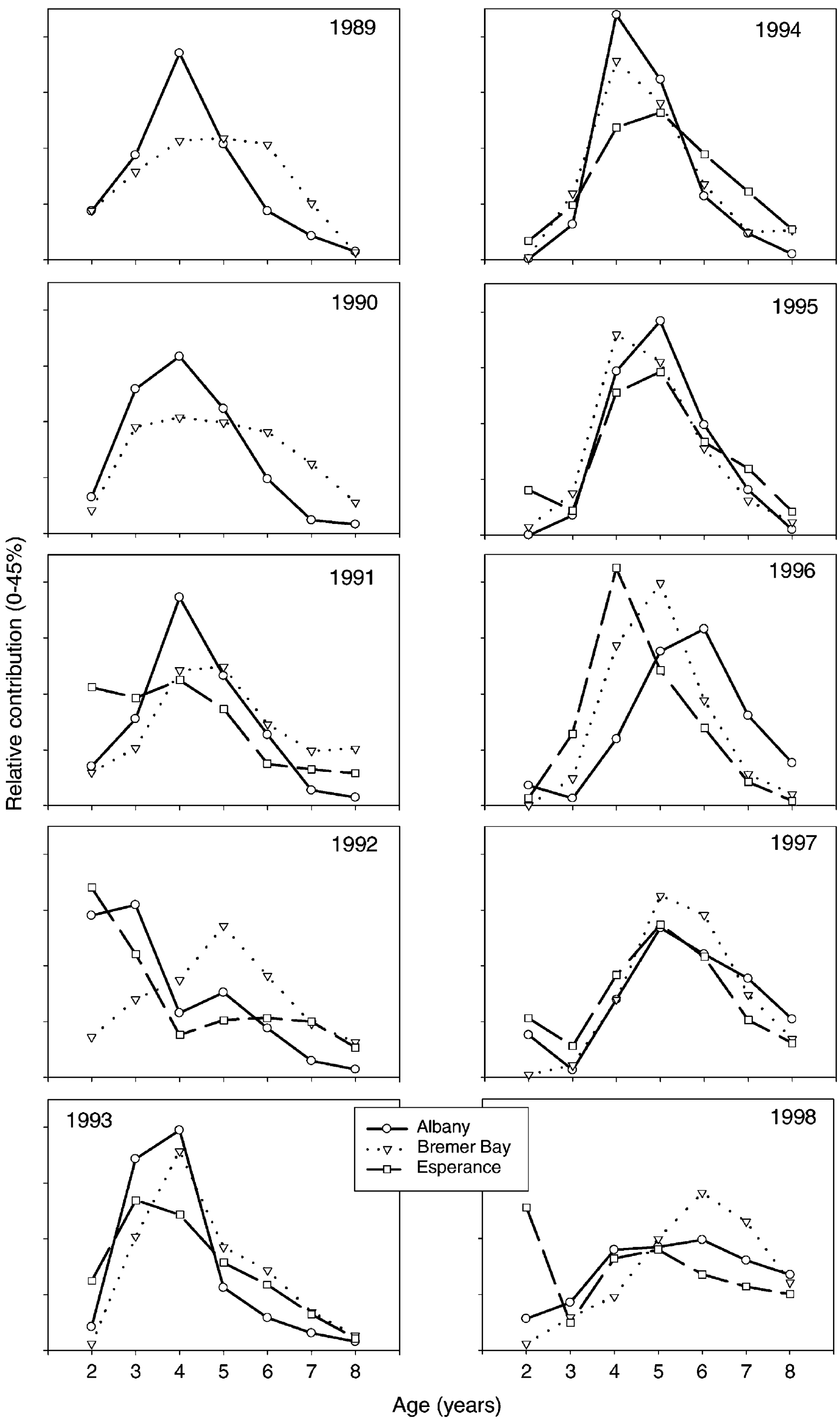

Fig. 5. Annual relative age composition for commercial catches of *S. sagax* at three fishing zones on the southern coast of WA between 1989 and 1998. The few data from Esperance for 1989–1990 were not sufficient to warrant inclusion in this study.

the peak spawning period for *Sardinops* at Esperance was during autumn (March–May). The high egg concentrations at Esperance and very low concentrations at Albany in April 1995, opposite to the pattern in January 1994, confirmed this difference in spawning times between these regions (Fig. 3).

