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Have recent mass mortalities of the sardine *Sardinops sagax* facilitated an expansion in the distribution and abundance of the anchovy *Engraulis australis* in South Australia?

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ABSTRACT: This paper examines the hypotheses (1) that *Sardinops sagax* and *Engraulis australis* are spatially segregated and do not interact directly, and (2) that recent mass mortalities of *S. sagax* have facilitated an expansion in the distribution and abundance of *E. australis*. In South Australian waters, *S. sagax* and *E. australis* both spawn during summer and autumn. Eggs and larvae of both species occur over the continental shelf, and are abundant in areas where upwelling occurs (e.g. off the Coffin Bay Peninsula and the western tip of Kangaroo Island) and frontal systems form (e.g. in Investigator Strait and the entrance of Spencer Gulf). After the mass mortality events in 1995 and 1998, eggs and larvae of *S. sagax* were confined mainly to these areas, and estimates of the total abundance of *S. sagax* eggs and larvae in South Australian waters fell by between 48 and 83% respectively. Between 1996 and 1999, densities of *E. australis* eggs and larvae increased in both key spawning areas and the central and eastern Great Australian Bight, and total abundance of eggs and larvae increased by over 215 and 285% respectively. These results indicate that (1) *S. sagax* and *E. australis* are not spatially segregated and may interact directly, and (2) the mass mortalities of *S. sagax* may have facilitated an expansion in the distribution and abundance of *E. australis*. Hence, fluctuations in the relative abundance of *S. sagax* and *Engraulis* spp. observed in the world's productive boundary current systems may also be possible in Australian waters.

KEY WORDS: Sardine · Anchovy · Distribution and abundance · Eggs and larvae · Depth · Temperature · Spawning season · Spawning area · Competition

INTRODUCTION

The sardine *Sardinops sagax* and the anchovies *Engraulis* spp. dominate the clupeoid assemblages of the productive coastal seas of the Kuroshio, Californian, Humbolt and Benguela boundary current systems, and the less productive waters of temperate and subtropical Australasia (Parrish et al. 1989). Fluctuations in the relative abundance of *S. sagax* and the local species of *Engraulis* have been recorded in Japan, California, Peru and South Africa, but not in Australia or New Zealand (Lluch-Belda et al. 1989, 1992a,b, Lluch-Cota et al. 1997, Schwartzlose et al. 1999). In a recent review of world-wide, large-scale fluctuations in the abundance of these genera, Schwartzlose et al. (1999) asserted that there may be 'almost no direct interaction' between sardine and anchovy in Australia, as the species are spatially segregated with *S. sagax* occur-

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Table 1. *Sardinops sagax* and *Engraulis australis.* Total numbers of samples and eggs and larvae collected during each month and each year. Number of positive (+ve) sites = number of sites in which eggs or larvae of each species were found. In 1997, *S. sagax* larvae and *E. australis* eggs and larvae were not counted

	No. of samples				*S. sagax*		*E. australis*	
Year	Jan	Feb	Mar	Total	No. eggs (+ve sites)	No.larvae (+ve sites)	No. eggs (+ve sites)	No. larvae (+ve sites)
1995	52	–	45	97	1197 (59)	457 (42)	316 (40)	95 (27)
1996	64	90	–	154	116 (43)	135 (49)	188 (45)	85 (38)
1997	–	82	107	189	721 (97)	–	–	–
1998	–	54	110	164	2738 (110)	1829 (127)	495 (55)	259 (91)
1999	–	144	68	212	392 (49)	477 (83)	2731 (84)	904 (145)

ring mainly over the continental shelf and the Australian anchovy *E. australis* found mostly in bays, inlets and estuaries.

Although the Australian population of *Sardinops sagax* is not known to have undergone fluctuations in abundance of the type observed in other ecosystems, it has been affected by 2 recent mass mortality events (Fletcher et al. 1997, Griffin et al. 1997, Hyatt et al. 1997, Jones et al. 1997, Whittington et al. 1997, Gaughan et al. 2000, Ward et al. 2001). These events occurred in 1995 and 1998/99, spread throughout the entire Australian range of the species and are thought to have killed more fish over a larger area than any other single-species fish-kill recorded (Jones et al. 1997). Several papers have discussed the nature of the disease agent and the spread of the 1995 event (Griffin et al. 1997, Hyatt et al. 1997, Jones et al. 1997, Whittington et al. 1997); however, few data have been published on the effects of the events on patterns of distribution and abundance (Fletcher et al. 1997, Gaughan et al. 2000, Ward et al. 2001). No previous study has investigated the hypothesis that these decreases in the abundance of *S. sagax* have facilitated expansions in the distribution and abundance of other planktivorous clupeoids, such as *Engraulis australis*.

South Australia lies at the centre of the Australian distribution of both *Sardinops sagax* and *Engraulis australis*, yet most studies of these species have been conducted off the eastern and western coasts of the continent (e.g. Fletcher et al. 1994, Hoedt & Dimmlich 1995). Unlike the pelagic ecosystem off the eastern and western coasts, the hydrography of South Australia is not dominated by south-flowing, oligotrophic waters of tropical origin (Middleton 1995, Schwartzlose et al. 1999, Ward & Staunton-Smith in press). Rather, productivity in shelf waters is enhanced during summer and autumn (December to April) by upwelling events that intrude into surface waters off the western Eyre Peninsula, around Cape Borda (Kangaroo Island) and along the state's south-eastern coastline (Lewis 1981, Griffin et al. 1997). In addition, planktonic organisms are concentrated during summer and autumn by frontal systems that form at the entrance of Spencer Gulf and in Investigator Strait (Bruce & Short 1990). Not surprisingly, the spawning seasons of *S. sagax* and *E. australis* in South Australian waters coincide with the seasons during which these oceanographic phenomena occur (Ward unpubl. data).

Direct quantification of the distribution and abundance of small pelagic fishes is complicated by factors such as their highly aggregated distribution, extreme mobility and high capacity for net avoidance, temporal variations in their depth preferences and schooling behaviour, and difficulties in identifying species using remote-sensing techniques (Ward et al. 1998). Much of the data available on the patterns of distribution and abundance of *Sardinops sagax* and *Engraulis* spp. in other ecosystems have been obtained from ichthyoplankton surveys (Smith 1973, 1990, Crawford 1981a,b, Lasker 1985).

