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The 1995 mass mortality of pilchard: no role found for physical or biological oceanographic factors in Australia

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Abstract. An unprecedented mass mortality of pilchard, *Sardinops sagax*, occurred in Australia in 1995, spreading east and west from the Great Australian Bight at approximately 0.5 m s⁻¹ and 0.3 m s⁻¹ respectively to span the 6000-km range of the species from Noosa, Queensland, to Geraldton, Western Australia. Mortalities with the same clinical signs of hypoxia also occurred in New Zealand. Upwelling and phytoplankton blooms preceded the first mortalities, leading to widely publicized speculation that environmental stress caused the mortalities. However, upwellings as strong as in February 1995 off Eyre Peninsula occur as often as once every three or four years, and environmental conditions surrounding mortalities elsewhere were normal. Phytoplankton blooms were absent through much of the range; where they did accompany mortalities they were of widely differing species. Hence, the hypothesis that environmental stress caused the mortalities is quite confidently rejected. The hypothesis that ocean currents were a vector of an aetiological agent is also rejected, since the Leeuwin and East Australian currents were both flowing strongly against the spread of mortalities. Other potential vectors exist, however, so the hypothesis that an introduced pathogen was responsible cannot be rejected.

Introduction

A mass mortality of adult (12–18 cm standard length, SL) pilchard, *Sardinops sagax*, occurred in Australian and New Zealand waters in 1995. In Australia, mortalities spanned the 6000-km range of the species, starting in early March off the Eyre Peninsula in South Australia (SA) and ending in June off Noosa to the east and Geraldton to the west (Fig. 1). It was the most widespread mortality of the species known to have occurred. Masses of dead pilchards were found floating on the surface at sea, washed up on beaches and in the stomachs of benthic fish. Death was clearly due to hypoxia. Presence of a Herpes-type virus in the gill epithelium correlated strongly with moribundity, but no cytopathic effect has been demonstrated (Hyatt *et al.* 1996, Whittington *et al.* 1996). Even if the virus was the aetiological agent, it is unclear why the epizootic occurred.

The sudden occurrence of widespread mortalities suggests that the whole population had been exposed to an extreme level of stress or to an agent to which it had no accumulated resistance. The wave-like spread of mortalities away from a source region leads us to consider two general hypotheses: (1) a pre-existing syndrome was triggered sequentially along the continental shelf by a propagating environmental anomaly, and (2) an exotic pathogen was dispersed from a single source by ocean currents, fish-to-fish contact, predators or ballast water. We also briefly consider a third

hypothesis, which combines elements of the first two by postulating that there was enough resistance to an exotic pathogen for it to spread before virulence was triggered by a natural event, e.g. spawning or the onset of winter.

It is beyond the scope of this paper to explain the outbreak and spread of mortalities; we merely consider the hypotheses above with reference to the surrounding environmental conditions. We do not consider hypotheses (for example, overcrowding or increased vector density) that do not invoke oceanographic factors, nor do we address the consequences of the mass mortality of this important prey species. We note, however, that despite the magnitude of the event, the pilchard catch for 1995 was similar to that of recent years, with 3338 t being landed in South Australia (D. Mackie, Primary Industries South Australia, personal communication) and ~9000 t being landed in Western Australia (W. J. Fletcher, West Australia Fisheries, personal communication).

Hypothesis 1: Pre-existing syndrome triggered by environmental stress

No substantial pilchard mortality spanning more than a single estuary or region of Australia has ever been documented, although anecdotal reports of larger kills in the 1940s and 1950s do exist. More importantly, there are no reports of mortalities sharing the same clinical signs as the

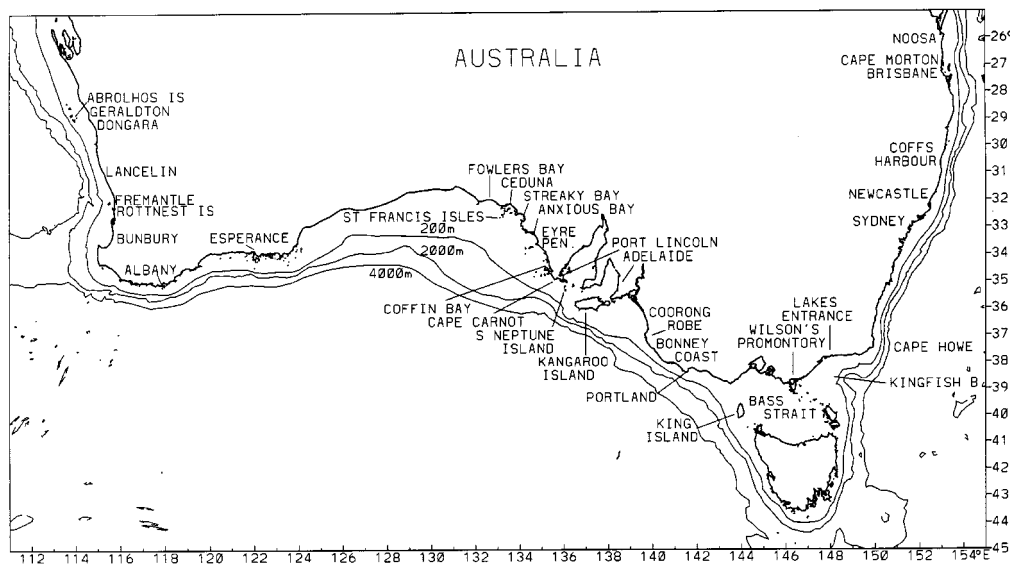


Fig. 1. Bathymetric map showing locations referred to in the text.