3.2. Gonadosomatic indices

GSI differed significantly between year, month and region, as well as for the covariate age and each interaction term (Table 2). Since ANOVA models with large numbers of residual degrees of freedom will often provide results with all terms significant, it is instructive to examine the proportional contribution of each term to the total explained variance and the *F*-values for individual terms. High *F*-values for month and age reflect, respectively, the expected seasonality of spawning and increase in reproductive capacity with size. The next highest *F*-value was for region, which indicates that this effect can be considered as important. The significant region × month effect had the highest *F*-value of the interaction terms, but accounted for only 7.7% of the explained variance. Data pooled across years and ages shows some key differences in annual spawning patterns (Fig. 4). GSI was high in Albany from January–February to July–August, in Bremer Bay from March–April to May–June and in Esperance only in March–April (Fig. 4). The longer term pattern is thus for the length of the spawning season to decrease from west to east.

3.3. Age composition

Differences in relative age composition between regions were apparent in most years between 1989 and 1998 (Fig. 5). There was a high degree of similarity between all three regions in 1995 and 1997 but in other years there were large differences in the contribution by some age classes (Fig. 5). Cross-validation by

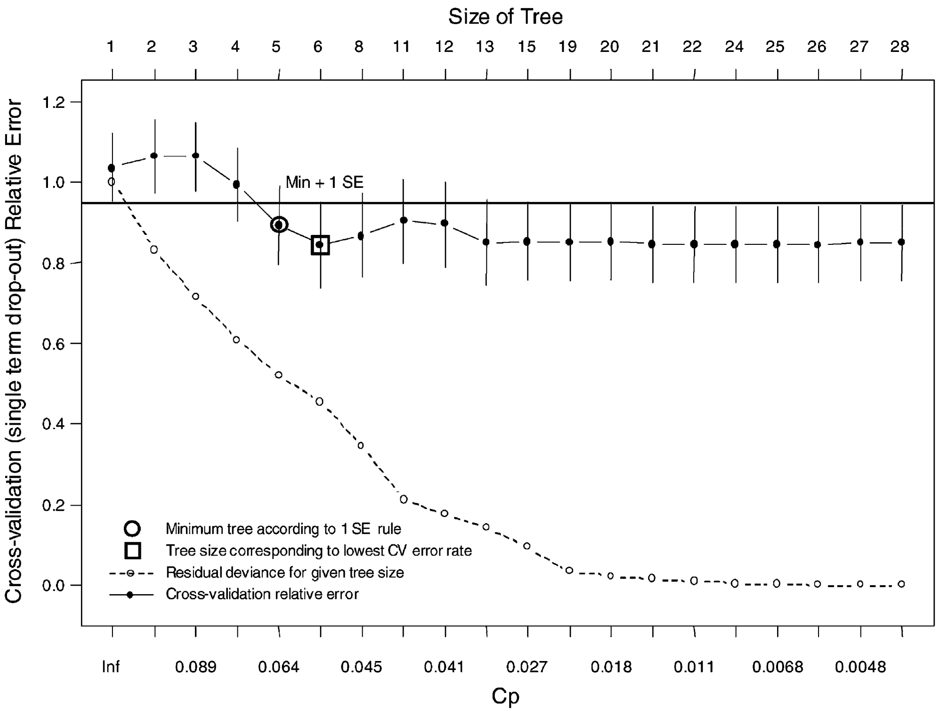

Fig. 6. Cross-validation error plot for MRT of *S. sagax* age-distribution characteristics. Residual deviance decreases with given tree-size (lower dashed line, open circles). Cross-validation relative error (±1 S.E.) by single-case deletion (filled circles) identified a minimum relative error at tree-size 6, with a tree-size of 5 suggested by the 1 S.E. rule. The dashed horizontal line is positioned at the minimum cross-validated error plus 1 S.E.