This paper describes and compares the distribution and abundance of the eggs and larvae of *Sardinops sagax* and *Engraulis australis* in South Australia. Findings are used to examine the hypotheses that (1) these species are spatially segregated and do not interact directly in Australian waters and (2) the decline in the abundance of *S. sagax* resulting from 2 mass mortality events has facilitated an expansion in the distribution and abundance of *E. australis*.

MATERIALS AND METHODS

Plankton surveys. Each year between 1995 and 1999, plankton samples were collected during January to March from sites located throughout South Australian waters (Table 1, Fig. 1). A total of 816 samples was collected using paired CalVet nets (0.225 m diameter, 500 µm mesh) towed vertically at approximately 1 m s^{-1}. Nets were deployed to within 10 m of the seabed in waters less than 80 m deep and to a depth of 70 m in waters deeper than 80 m. The distance travelled by each net was estimated using flowmeters. The volume of water filtered was calculated by multiplying

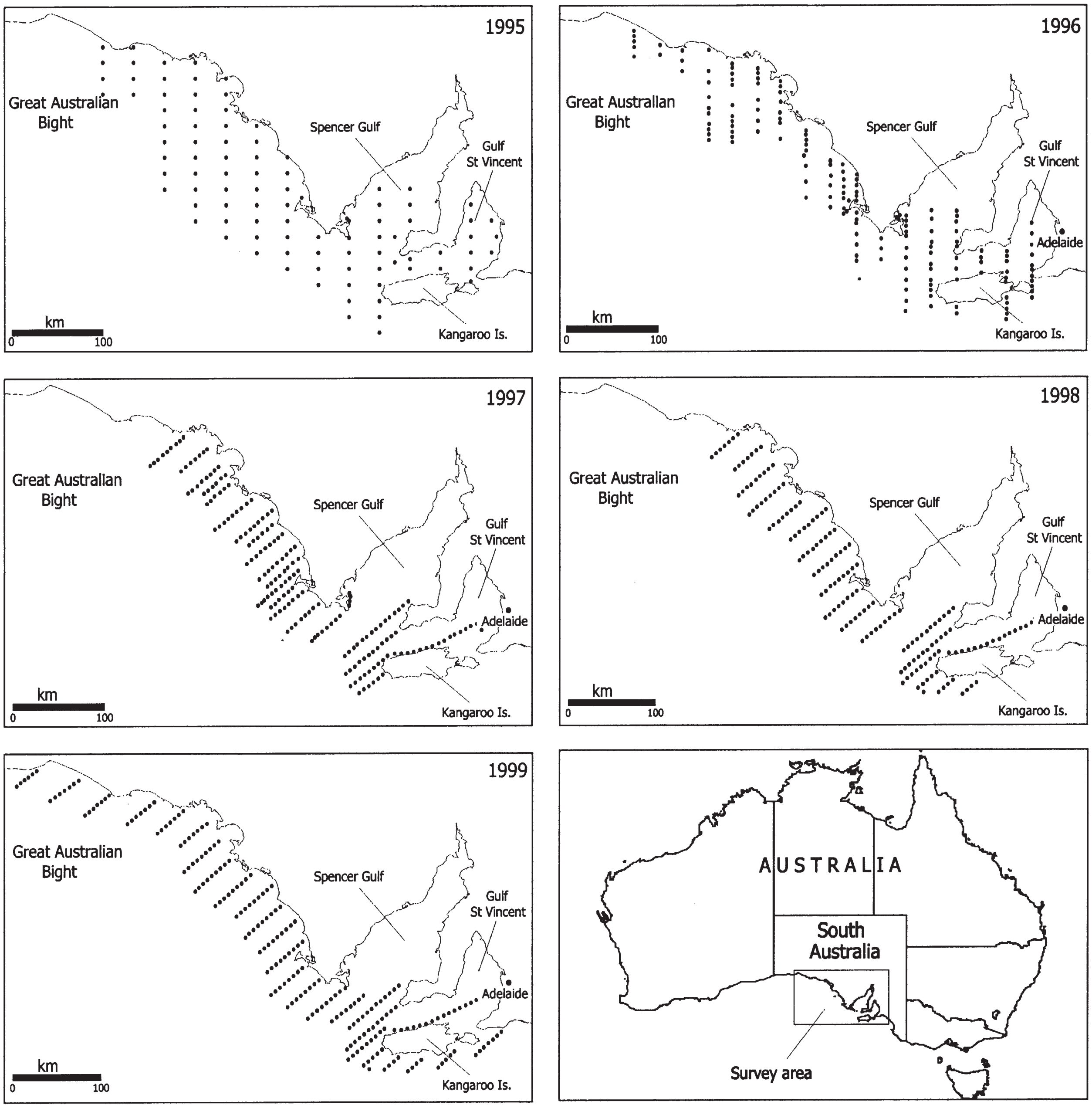

Fig. 1. Maps showing locations referred to in text, and sites at which plankton samples were collected in South Australia between 1995 and 1999. Dots indicate stations along sampling transects

the distance towed by the surface area of the net. Depth and sea surface temperature were recorded at each site. Samples were stored in 5% formaldehyde.

Laboratory analyses. Plankton samples were rinsed of formalin and sorted using a dissecting microscope. Eggs and larvae of *Sardinops sagax* and *Engraulis australis* were identified using standard references (e.g. Lasker 1985, Gaughan et al. 1996, Neira et al. 1998). In 1997, *S. sagax* larvae and *E. australis* eggs and larvae were not enumerated.

Data analysis. The density (per 100 m^3) of *Sardinops sagax* and *Engraulis australis* eggs and larvae in each sample (D_v) was calculated using the equation: $D_v = (100 \times N)/V$, where N is the total of eggs/larvae in each sample and V is the volume of water sampled (m^3).

A ln $(x + 1)$ transformation was used to normalise the distributions of egg and larval densities. To overcome inter-annual changes in the sampling regime, each site was assigned to a 6 × 6 nautical mile grid-square. Effects of grid-square, depth, temperature, month and

Table 2. *Sardinops sagax* and *Engraulis australis*. Total sampling area and estimated total area in which eggs and larvae were present. Estimates of total area of occurrence for 1999 only take into account sites that were also sampled in 1998

Year	Sampling area (km^2)	*S. sagax*		*E. australis*	
		Eggs	Larvae	Eggs	Larvae
1995	111 719	69 375	51 478	45 610	33 834
1996	76 070	17 990	21 841	19 880	17 394
1997	49 825	26 275	–	–	–
1998	49 405	33 801	39 928	18 413	24 090
1999	67 653	11 436	21 366	17 690	32 986

year on egg and larval densities were examined using univariate general linear models with Type III sums of squares.