1995 event. Documented earlier mortalities occurred at (1) Hawley Beach, Tasmania, on 6 January 1982, where pilchards appeared on the beach with their stomachs burst and with bleeding from the gills and anus, apparently from having been crushed (Copas 1982), (2) Investigator Strait, SA, on 29 March 1990, where pilchards were found in the stomachs of (benthic feeding) King George whiting (K. Jones, SARDI, personal communication) and (3) Port River Estuary, Adelaide, on 19 January 1991, where deaths of juvenile and adolescent pilchards were tentatively associated with a mixed dinoflagellate bloom of *Alexandrium minutum* (toxic) and *Scrippsiella* spp. (non-toxic) occurring in warm (23–25°C) water (K. Jones, personal communication). Other, undocumented, smaller kills are often attributed to pollution, seismic exploration or dumping by fishing vessels.

Hence, there is no documented evidence to suggest that the 1995 mortality was a recurrence of an existing syndrome. This is insufficient information to rule out the hypothesis, since smaller mortalities may have occurred unnoticed, but, for the hypothesis to be tenable, an environmental anomaly of unprecedented proportions must have been involved.

Outbreak—correlation with upwelling

Before considering the mechanism involved, we examine the possible correlation of the initial outbreak of mortalities with a strong upwelling episode that occurred in the region.

Pilchard deaths were first observed on 15 March 1995, 50 km offshore from Anxious Bay on the Eyre Peninsula (Fig. 1). The peninsula is sparsely populated, but it is unlikely

that an outbreak earlier than mid March or outside the Anxious Bay area had gone undetected, because many lobster fishers work those waters and their observations have been recorded (K. Jones, personal communication). It is less clear where and when those fish were exposed to whatever caused their deaths, because they could have moved some distance, X , given by $X = T_{inc} (V_{swim} + V_{curr})$, where T_{inc} is the delay between exposure and death (for example the incubation period of a pathogen) and V_{swim} and V_{curr} are the swimming and current velocities averaged over T_{inc} , respectively. To do space- and time-lagged correlations of the mortalities with environmental conditions, bounds must be estimated for T_{inc} , V_{swim} and V_{curr} in order to limit the set of sensible lags.

Whittington *et al.* (1996) report a lag of 4 days between fish being lesion-free at a particular location and subsequent mortalities. The major environmental anomaly, however, predated the outbreak of mortalities by 2 to 3 weeks (see below). We therefore choose 3 weeks as a maximum time lag so as not to exclude the major environmental anomaly *a priori*, but we expect 4 to 10 days to be the lags of greatest interest.

The optimum swimming speed is about 1 body length s^{-1} for a variety of fish species (Trump and Leggett 1981) and sizes (Ware 1978). During foraging this rate may increase to 3 body lengths s^{-1} (Ware 1978). Newman (1970) found maximum migration rates of pilchards off South Africa to be 0.06 $m s^{-1}$ over 1800 km, but up to 0.18 $m s^{-1}$ over 240 km. Here we assume $V_{swim} < 0.5$ to 2 body lengths s^{-1} , i.e. 0.06 to 0.24 $m s^{-1}$ or 35–140 km per week. It is unknown, however, in which direction, if any, pilchards were likely to be swimming at the time.

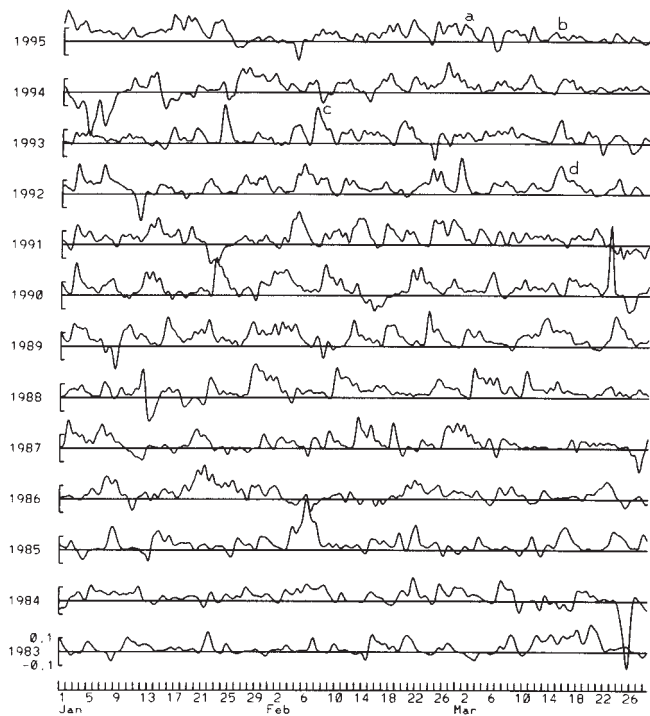


Fig. 2. The upwelling-producing component of the wind stress (N m^{-2}) at Neptune Island (Bureau of Meteorology station 18115). Stress is estimated from the three-hourly velocity observations using the neutral steady state formula of Large and Pond (1981), filtered by convolution with a Hanning window of width 15 h at half amplitude, then resolved along 315T. The symbols 'a' to 'd' are centred at the times of the corresponding panels of Plate I.