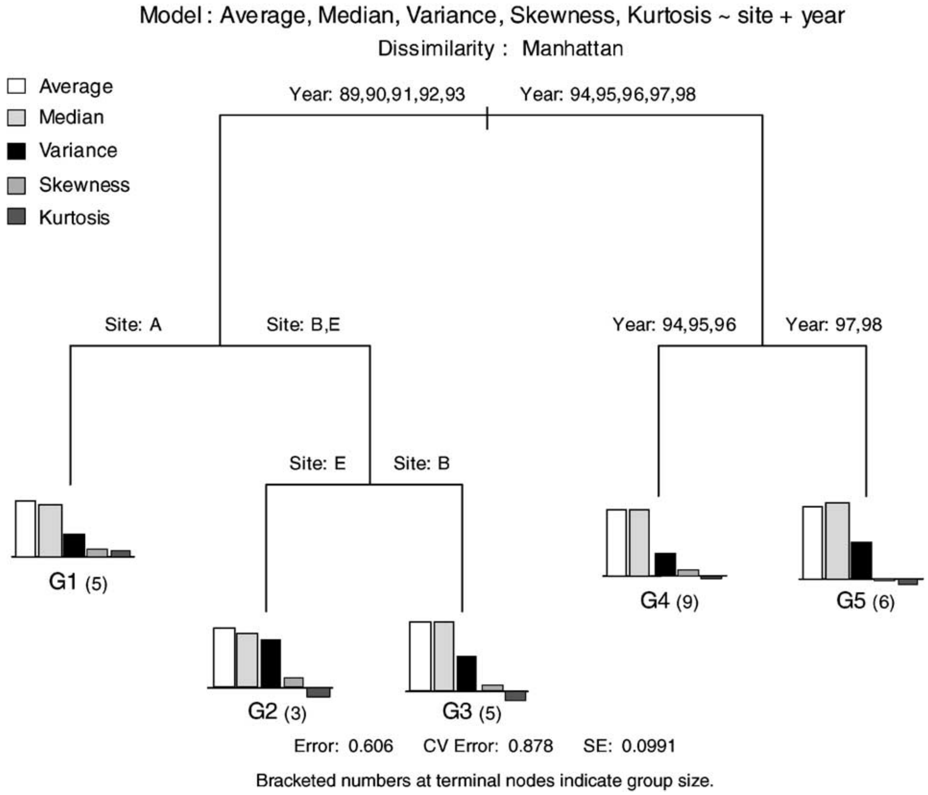

Fig. 7. MRT of *S. sagax* age-distribution characteristics. Classification terms are *site* (Albany, Bremer Bay and Esperance) and *year* (1989–1998). Response is multivariate location determined by five summary statistics calculated for each site–year combination, namely the distribution average, median, variance, skewness and kurtosis. Group mean responses are indicated by barcharts at terminal nodes.

single-case deletion (Fig. 6) suggested a MRT of five terminal nodes (Fig. 7). The MRT model explained 40% of the variation in the data, resulting in a poor model in a predictive sense. Nonetheless, the technique adequately discriminates the region–year distributions on the basis of their shape (Fig. 8). The MRT analysis supported the observed differences in the period from 1989 to 1993, firstly with Albany separating from Bremer Bay and Esperance and then these latter two regions also separate (Fig. 7). In the period from 1994 to 1998 the primary separation was by year, with 1994–1996 different to 1997–1998. Examination of the annual catch curves for the 1994–1996 and 1997–1998 groups (Fig. 5) indicates that this 5-year period was characterised by the progressive ageing of two dominant year classes, and a concomitant increase in modal age, that resulted from strong recruitment in the early 1990s. For example, 3–5-year olds dominated the catch in Albany in 1994–1996, respectively. The difference between 1994–1996 and 1997–1998 was that the former period had very low levels of recruitment, while in the latter period recruitment had improved.