To calculate the total abundance of eggs and larvae of each species in each year, the survey area was divided into a series of contiguous polygons approximately centred on each site. The size of each polygon was determined using geographical information software (Mapinfo©). The density (per km^2) of the eggs and larvae of each species in each polygon (D_a) was estimated according to the equation: $D_a = (N/V) \times M \times 10^6$ where M is depth in metres for sites located in less than 70 m of water and 70 m for deeper sites. Weighted mean D_a in grids containing eggs/larvae were calculated by weighting the density for each grid by its area. Total egg/larval abundance for each species in each year in each state was estimated by multiplying weighted mean D_a by the sum of the area of the grids that contained those eggs/larvae.

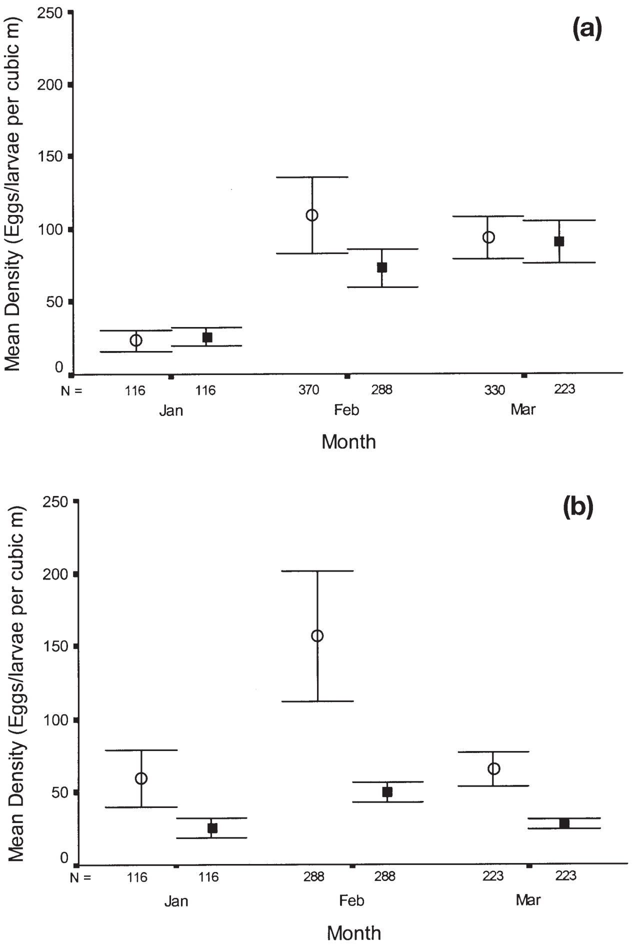

Fig. 2. (a) *Sardinops sagax* and (b) *Engraulis australis*. Mean monthly densities (± SE) of eggs (○) and larvae (■) in South Australia

RESULTS

Total sample

The sampling strategy and size of area sampled varied between years (Fig. 1). In 1995, the primary goal was to identify the extent of the spawning grounds of *Sardinops sagax*, and so a large area (111 719 km^2) containing relatively few sites (97) was sampled (Tables 1 & 2, Fig. 1). In 1996, the size of sampling area was reduced to 76 070 km^2 but more samples (154) were collected. From 1997 onwards, transects were orientated in a NE-SW (cf. North-South) direction, sampling was confined to key spawning areas, and between 164 and 212 samples were collected (Tables 1 & 2, Fig. 1).

Totals of 5164 eggs and 2898 larvae of *Sardinops sagax* and 3730 eggs and 1343 larvae of *Engraulis australis* were collected (Table 1). Higher numbers of *S. sagax* eggs and larvae were collected in 1995 and 1998, the years immediately preceding the mortality events, whereas higher numbers of *E. australis* eggs and larvae were collected in 1998 and 1999, the last 2 years of the study (Table 1). In contrast, relatively low numbers of *S. sagax* eggs and larvae were collected in 1996 and 1999, the years immediately following the mortality events, whereas relatively low numbers of *E. australis* eggs and larvae were collected during the first 2 yr of the study (Table 1).

Month

Although relatively low densities of eggs and larvae of both species were recorded during January (Fig. 2), the effect of month on mean densities was statistically significant for *Engraulis australis* eggs only (Tables 1 & 3). The lower than expected densities of eggs and larvae of both species collected in 1995, may reflect the fact that most sampling in that year was conducted during January (i.e. prior to the peak spawning season) (Table 1).

Table 3. *Sardinops sagax* and *Engraulis australis*. Results of univariate general linear model of mean transformed densities of eggs and larvae. Degrees of freedom, mean squares (in *italics*) and *F*-values are given above p-values. Significant p-values are in **bold**-face

Species	Grid	Depth	Temp	Month	Year	Corrected model	Error
S. sagax							
Eggs	415	13	9	2	4	448	365
df = 814	*4.605*	*6.826*	*10.839*	*2.315*	*55.048*	*6.322*	*3.837*
R^2 = 0.67	1.20	0.78	2.83	0.603	15.127	1.1.647	
	0.037	**0.045**	**0.003**	0.548	**<0.0001**	**<0.0001**	
Larvae	371	12	9	2	3	403	221
df = 625	*3.899*	*2.238*	*9.029*	*0.197*	*51.823*	*6.035*	*3.247*
R^2 = 0.77	1.19	0.68	2.76	0.60	15.823	1.843	
	0.076	0.767	**0.004**	0.942	**<0.0001**	**<0.0001**	
E. australis							
Eggs	371	12	9	2	3	403	221
df = 625	*4.582*	*5.407*	*11.484*	*16.343*	*26.477*	*5.552*	*4.700*
R^2 = 0.68	0.98	1.15	2.44	3.48	5.63	1.81	
	0.588	0.321	**0.011**	**0.033**	**0.001**	**0.083**	
Larvae	371	12	9	2	3	403	221
df = 625	*3.187*	*2.794*	*3.280*	*0.480*	*18.192*	*4.418*	*3.442*
R^2 = 0.65	0.93	0.81	0.95	0.14	5.29	1.28	
	0.743	0.638	0.480	0.870	**0.002**	**0.0001**	

Depth

Large numbers of eggs and larvae of both species were collected from sites located in depths between 20 and 140 m (Fig. 3), and the depth in which a site was located was not an important determinant of egg or larval density of either species (Table 3).