To estimate V_{curr} we refer to wind and sea surface temperature data. Moderately strong (10 m s^{-1}) upwelling-favourable winds blew (with a few interruptions) between 17 February and 6 March (Fig. 2). Good (relatively cloud free) Advanced Very High Resolution Radiometer (AVHRR) sea surface temperature (SST) images are available for 17, 19, 20, 23 and 24 February and 2 and 3 March. Upwelling first appears off the Eyre Peninsula and Bonney coast in the 19 February image (not shown) and is most evident on 2 March (Plate Ia), when large plumes of cold water can be seen originating from the Cape Carnot area ($100 \text{ km} \times 25 \text{ km}$ of 14°C water) and the Bonney coast ($300 \text{ km} \times 50 \text{ km}$ of 11°C water). On the assumption that the plumes surfaced where they attach to the coast and that they were advected away by the alongshore current, the 100-km length of the Cape Carnot plume 11 days after the onset of upwelling suggests that V_{curr} is 0.11 m s^{-1} , or 60 km per week north-westward.

The fish found dead off Anxious Bay on 15 March could therefore have been up to 200 km ($140 + 60$) south-east (off Cape Carnot) a week earlier on 8 March, 400 km south-east (off Kangaroo Island) 2 weeks earlier on 1 March, or 600 km

south-east (off Robe) three weeks earlier on 22 February if they swam at $2 \text{ body lengths s}^{-1}$ to the north-west. At only $0.5 \text{ body length s}^{-1}$ they could have been off Cape Carnot on 28 February, but the transit from the Bonney coast would have taken much longer than our assumed maximum incubation period of three weeks, and upwelling was not occurring there that early.

The fish found dead farther north near St Francis Isles and Fowlers Bay, on 16 and 17 March, respectively, could not at any plausible swimming speed have been off the Bonney coast after or when there was upwelling. They could, however, have been off Cape Carnot on 28 February if they subsequently swam north-westwards at $1.5 \text{ body lengths s}^{-1}$ with a favourable current of 0.11 m s^{-1} .

It therefore seems possible to link all the initial mortalities observed from Anxious Bay to Fowlers Bay with the Cape Carnot upwelling, but not with the Bonney coast upwelling, assuming incubation periods of up to 3 weeks.

Weak upwelling-favourable winds continued through the remainder of March, and all the SST images show some degree of weaker upwelling. The 16 March image (Plate Ib) is the clearest of these, showing cold (14°C) water upwelling close (within 5 km) to the coast from Cape Carnot to Streaky Bay. Upwelling could still therefore have been a factor if only short (a few days) incubation periods are assumed.

The possible roles of upwelling

Upwelling brings water to the surface that is often cold, low in oxygen and high in nutrients and other breakdown products. Each of these differences from the surface waters potentially stresses fish. Möller and Anders (1986) suggest that the incidence of all fish diseases is influenced by temperature. Many viruses, particularly Herpes viruses, are thought to exist as latent infections, only becoming patent when the fish are stressed by, for example, temperature changes, crowding, or pollution (Sinderman 1990). High concentrations of nutrients stress fish indirectly by allowing phytoplankton to bloom, which in turn stresses the fish by releasing toxins, depleting oxygen or damaging gills.

Because many potential stresses happen at once it is often unclear which actually contribute to subsequent mortalities. For example, regular mass mortalities of fish, especially pilchards, follow upwelling off south-western Africa near Walvis Bay where the benthic environment is highly organic, is anoxic and has a high hydrogen sulfide content (Brongersma-Sanders 1957). Mortalities are often preceded by red-to-brown discolouration of the sea by algal blooms, including those of a small dinoflagellate tentatively identified as *Glenodinium* sp.

The satellite data of Plate I show that the temperature of the upwelled water was 4° cooler at about 14°C . Reference to the data of Cresswell (1995) and Lewis (1981) suggests that it probably had a nitrate concentration of about $4 \mu\text{mol}$

L^{-1} . Assuming a N:chlorophyll-*a* (Chl-*a*) ratio of 8 (Yoder 1979), full utilization by phytoplankton and minimal zooplankton grazing, this amount of nitrate could yield mild bloom conditions of 6–8 mg Chl *a* m^{-3} .

Pilchard change diet from zooplankton to phytoplankton at maturity (King and Macleod 1976), suggesting a possible role for phytoplankton (see below) since only adult pilchard were affected. In addition, the consistent association of virus with moribundity (Whittington *et al.* 1996) suggests a possible role for the virus. In either case, it is necessary to know whether the upwelling event of 1995 really was extraordinary.

Comparison with past upwellings

Upwelling along the Eyre Peninsula has not previously been studied in any detail. Upwelling has, however, been studied off the nearby Bonney coast (Rochford 1977, Lewis 1981, Schahinger 1987), this being one of the few strong upwelling regions off Australia, and the winds that drive that upwelling during late summer blow also along the Eyre Peninsula coastline. The widening of the shelf to the north-west, however, leads to less upwelling there for a given wind strength. Indeed, on 2 March 1995 (Plate Ia) the upwelling off the Bonney coast was much more widespread and colder (11°) than that off the Eyre Peninsula.

Since it is the wind that drives the upwelling along the South Australian coast, one can reasonably expect that for the upwelling of March 1995 to be unusual, so should have been the wind.

The strength of the upwelling-favourable component of the wind stress at South Neptune Island in February–March 1995 (Fig. 2) was only moderate (0.13 N m^{-2} on 21 February) compared with many events during the twelve previous years; 0.23 N m^{-2} on 7 February 1993 and 1 March 1992 or 0.30 N m^{-2} on 6 February 1985, for example. The duration of the event, however, was relatively long. A simple index of upwelling that includes both the strength and duration of the wind is the 15-day mean of the upwelling-producing component of the wind stress. Computation of this also suggests that February–March 1995 was typical of earlier years.