4. Discussion

4.1. Overview of stock structure

The wide distribution of *Sardinops* eggs between Albany and Esperance during individual surveys (Fig. 3) shows that there is a wide distribution of mature *Sardinops* off southern WA. The more or less continuous occurrence of *Sardinops* eggs also indicates that regional differences in seasonal availability of *Sardinops* cannot be attributed to one highly mobile

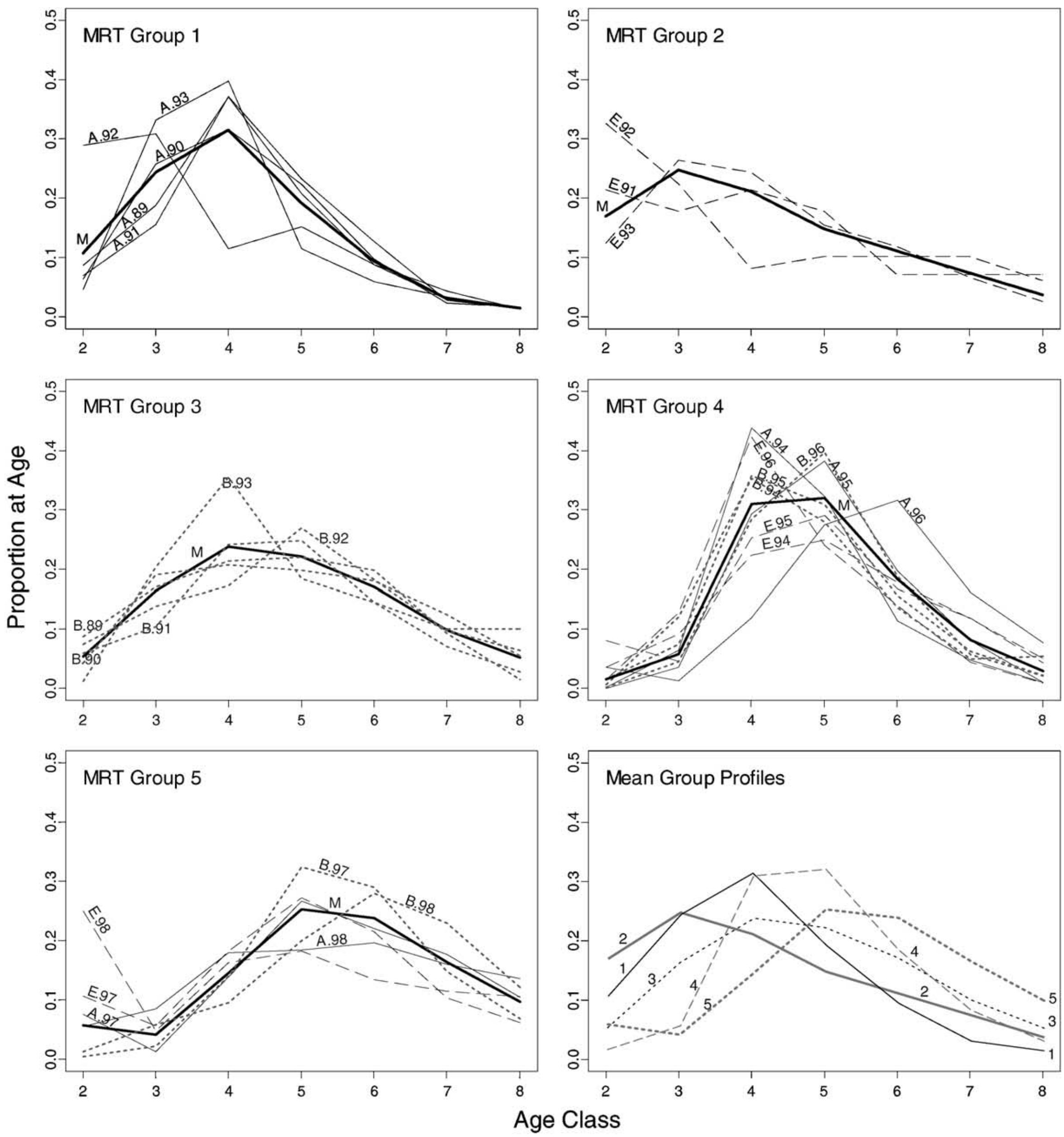

Fig. 8. Individual age distributions comprising each of the five groups determined by MRT analysis. Site–year profiles are labelled in the form A, B or E (for Albany, Bremer Bay or Esperance) followed by the year (1989–1998); heavy lines show the mean profile for each group, and the bottom right panel plots each of the mean profiles.

Sardinops stock that undertakes an annual, cyclic migration along the coast.

Given the less conservative distribution patterns for planktonic fish eggs compared to the population that spawned them, as seen from 30-year data sets for three ground fish stocks in the northeast Atlantic (Begg et al., 1999), and the eastward transport of southern WA *Sardinops* eggs during winter of up to 40 km per day

(Fletcher et al., 1994), we consider that the pattern of high and low abundances provide support for the concept of separate concentrations of spawning adults. However, rather than simply being spatially separated units with more or less persistent geographic demarcations, the areas of high concentrations of spawners are linked by areas of lower concentrations along a continuous distribution. The adult groups are thus distinct rather than strictly separate. The decrease in egg concentration east of Cape Riche has, however, been particularly persistent, having previously been observed during 1991 (Fletcher et al., 1994). Analyses of egg distributions in more recent years are currently being undertaken (D. Gaughan, unpublished data) and preliminary results also suggest the presence of centres of spawning. These new data may assist in assessing if the observed shifts in the locations of peak spawning in the region between Bremer Bay and Esperance are important to the population dynamics of *Sardinops* in southern WA.

Differences in GSI between regions represents a fundamental biological difference and thus provides strong support for the FDAA hypothesis. A significant difference in GSI would not be expected if there was a single, well mixed stock of adults with even exposure to the range of conditions that influence reproductive condition. The relatively high *F*-value for the month $\times$ region term compared to the other interaction terms also provides a degree of support for the notion of different spawning periods between regions.

An important feature of the FDAA hypothesis, viewed retrospectively, is that it reflects the restricted extent of the fishing grounds in each of the three regions on the south coast of WA (see Fig. 1). When fishing (and thus sampling) is spatially restricted with respect to the extent of the breeding stock, clinal changes, in this case shortening of the spawning season from west to east, will manifest as different spawning patterns. That is, despite that changes may be gradual over long distances, samples from small areas along the distribution will show significant differences. Thus, the hypothesised FDAAs are inextricably linked to the fact that each of the three commercial fleets predominantly operate within 20 km of port. While we appreciate from the egg distribution patterns that there is a more or less continuous distribution of *Sardinops* between the three regions examined in this study, we also contend that for the purposes of fisheries management this observation does not invalidate the need to recognise the importance of regional differences in certain aspects of the reproductive biology.