Sea surface temperature

Eggs and larvae of *Sardinops sagax* and *Engraulis australis* were collected commonly from sites with sea surface temperatures (SSTs) ranging from 15.5 to 23.5°C, and mean densities were high in sites with SSTs between 15.5 and 17.5°C and between 19.5 and 22.5°C (Fig. 4, Table 3).

Spatial distribution

In 1995 and 1998, the years immediately preceding the mass mortality events, *Sardinops sagax* eggs were obtained from approximately 60% of sites, and sites containing eggs were located throughout the

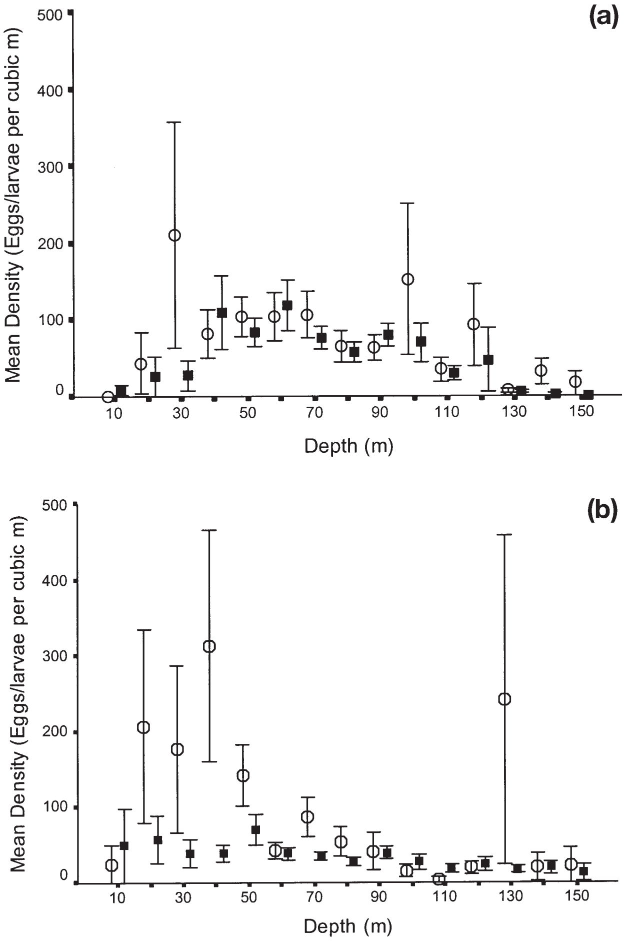

Fig. 3. (a) *Sardinops sagax* and (b) *Engraulis australis*. Effect of depth on mean densities (±SE) of eggs (○) and larvae (■) in South Australia

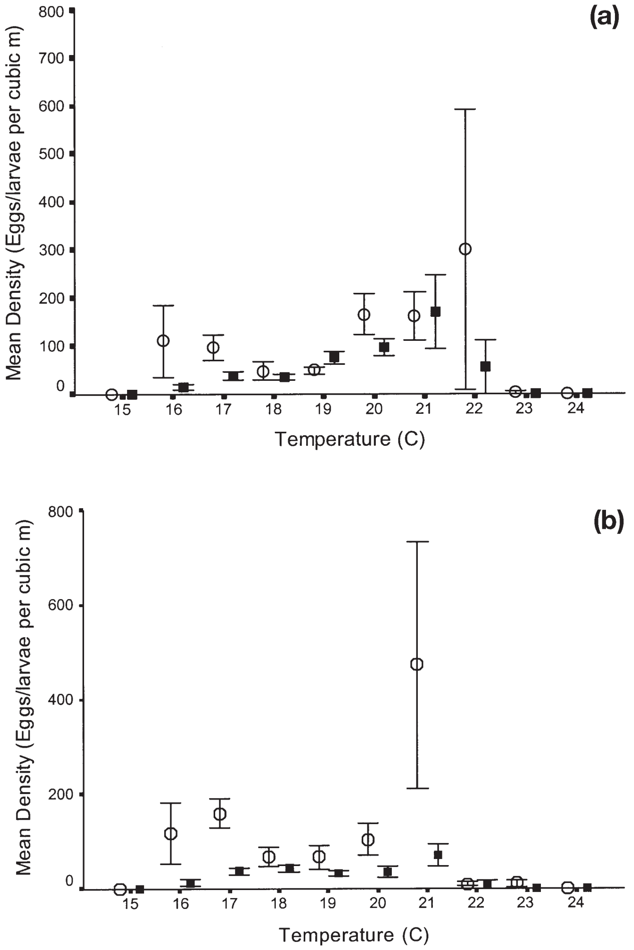

Fig. 4. (a) *Sardinops sagax* and (b) *Engraulis australis.* Effect of sea surface temperature on mean densities (+ SE) of eggs (○) and larvae (■) in South Australia

survey area (Table 1, Fig. 5). The relatively small numbers of eggs collected in sites east of Coffin Bay Peninsula in 1995 may reflect the fact that these sites were sampled during January, i.e. prior to the peak spawning season. In 1996 and 1999, the years immediately following the mass mortality events, *S. sagax* eggs were obtained from <30% of sites (Table 1, Fig. 5); few *S. sagax* eggs and larvae were collected from the central and eastern Great Australian Bight (Figs. 5 & 6). In 1996, most *S. sagax* eggs and larvae were collected from sites off the Coffin Bay Peninsula and the western tip of Kangaroo Island and in Investigator Strait and the entrance to Spencer Gulf. In 1999, egg and larval densities were again relatively high at sites near Cape Borda and in Investigator Strait and the entrance to Spencer Gulf, but few eggs or larvae were collected from stations near the Coffin Bay Peninsula, where the fishery is centred (Ward et al. 1998).