The other variable determining the nature of upwelling is the density profile of the water column, since this affects the internal Rossby radius (within which distance from the coast the water first upwells) and the thickness of both the top and bottom Ekman layers. The only routinely monitored proxy variable for this parameter is coastal sea level. Monthly averaged sea level was slightly low at Port Stanvac (Adelaide, -0.07 m) and Portland (-0.06 m) in January 1995 but within 0.03 m of normal at Thevenard (Ceduna) in January and Port Stanvac and Portland in February and March (Anon. 1995a). Hence, there is no evidence of a

large-scale perturbation of the density profile, due for example to a passing Kelvin wave as speculated by O'Neill (1995).

We have examined the SST images of South Australian waters for February and March from 1991 through 1995. Unfortunately, cloud cover was such that the degree of upwelling could not be assessed for many of the wind events. Nevertheless, several images of upwelling comparable to, or stronger than, the 1995 upwelling were found. The most recent evident upwelling similar to that of 2 March 1995 is for 9 February 1993 (Plate Ic) following the strong wind mentioned above. The image showing the strongest upwelling was for 18 March 1992 (Plate Id) following a fairly prolonged (3-day) period of moderate to strong (greater than 0.1 N m^{-2}) upwelling winds.

To estimate how often such upwellings occur, we must rely on the wind data because of the cloud problem. However, not all strong upwelling-favourable winds lead to strong upwelling. For example, the image for 17 March 1989 (not shown), shows that even though the wind was as strong as and more prolonged than in March 1992, the upwelling as evidenced by SST was as widespread but warmer at $14\text{--}15^{\circ}\text{C}$ (compared with $12.5\text{--}13^{\circ}\text{C}$; the difference exceeding the 0.6°C r.m.s. error (Pearce *et al.* 1989) of AVHRR SST estimates). Furthermore, the strong wind on 5 February 1991 did not result in any apparent upwelling off the Eyre Peninsula, and resulted in only weak upwelling off the Bonney coast. From the available images, it appears that the amount of upwelling for given wind is greater on average in March than in February, presumably owing to the weakening pycnocline. Fig. 2 therefore suggests that the next most recent strong upwelling events occurred around 6 March 1988, 1 March 1987, 6 February 1985 (because the wind was extremely strong) and 16 March 1983. The 1983 and 1985 events were observed by Schahinger (1987).

On the assumption that SST and wind forcing are valid indicators of upwelling in this area, the upwelling of late February to early March 1995 was certainly a strong one, perhaps occurring only once every three or four years, according to observations during the last 13 years. But stronger upwellings appear to have occurred, the last as recently as 18 March 1992 (after which no reports of mortalities followed (K. Jones, personal communication)). Hence, there is no correlative evidence to suggest that the upwelling off the Eyre Peninsula in February–March 1995 was largely responsible for initiating the outbreak of mortalities.

Spread—correlation with environmental anomalies

The salient features of the epidemiology (Whittington *et al.* 1996, Fletcher *et al.* in press) were (1) locations of sightings proceeding monotonically away from South

Australia at fairly constant speeds: typically 0.5 m s^{-1} to east and 0.35 m s^{-1} to west, (2) mortalities occurring for several weeks in South Australian waters, but for only a few days elsewhere and (3) sightings spanning the range of the species, closely spaced in populated regions, except for the 800 km stretch from Robe to central Bass Strait.

Plate II shows the advancing front of sightings overlaid on composite maps of the SST. The mis-match of mortalities with the regions of lowest SST (the upwelling regions of the Bonney Coast and Lakes Entrance) is clear, again suggesting that upwelling did not play a role. Comparison of the SST maps with those for 1990–94 (not shown) reveals no noticeable SST anomalies at all in 1995. Instead, normal conditions for February to June of warm waters flowing southwards in the Leeuwin Current (Cresswell *et al.* 1989; Smith *et al.* 1991) and East Australian Current, EAC (Ridgway and Godfrey 1997) prevailed. There is no obvious correlation (at any lag up to 3 weeks) between the SST and the sightings. The deaths were occurring in the very different surface temperatures (16 to 22°) that are normal across the range of the species.

The weakness of Plate II is that it shows only surface data (temperature only) which is time- and space-averaged. We now look in more detail for evidence of environmental anomalies, using also the (limited) *in situ* data available.

East of Eyre Peninsula

The AVHRR SST image of 11 May 1995 for New South Wales (NSW) waters shows slightly cooler surface waters in the inner shelf (20°C) than over the outer shelf in the EAC (25°C). This does not in itself indicate upwelling, since the EAC waters will be warmer than resident NSW waters. By late May (last panel of Plate II), SST imagery shows the cooler 19°C water over all the shelf south of 32°S . This cooling is more likely to be due to the loss of the surface SST expression of the EAC extension by mixing and radiation, rather than to upwelling.

In situ temperature observations are few, but the available data are consistent with the satellite estimates. At the Esso-BHP Kingfish B oil platform, for example, the temperature at 8 m decreased fairly smoothly from 17° to 16°C between 13 April and 10 May (Lawson and Treloar Pty Ltd, personal communication for Esso-BHP), as is normal for the period. Eight km west of Gabo Island on 13 May, the water temperature, salinity and oxygen saturation were 16.0 – 15.7°C , 35.4 and 100% , respectively, down to 35 m (F. J. Neira, VFRI, personal communication).

At Sydney Water's Ocean Reference Station in 60 m of water 3 km off Bondi, the temperature profile during May 1995 (mortalities at Sydney were sighted on 15 May) was typical for that time of year, showing strong stratification (15°C to 22°C) during southward currents, or isothermal conditions (19°C top to bottom) indicative of local

downwelling during brief periods of flow to the north associated with local and remote southerly winds (Griffin and Middleton 1992).