The separation of the age compositions from Albany, Bremer Bay and Esperance by the MRT analysis for the years between 1989 and 1993 provides support for the FDAA hypothesis. In contrast, the MRT analysis detected a stronger similarity between years for the latter 5-year period. However, the similarities across region for the years 1994–1996 and 1997–1998 appear to be due to patterns in recruitment rather than mixing of adults across regions. Although similarities in annual recruitment patterns between regions represents only one of several possible explanations for the results from 1994 to 1998, this concept of a positive relationship between recruitment level across each region is supported by anecdotal information. Such information formed the basis of the recruitment–pool hypothesis (Gaughan et al., 2001b); briefly, this hypothesis states that recruitment to each of the southern WA FDAAs results from a common pool of westward migrating juveniles. The lack of separation by region in the subsequent 5 years does not therefore provide evidence to support the hypothesis of wide-scale mixing of mature *Sardinops* across southern WA. Given that Frank's (1992) dispersal hypothesis suggests that a positive relation in annual recruitment levels between different stocks is possible in the absence of adults of these stocks mixing, further detailed analysis of the catch-at-age data, and in particular the recruitment component, is warranted. Furthermore, because Frank (1992) suspected that the level of juvenile dispersal may be density dependent in some cases, examination of the time series of age data presented here, and extended with that collected subsequently, will help to further elucidate the population dynamics of *Sardinops* off the south coast of WA. Of particular interest will be whether or not the spatial dynamics can be expected to change as the size of the entire south coast breeding stock fluctuates.

The regional differences in female GSIs and in age compositions indicate that there is minimal alongshore mixing of adult *Sardinops* off southern WA, which supports the relationship between oxygen isotope ratios and the temperature cline between Albany and Esperance found by Edmonds and Fletcher (1997). If regular alongshore migrations do occur, their magnitude is likely to be in the order of tens rather than hundreds of kilometres.

4.2. Basis of stock structure

The occurrence of FDAAs may be related to spatial variability of habitat quality in an oligotrophic ecosystem. The southern WA coast may thus have localised areas for which a suite of various factors provide the best combination of benefits to maximise fitness (e.g. survivorship, growth, egg production, egg quality) of *Sardinops*, as in MacCall's (1990) basin model. Recruit aged *Sardinops* are possibly attracted to particular inshore regions because of better conditions, e.g. assumed higher productivity associated with terrestrial run-off and or seagrass meadows. Spatially, consistent patchiness of preferred habitat may be responsible for adults maintaining affiliation with a particular geographic area once recruited. This simple model may explain the lack of significant mixing of mature *Sardinops* over even relatively short distances (e.g. 150 km).

Alternatively, persistence of regional FDAAs may also, or in part, be due to natal homing, a phenomenon that Fréon and Misund (1999) contend "may occur in pelagic fish more frequently than expected", and which forms part of Cury's (1994) éternal retour (perpetual return) hypothesis, in which homing forms part of a continuum of reproductive strategies that all rely on imprinting. Natal homing relies upon the premise that local conditions are memorised, or imprinted, at a very early life-history stage. It is assumed that because this learning is at the level of the individual the process occurs afresh for each new generation (Cury, 1994). In the case of small pelagic fish, Cury (1994) considered that homing may be directed towards a set of environmental conditions rather than some specific geographical location. If FDAAs of *Sardinops* along the southern coast of WA are related to natal homing, the west–east cline in temperature across this region may provide a homing cue. Also, any imprinting that occurs must be for an alongshore "section" of coast because of the potential for rapid transport of eggs and larvae away from the spawning area (Fletcher et al., 1994; Gaughan et al., 2001b).

We have suggested here only two alternative explanations for *Sardinops* FDAAs along southern WA, both of which were developed with regard to the concept of preferred habitats within a framework of a limited carrying capacity of the environment. Both explanations are thus based on mature *Sardinops* remaining in an area once recruited, but the first does not consider the source of the recruits, which may originate from more than one region. The second assumes recruits to a region originated from that same region. Further development of these or other hypotheses require more information on the juvenile stages of *Sardinops* off southern WA. Another oxygen/carbon stable isotope study currently underway aims to gain further insight into where *Sardinops* from each of the southern WA fisheries spent their pre-recruit period. However, because this other study will not be able to determine the origin of recruits in each region, further assessment of the above hypotheses may best be achieved by examination of nuclear DNA. Although examination of allozyme loci has shown little differentiation amongst southern WA *Sardinops* (Dixon et al., 1993), Ruzzante et al. (1996) found with Atlantic cod off Newfoundland that subgroups not previously detected using allozyme loci could be differentiated by examination of nuclear DNA microsatellite loci. Study of nuclear DNA of *Sardinops* in WA would help to clarify whether the FDAAs contribute to a single breeding stock that shares recruits or that they should be considered as independent management units.