Eggs and larvae of *Engraulis australis* were collected from 29 and 25% of sites respectively in 1996 and 39 and 68% of sites respectively in 1999 (Table 1, Figs. 7 & 8). In 1995, when sites east of the Coffin Bay Peninsula were sampled during January, few *E. australis* eggs or larvae were obtained from this area. In 1996, *E. australis* eggs or larvae were collected mainly from sites near the Coffin Bay Peninsula, the western tip of Kangaroo Island, Investigator Strait and the entrances of Spencer Gulf and Gulf St. Vincent (Figs. 7 & 8). In contrast, during 1998 and 1999, *E. australis* eggs and larvae were also highly abundant at sites located in the central and eastern Great Australian Bight.

Mean density

The effect of the second mass mortality event can be seen in the 60% decrease in the mean density of *Sardinops sagax* eggs from 360 (±78 SE) eggs per 100 m^3 in 1998 to 148 (±32 SE) eggs per 100 m^3 in 1999. Similarly, between 1998 and 1999 the mean density of *S. sagax* larvae fell by 50% from 208 (±30 SE) to 99 (±11 SE) larvae per 100 m^3 (Fig. 9). The effect of the first mortality event on mean density of *S. sagax* eggs and larvae was difficult to discern, perhaps because in 1995 many samples were collected in early January, prior to the peak spawning season, and the estimate of mean egg density for that year was thus negatively biased.

The scheduling of the first sampling cruise also affected estimates of the mean density of *Engraulis australis* eggs and larvae for 1995. It is therefore more appropriate to examine changes in mean density by comparing estimates for 1996 and 1999. Between these years, mean densities of *E. australis* eggs and larvae increased by 315%, from 138 (±25 SE) to 572 (±9 SE) eggs per 100 m^3 and by 30% from 81 (±79 SE) to 105 (±12 SE) larvae per 100 m^3 (Fig. 9).

Total abundance

Underestimation of egg and larval densities for 1995 resulting from the timing of the first research cruise ensures that estimates of the effect of the first mortality event are conservative. Between 1995 and 1996, estimates of total abundance of eggs and larvae of *Sardinops sagax* declined by 77 and 48% respectively. Estimates of the area in which eggs and larvae were present during 1999 were based only on sites that were also sampled in 1998. Between 1998 and 1999 estimates of the total abundance of *S. sagax* eggs and larvae fell by 83 and 78% respectively (Fig. 10).

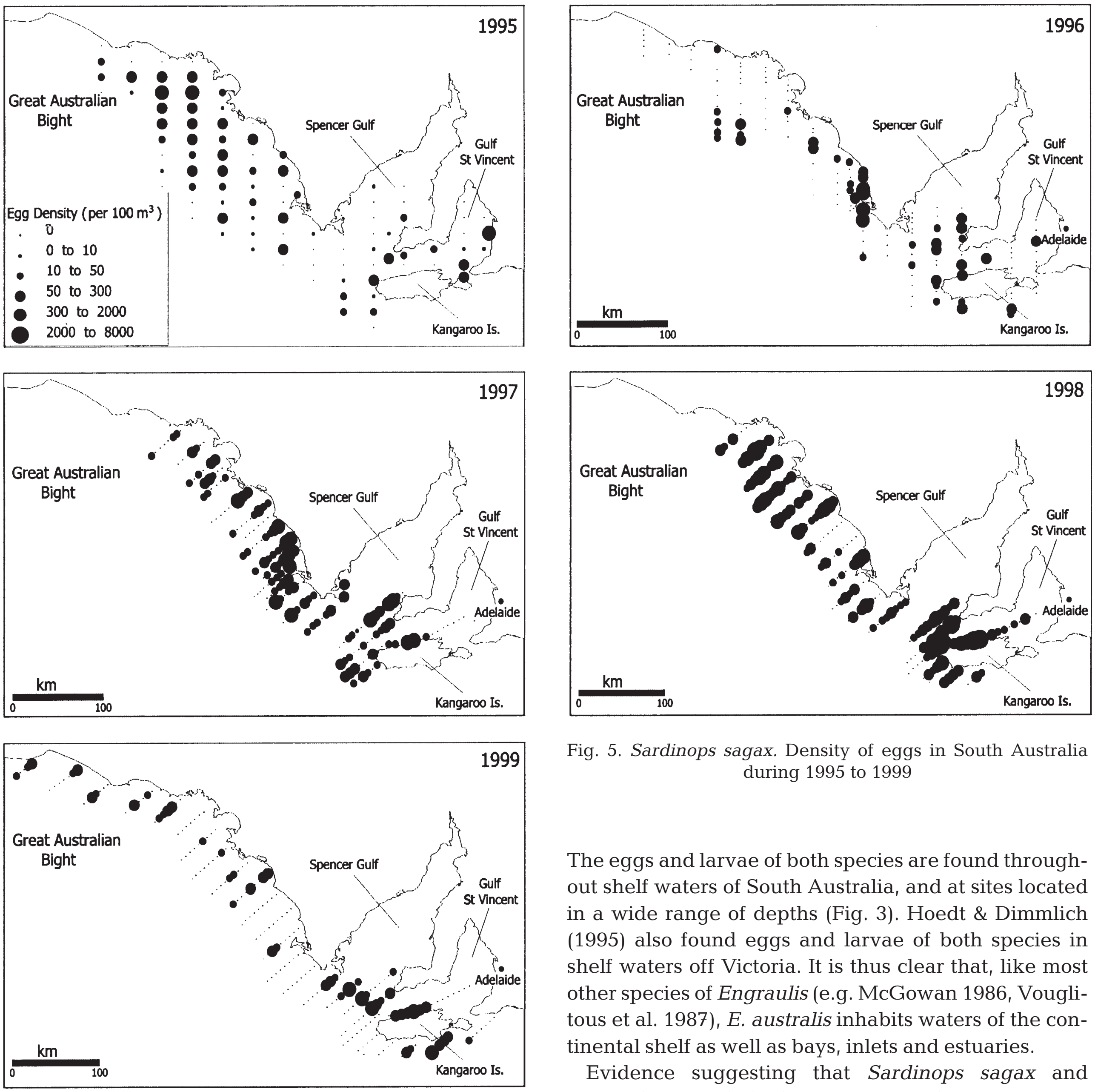

Fig. 5. *Sardinops sagax.* Density of eggs in South Australia during 1995 to 1999

Between 1996 and 1999, estimates of the total abundance of *Engraulis australis* eggs and larvae increased by approximately 286 and 215% respectively (Fig. 10).