Farther offshore at the CSIRO Port Hacking (Sydney) 100 m station at the bottom, temperature and nitrate were 19.5°C , $3.2 \mu\text{mol L}^{-1}$ on 13 April and 16.6°C , $7.6 \mu\text{mol L}^{-1}$ on 25 May 1995. The surface values were 19.9°C , $0.8 \mu\text{mol L}^{-1}$ and 19.0°C , $1.4 \mu\text{mol L}^{-1}$ respectively, indicating only weak, if any, upwelling. On 25 May, dissolved oxygen was slightly lower (6.14 mg L^{-1}) at the bottom than at the surface (7.35 mg L^{-1}). The 1995 data are very close to the mean values for the seasonal cycle of each quantity, as shown in Fig. 3.

On 19 May 1995 an expendable bathythermograph line was completed across the Tasman Sea into Sydney (finishing at the 200-m isobath) as part of the World Ocean Circulation Experiment. The section did not show any large anomalies relative to the range of variability in sections collected quarterly since 1991 (G. Meyers, CSIRO, personal communication). The along-track averaged thermal structure to 700 m was essentially the same (1 – 2°C cooler) as at the same time in 1994. The bottom temperature at the shelf break was 19°C , indicating an absence of any large-scale thermocline rise.

Sampling was performed off Cape Morton ahead of the kill front on 20 May and again behind it on 6 June by the Southern Fisheries Centre of Queensland Department of Primary Industries (A. Butcher, personal communication). The observed temperature drop from 23 – 23.7°C to 20.1 – 21.2°C is typical for this location and time of year. On 30 May 1995 CSIRO completed a line of stations from the

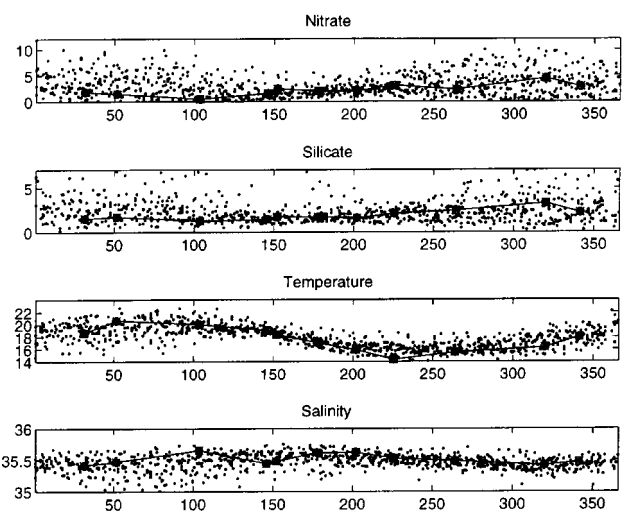


Fig. 3. Depth-averaged nitrate and silicate concentrations (both $\mu\text{mol L}^{-1}$), temperature ($^\circ\text{C}$) and salinity from the CSIRO Port Hacking 50-m station versus day number, 1970–95. Measurements were taken at 10-m intervals from surface to bottom. 1995 data are shown as linked symbols. Mortalities were first sighted at Sydney on Day 134 of 1995 (15 May).