4.3. Management implications

Based on the evidence that large-scale movement or mixing of adult *Sardinops* along the south coast of WA does not occur, migration of *Sardinops* between regions cannot be relied upon to reduce the impact of any localised over-exploitation. Likewise, any measurable increase in the number of individuals within a particular region depends on recruitment. The relative contribution of each FDAA to overall levels of recruitment and population size is not known. This uncertainty requires that exploitation at a level that may seriously impact egg production in any one region cannot be allowed because recruitment to all regions may suffer. Likewise, an apparently healthy FDAA of *Sardinops* in one or two regions on the south coast may not necessarily contribute to rebuilding those in other regions that may be at low levels. If the FDAAs proposed here actually represent independent subgroups with autochthonous recruitment, and thus may be genetic subgroups not detectable using allozyme loci, depletion in any one region could pose a direct threat to the intra-specific genetic diversity and hence long term productivity (Cury and Anneville, 1998) of *Sardinops* in southern WA.

5. Conclusions

The results of this study do not entirely support the previous work on *Sardinops* in WA that indicated separate adult assemblages exist along the south coast of WA (Edmonds and Fletcher, 1997). Rather than clear demarcations between the proposed assemblages, the west–east cline in certain aspects of reproductive biology and a continuous but uneven distribution of Day 1 eggs lead to a modification of the hypothesis for separate groups. Thus instead of being thought of as separate, these assemblages are considered as distinct; for the purposes of management they are deemed to constitute distinct reproductive units within a single breeding stock and are thus termed FDAAs. The prime benefit of this study is that conjecture over the presence of alongshore migration and high levels of mixing of adult *Sardinops* between regions can be confidently addressed during future management deliberations. The low level of mixing by adults and continued uncertainty over the origin and movement of pre-recruits warrants management techniques that consider both the individual regions (i.e. the FDAAs) and the south coast as a whole (i.e. the entire breeding stock). The *Sardinops* fisheries in WA are currently managed with consideration given to both of these levels of management unit, an essential strategy under a precautionary approach to management (Stephenson, 1999).

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References

Begg, G.A., Waldman, J.R., 1999. An holistic approach to fish stock identification. Fish. Res. 43, 35–44.

Begg, G.A., Hare, J.A., Sheehan, D.D., 1999. The role of life history parameters as indicators of stock structure. Fish. Res. 43, 141–163.

Bembo, D.G., Carvalho, G.R., Cingolani, N., Pitcher, T.J., 1996. Electrophoretic analysis of stock structure in northern Mediterranean anchovies, *Engraulis encrasicolus*. ICES J. Mar. Sci. 53, 115–128.

Box, G.E.P., Cox, D.R., 1964. An analysis of transformations (with discussion). J. R. Statist. Soc. B 26, 211–252.

Breiman, L., Friedman, J.H., Olshen, R.A., Stone, C.G., 1984. Classification and Regression Trees. Wadsworth, Belmont, CA.

Cury, P., 1994. Obstinate nature: an ecology of individuals. Thoughts on reproductive behavior and biodiversity. Can. J. Fish. Aquat. Sci. 51, 1664–1673.

Cury, P., Anneville, O., 1998. Fisheries resources as diminishing assets: marine diversity threatened by anecdotes. In: Durand, M.-H., Cury, P., Mendelssohn, R., Roy, C., Bakun, A., Pauly, D. (Eds.), Global Versus Local Changes in Upwelling Systems, pp. 537–548.

De'ath, G., 1999. New statistical methods for modelling species–environment relationships. Ph.D. Thesis. James Cook University, Queensland.