DISCUSSION

The assertion by Schwartzlose et al. (1999) that in Australia *Sardinops sagax* and *Engraulis australis* are spatially segregated, with *S. sagax* occurring mainly over the continental shelf and *E. australis* found mostly in bays, inlets and estuaries, appears to be incorrect. The eggs and larvae of both species are found throughout shelf waters of South Australia, and at sites located in a wide range of depths (Fig. 3). Hoedt & Dimmlich (1995) also found eggs and larvae of both species in shelf waters off Victoria. It is thus clear that, like most other species of *Engraulis* (e.g. McGowan 1986, Vouglitous et al. 1987), *E. australis* inhabits waters of the continental shelf as well as bays, inlets and estuaries.

Evidence suggesting that *Sardinops sagax* and *Engraulis australis* both spawn in a wide range of temperatures is consistent with findings obtained in other studies of these genera (e.g. Lluch-Belda et al. 1991). The dual peaks in the spawning activity of *S. sagax* at temperatures of 15 and 23°C observed in the California Current (Lluch-Belda et al. 1991) are remarkably similar to the bi-modal pattern of egg abundance suggested by data obtained in the present study (Fig. 4). In contrast, Lluch-Belda et al. (1991) observed only 1 spawning maximum for *E. mordax*, whereas data presented here for *E. australis* suggest the possibility of bimodality. The occurrence of dual peaks in spawning activity is surprising, as the optimum spawning temperature would be expected to occur around the mid-

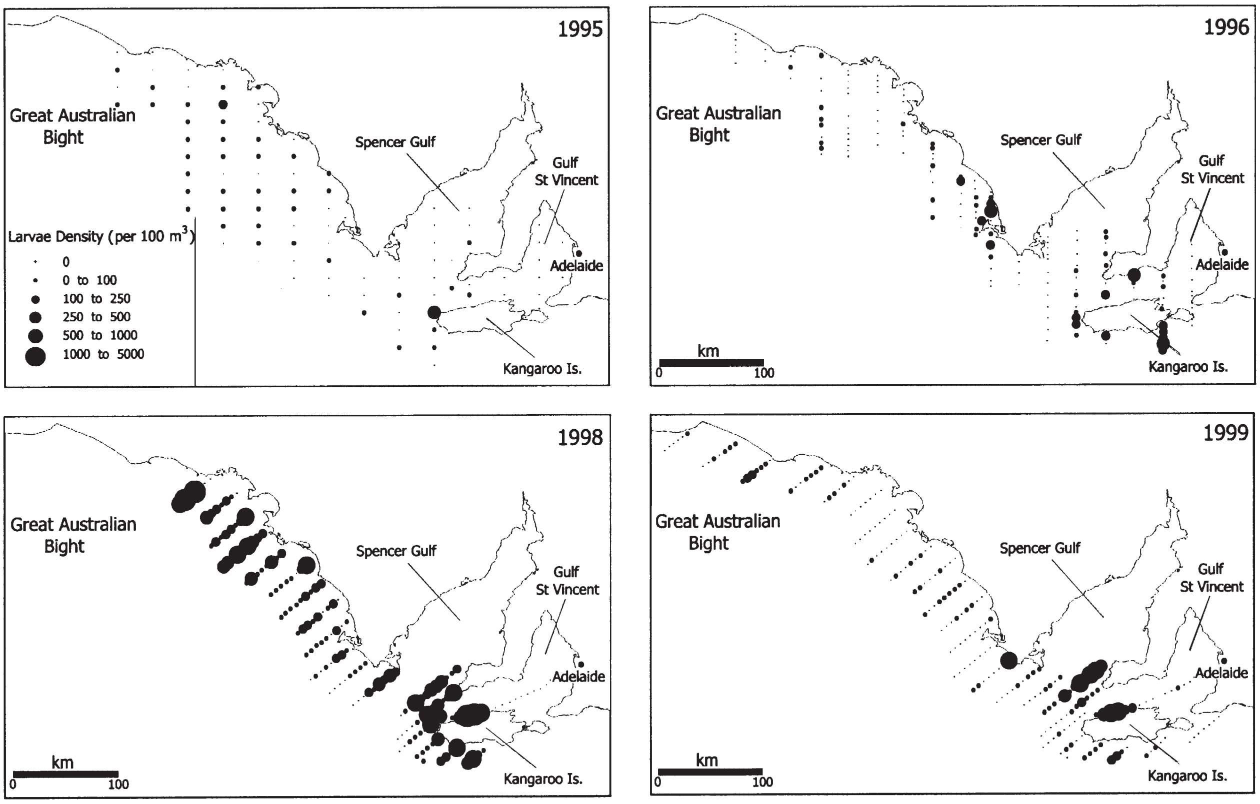

Fig. 6. *Sardinops sagax.* Density of *S. sagax* larvae in South Australia during 1995 to 1999