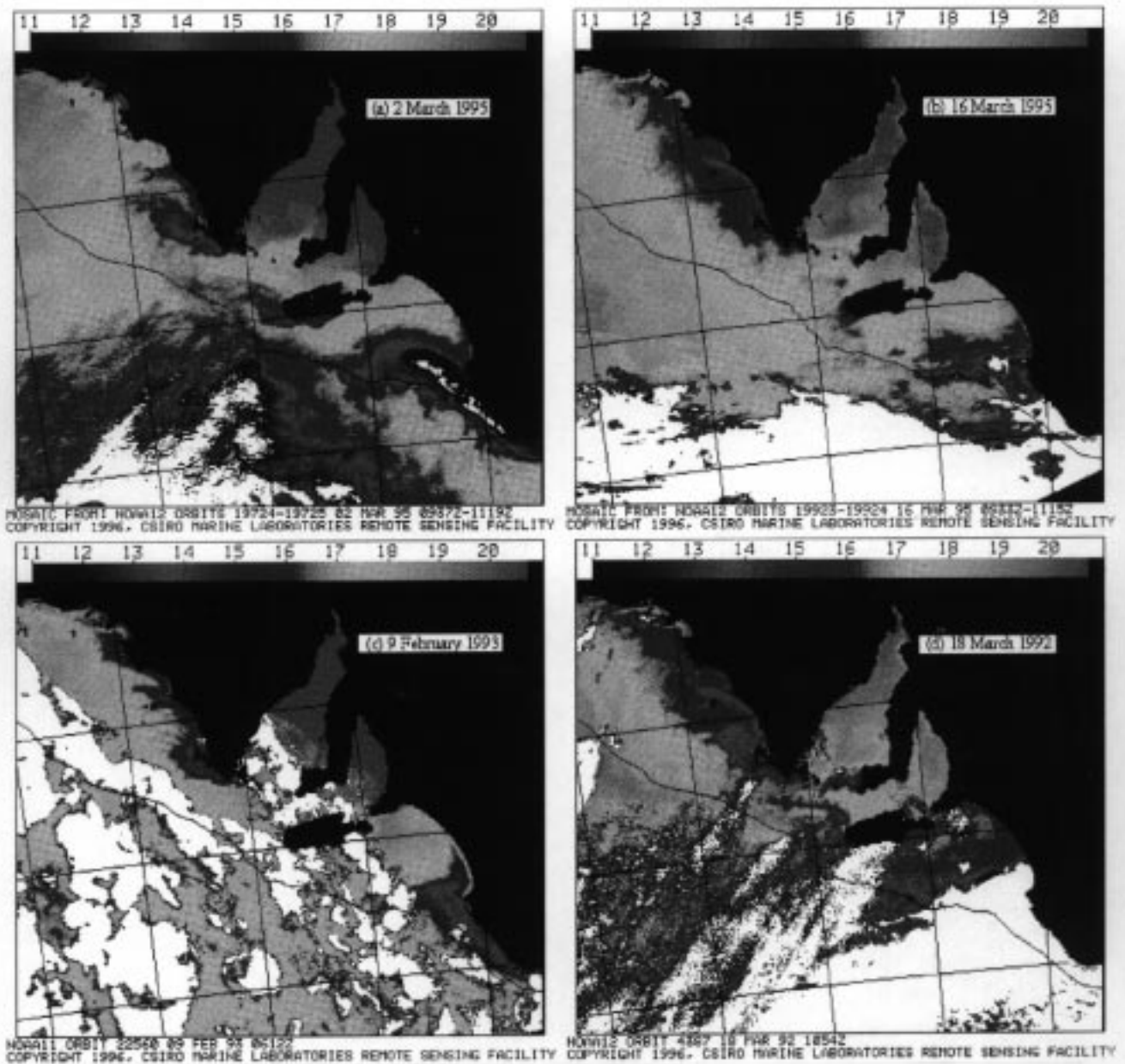


Plate I. AVHRR sea surface temperature images of the Eyre Peninsula to Bonney coast region showing (a) developed upwelling off Cape Carnot before outbreak of mortalities, (b) diffuse upwelling concurrent with mortalities, (c) the most recent similar upwelling and (d) the most intense upwelling evident in imagery since 1991. Any temperature less than 11°C is coded white since it is probably due to cloud.

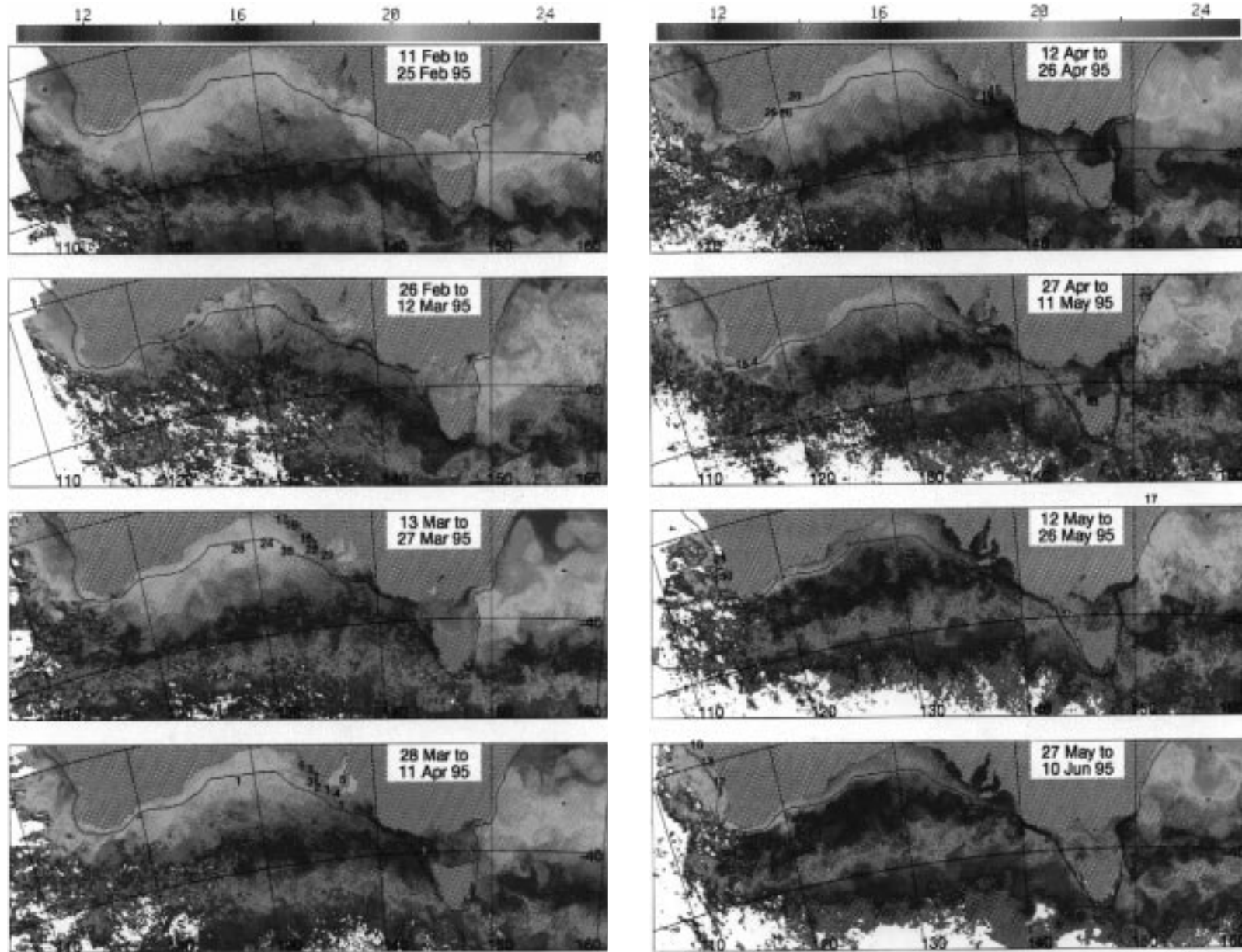


Plate II. Locations of the first sightings of dead pilchards for each region (denoted by day of the month) overlaid on composite NOAA-12 AVHRR SST images. Each panel covers a 15-day period. The sightings data are divided on month boundaries; the SST data-window leads by an anticipated 'incubation period' of three days. Each pixel is coded to represent the 94th percentile of the SST estimates available within the period, in order to reject clouds wherever possible.