Devereux, I., 1967. Temperature measurements from oxygen isotope ratios of fish otoliths. Science 155, 1684–1685.

Dixon, P.I., Worland, L.J., Chan, B.H.Y., 1993. Stock identification and discrimination of pilchards in Australian waters, using genetic criteria. Final Report to Fisheries Research and Development Corporation. Project No. 25/89. Fisheries Research and Development Corporation, Canberra.

Edmonds, J.S., Fletcher, W.J., 1997. Stock discrimination of pilchards, *Sardinops sagax*, by stable isotope ratio analysis of otolith carbonate. Mar. Ecol. Prog. Ser. 152, 241–247.

Fletcher, W.J., 1991. A test of the relationship between otolith weight and age for the pilchard *Sardinops neopilchardus*. Can. J. Fish. Aquat. Sci. 48, 35–38.

Fletcher, W.J., 1995. Application of the otolith weight–age relationship for the pilchard, *Sardinops sagax neopilchardus*. Can. J. Fish. Aquat. Sci. 52, 657–664.

Fletcher, W.J., Blight, S.J., 1996. Validity of using translucent zones of otoliths to age the pilchard *Sardinops sagax neopilchardus* from Albany, Western Australia. Mar. Freshw. Res. 47, 617–624.

Fletcher, W.J., Tregonning, R.J., Sant, G.J., 1994. Interseasonal variation in the transport of pilchard eggs and larvae off southern Western Australia. Mar. Ecol. Prog. Ser. 111, 209–224.

Fletcher, W.J., Lo, N.C.-H., Hayes, E.A., Tregonning, R.J., Blight, S.J., 1996. Use of the daily egg production method to estimate the stock size of Western Australian sardines (*Sardinops sagax*). Mar. Freshw. Res. 47, 819–825.

Frank, K.T., 1992. Demographic consequences of age-specific dispersal in marine fish populations. Can. J. Fish. Aquat. Sci. 49, 2222–2231.

Fréon, P., Misund, O.A., 1999. Dynamics of pelagic fish distribution and behaviour: effects on fisheries and stock assessment. Fishing News Books. Blackwell Science Publications, Oxford.

Gaughan, D.J., Fletcher, W.J., White, K.V., 2001a. Growth rate of larval *Sardinops sagax* from ecosystems with different levels of productivity. Mar. Biol. 139, 831–837.

Gaughan, D.J., White, K.V., Fletcher, W.J., 2001b. The links between functionally distinct adult assemblages of *Sardinops sagax*: larval advection across management boundaries. ICES J. Mar. Sci. 58, 597–606.

Hall, N.G., 2000. Modelling for fishery management, utilising data for selected species in Western Australia. Ph.D. Thesis. Murdoch University, Perth.

Lenanton, R.C.J., Joll, L., Penn, J.W., Jones, K., 1991. The influence of the Leeuwin Current on coastal fisheries in Western Australia. J. R. Soc. West. Aust. 74, 101–114.

MacCall, A.D., 1990. Dynamic geography of marine fish populations. Books in Recruitment Fishery Oceanography. Washington Sea Grant. University of Washington Press, Seattle, WA.

Pawson, M.G., Jennings, S., 1996. A critique of methods for stock identification in marine capture fisheries. Fish. Res. 25, 203–217.

Ruzzante, D.E., Taggart, C.T., Cook, D., Goddard, S., 1996. Genetic differentiation between inshore and offshore Atlantic cod (*Gadus morhua*) off Newfoundland: microsatellite DNA variation and antifreeze level. Can. J. Fish. Aquat. Sci. 53, 634–645.

Stephenson, R.L., 1999. Stock complexity in fisheries management: a perspective of emerging issues related to population sub-units. Fish. Res. 43, 247–249.

Therneau, T., 1998. RPART software and associated documentation from statlib@lib.statlib.cmu.edu