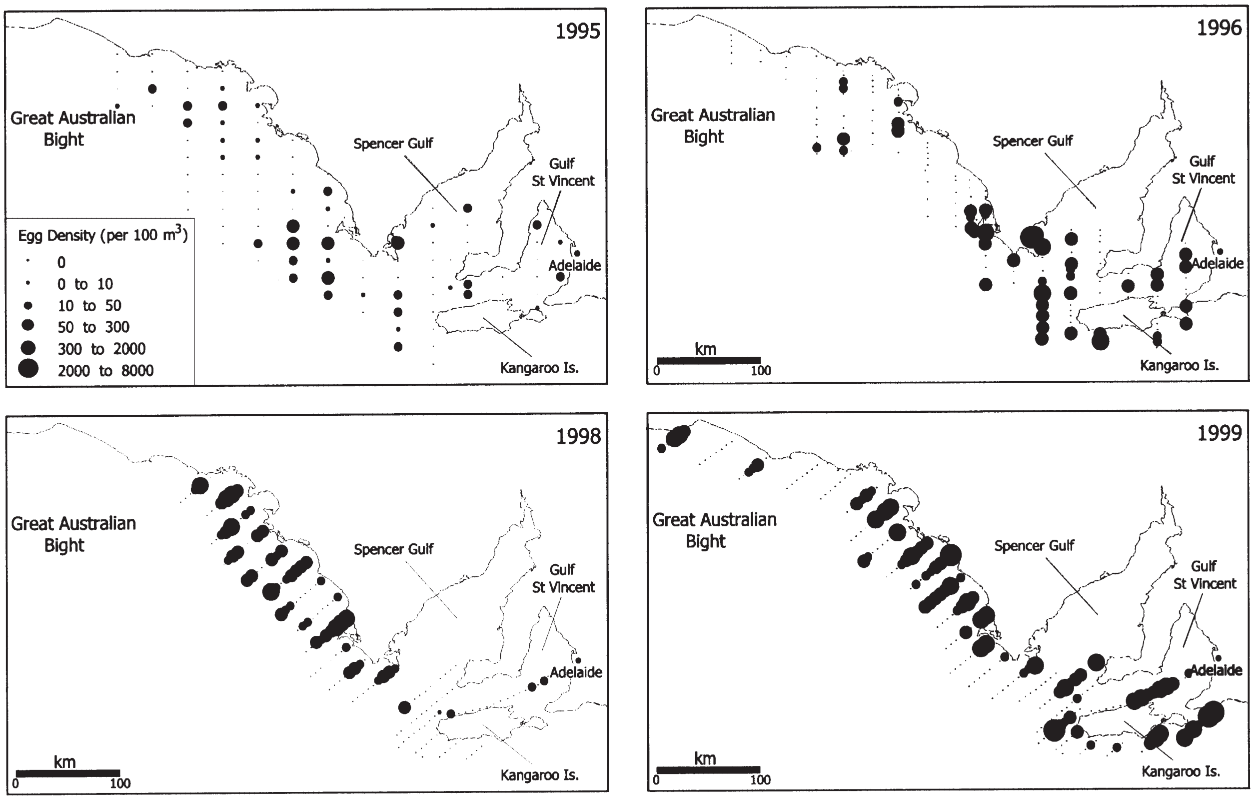

Fig. 7. *Engraulis australis.* Density of eggs in South Australia during 1995 to 1999

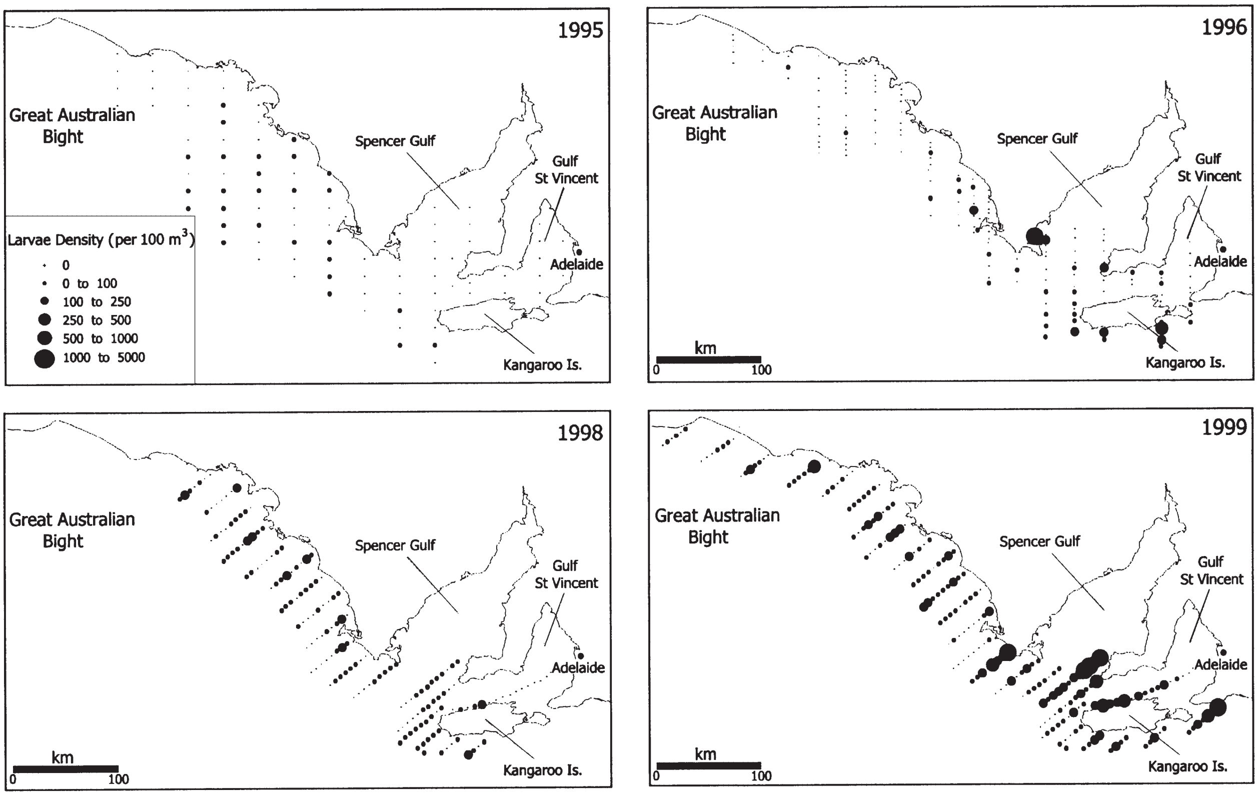

Fig. 8. *Engraulis australis.* Density of larvae in South Australia during 1998 to 1999

point between the extremes. Lluch-Belda et al. (1991) suggested that this hiatus may be related to upwelling. As the spawning seasons of *S. sagax* and *E. australis* coincide with months during which upwelling occurs and important spawning grounds for both species are located near upwelling areas such a link may also explain the patterns observed in South Australia.

The contraction, following the 2 mass mortality events, of spawning activity of *Sardinops sagax* into areas where upwelling occurs (e.g. off the Coffin Bay Peninsula and the western tip of Kangaroo Island) and frontal systems form (e.g. Investigator Strait and the entrance of Spencer Gulf) emphasises the importance of these locations for *S. sagax* in South Australia. The relatively low abundance during 1998 and 1999 of *S. sagax* eggs and larvae in waters around the Coffin Bay Peninsula, where the fishery is centred, provides evidence of the increased vulnerability to over-fishing of stocks that have been affected by mass mortality events (Ward & Staunton-Smith in press). These observations emphasise the need to establish conservative quotas in the years immediately following such events and the value of incorporating closure areas that include key spawning grounds into strategies for managing stocks of pelagic fishes.