20-m isobath to the 65-m isobath, just north of Coffs Harbour and close to the kill front at the time (G. Cresswell, personal communication). Normal temperatures of 21 to 22.5°C were observed.

Coastal trapped waves travel northwards along the east Australian coast, and are the only oceanic wave-like phenomenon possibly responsible for triggering mortalities sequentially along the coast. However, most of the energy is propagated much faster than the kill front via modes 1 and 2 (Griffin and Middleton 1991, McIntosh and Schahinger 1994) at 3.5 and 2 m s⁻¹, respectively (Church *et al.* 1986). The higher modes travel more slowly, and produce greater thermocline displacements (downward following strong eastward currents in Bass Strait or strong southerly winds on the east coast). There is no evidence to suggest that they were energetic in 1995.

West of Eyre Peninsula

Coastal trapped waves travel only eastwards in the Great Australian Bight so they cannot be used to explain the westward spread of mortalities.

In response to the spread of mortalities, CSIRO made two extra visits to the monthly observation station at Rottneest Island. Nutrient, temperature and salinity data are thus available for 27 April, 15 May, 25 May, 1 June (mortalities sighted) and 28 June 1995. Other data were acquired by Western Australia Fisheries Department and are discussed by Fletcher *et al.* (in press).

Whereas the temperature and silicate concentrations in 1995 were normal, salinity was high all year and nitrate was

high (for this location) on 25 May, 1 June and 28 June (Fig. 4). Salinity at Rottneest Island has been increasing gradually since 1992 for unknown reasons. The high nitrate concentration (3.2 $\mu\text{mol L}^{-1}$ at one depth) is intriguing and appears, from the lack of a corresponding salinity or silicate signal, to be of oceanic rather than terrestrial (Swan River) origin. We have no evidence, however, that the high nitrate led to any blooming of phytoplankton, and indeed, from the 25 May and 1 June surveys, the chlorophyll-*a* concentrations measured spectrophotometrically appeared normal at 0.25–0.46 mg m⁻³.

In addition to the Rottneest stations, RV *Franklin* was used for 2.5 days to obtain more comprehensive data, although these were only concurrent with or slightly ahead of, rather than well ahead of, the kill front. Temperature, salinity and nutrient sections (not shown) off Dongara and Geraldton on 14 June 1995 (Fig. 5) show that low-nutrient conditions

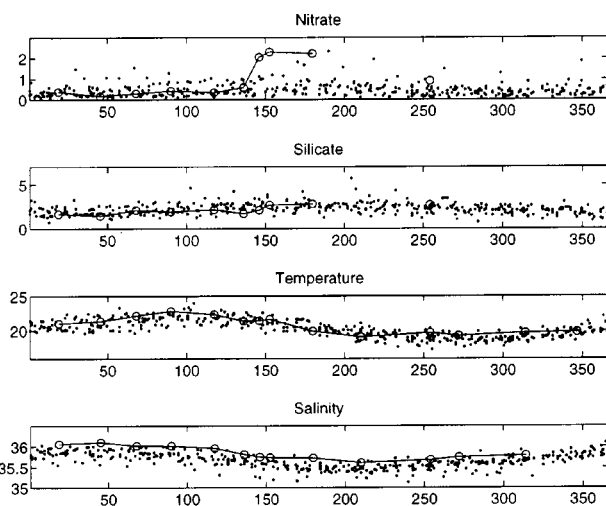


Fig. 4. Depth-averaged nitrate and silicate concentrations (both $\mu\text{mol L}^{-1}$), temperature ($^{\circ}\text{C}$) and salinity from the CSIRO Rottneest Island 50-m station *versus* day number, 1970–95. Measurements were taken at 10-m intervals from surface to bottom. 1995 data are shown as linked open circles. Mortalities were first sighted at Rottneest Island on Day 151 of 1995 (1 June).