The coincidental timing of the expansion of the *Engraulis australis* population and the declines in the abundance of *Sardinops sagax* resulting from the mortality events suggest that these species compete for resources. This interpretation contradicts the assertion by Schwartzlose et al. (1999) that there may be 'almost no direct interaction' between these genera in Australia, but is consistent with observations of these genera in other ecosystems (Lluch-Belda et al. 1992a,b). As appears to be the case in the Californian Current (Lluch-Belda et al. 1991), *S. sagax* seems to dominate the interaction.

Increases between 1996 and 1999 in estimates of the total abundance of *Engraulis australis* eggs and larvae reflect increases both in the areas occupied and in mean densities. The expansion of the distribution of *E. australis* into waters of the eastern Great Australian Bight is notable, as Schwartzlose et al. (1999, p 305) suggested that this species is 'not found in the GAB (Great Australian Bight)'. The increases in egg and larval density are also significant, as several other studies of these species have suggested that changes in total abundance are more usually reflected in changes in spawning area than changes in density (e.g. Smith 1990).

The apparent increase in the abundance of *Engraulis australis* does not provide unequivocal proof that long-term changes in the total and relative abundance of *Sardinops sagax* and *E. australis* have or will occur in Australia; a much longer time series of data would be

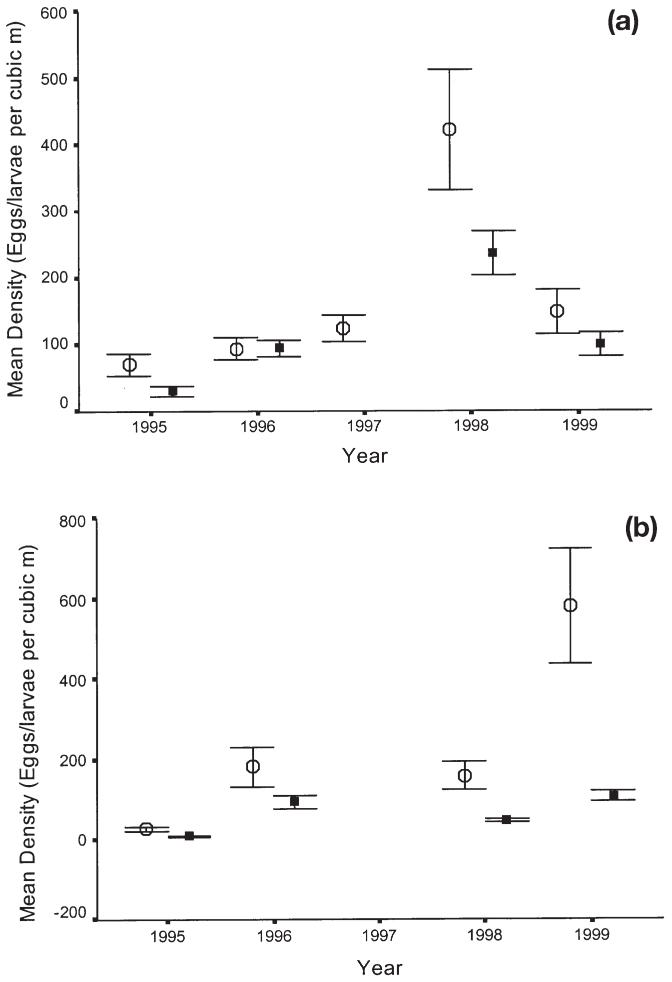

Fig. 9. (a) *Sardinops sagax* and (b) *Engraulis australis.* Mean density of eggs (○) and larvae (■) in positive sites in South Australia between 1995 and 1999

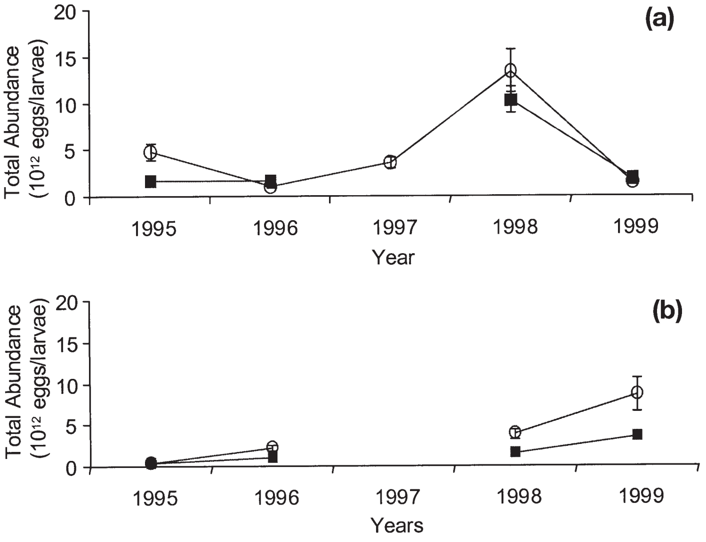

Fig. 10. (a) *Sardinops sagax* and (b) *Engraulis australis.* Estimates of the total abundance of eggs (○) and larvae (■) in South Australian waters between 1995 and 1996

required to assess this proposition. However, the data presented here do provide compelling evidence that these species occupy similar environments, interact directly and may undergo fluctuations in abundance of the type observed in the boundary current systems. Like the changes in abundance observed elsewhere, these fluctuations have the potential to alter the structure and function of pelagic ecosystems, and may affect populations of some predatory marine species adversely (Ward et al. 1998).

Unlike the fluctuations in the relative abundance of *Sardinops* spp. and *Engraulis* spp. observed in the boundary current systems, the changes described here may have been induced by human activities (e.g. Gaughan et al. 2000). Numerous papers and reports have suggested that imported frozen *S. sagax* used as fodder in the tuna mariculture industry is a potential source of the herpes virus(es) that caused the mass mortality events (Griffin et al. 1997, Jones et al. 1997, Gaughan et al. 2000, Ward et al. 2001). This link remains unproven, but the potential effects of such events on the structure and function of Australia's pelagic ecosystem are serious. Conservation and biodiversity legislation in many countries, including Australia, calls for a precautionary approach to the management of serious risks. A precautionary approach to risk assessment conflicts with the approach of the 'Office International des Epizooties', which requires importing countries to prove that there is a potential risk of introducing a specific disease before the importation of untreated fish products can be restricted (e.g. Gaughan et al. 2000, Jones in press).

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