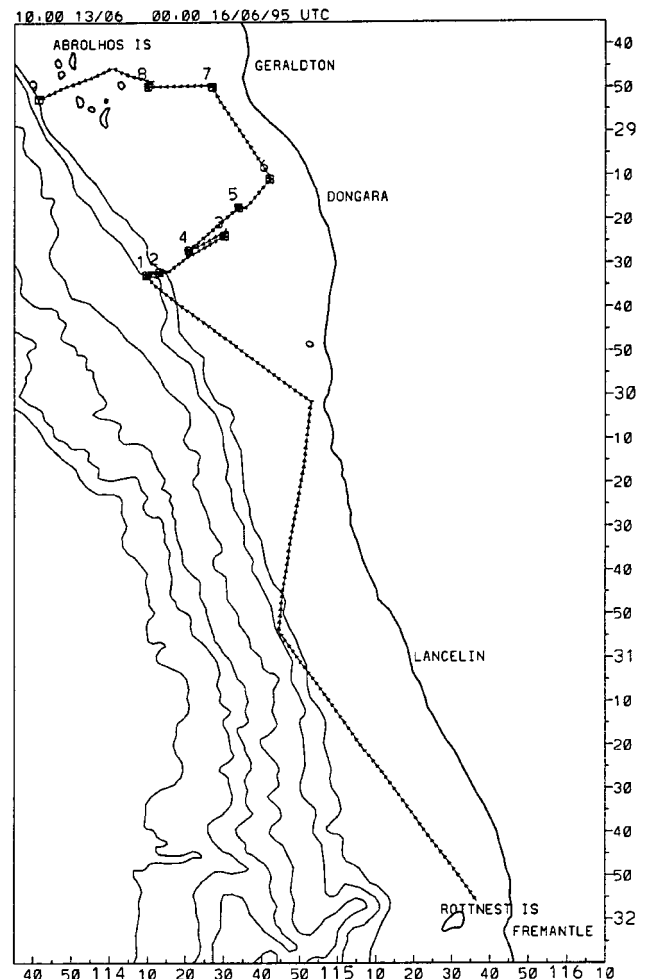


Fig. 5. Track of RV *Franklin* showing locations of nine stations. Dead pilchards were sighted by fishers near Station 3 as the survey commenced, hence the odd cruise track. Depth contours are 200 m, 500 m, 1000 m, 2000 m, 3000 m and 4000 m.

Table 1. Phytoplankton species compositions associated with pilchard mortalities in different geographic regions during 1995

Date	Locality	Collector	Taxa
Mar. 15	Morgan's Landing, Coffin Bay, SA	SARDI	toxic dinoflagellate <i>Gymnodinium mikimotoi</i>
Mar. 30	Coffin Bay, SA	SARDI	<i>G. mikimotoi</i>
Mar. 30	Maria Island, Tas.	DPIF	diatom bloom <i>Rhizosolenia phuketensis</i>
May 12–13	Wingan Inlet, Merimbula, Vic.	VFRI	gelatinous diatom blooms <i>Thalassiosira</i> spp.
mid May	Port Phillip Bay, Vic.	D. Hill, Univ. Melbourne	toxic dinoflagellate <i>Gymnodinium pulchellum</i>
May 30	North Rock, NSW	CSIRO	mixed diatom bloom <i>Chaetoceros</i> , <i>Lauderia</i> , <i>Pseudo-nitzschia</i> , <i>Rhizosolenia</i> , <i>Thalassiosira</i> , <i>Thalassiothrix</i> ; tropical cyanobacterium <i>Trichodesmium</i>
June 14–15	Rottneet I.–Geraldton, WA	CSIRO	diatoms <i>Bacteriastrum</i> , <i>Chaetoceros</i> , <i>Pseudo-nitzschia</i> , <i>Rhizosolenia</i> , <i>Thalassionema</i> , <i>Thalassiothrix</i> ; silicoflagellate <i>Dictyocha</i>
Aug. 31–Sept. 1	Tasman Bay, New Zealand	Cawthron Institute	diatom spring bloom <i>Coscinodiscus concinnus</i> , <i>Chaetoceros</i> spp., <i>Lauderia</i> , <i>Eucampia</i>

prevailed. The entire shelf to 140 m was occupied by warm (20.0–22.5°C), saline (35.64–35.68), low-nitrate (0.1–0.6 $\mu\text{mol L}^{-1}$) water.

Plankton

A role for plankton is suggested because only adult pilchard were dying. Adult pilchard are phytoplanktivorous and have a close spacing of gill lamellae, which makes them very sensitive to gill clogging even by non-toxic algal cells (Jones and Rhodes 1994). Widespread examination (under the aegis of the Australian Quarantine and Inspection Service) of pilchard stomach contents indicated that they were well fed. However, chemical and animal bioassays for the presence of algal toxins such as paralytic shellfish poisons, amnesic shellfish poisons or neurotoxic shellfish poisons were all negative. This, the general mismatch of mortalities with upwellings, and the inconsistent association of phytoplankton blooms (Table 1) with mortalities suggests phytoplankton were not a contributing factor in mortalities.

Gymnodinium mikimotoi causes necrosis and sloughing of epithelial tissues of gills and digestive system (Roberts *et al.* 1983), and it may account for the Coffin Bay mortalities of octopus, stingray and shellfish, but probably not the more widespread concurrent pilchard mortalities.

Thalassiosira spp. are non-toxic, mucilage-producing diatoms and were found associated with large quantities of 'slime' collected from gill-nets of fishers operating in eastern Victoria. However, it is almost certain that *Thalassiosira* spp. were not the primary cause of nearby pilchard mortalities since only pilchard were affected. No harmful impacts on finfish by *Thalassiosira* have ever been observed and no traces of this diatom were found in the gill lamellae of affected fish (F. J. Neira, personal communication).

Blooms of the toxic dinoflagellate *Gymnodinium pulchellum*, synonymous with the Japanese fish killer

Gymnodinium type '84K (Onoue *et al.* 1985) have been known in Port Phillip Bay since the 1950s (Wood 1965).

The mixed diatom bloom off North Rock (near Coffs Harbour) was normal for the region (Hallegraeff and Jeffrey 1993).

No phytoplankton blooms were recorded off the west coast, and the plankton composition and density sampled from Franklin (see Appendix for details) were consistent with the low nutrient concentrations observed. The total cell count averaged over all 23 Niskin bottle samples was only 27362 cells L^{-1} , the average chlorophyll-*a* concentration was only 0.36 mg m^{-3} , the average microzooplankton biomass was only 35 mg m^{-3} , and the average macrozooplankton biomass in bongo-net and surface-net samples was only 1.4 and 7.3 mg m^{-3} respectively. A large fraction (but low abundance) of *Chaetoceros* and *Dictyocha* species was found; some species (*C. convolutus*, *C. concavicornis* and *D. speculum*) have been implicated in the deaths of net-penned lingcod (Bell 1961) and salmon (Bruno *et al.* 1989; Rensel *et al.* 1989), but those species were not identified in the present plankton samples, and no *Chaetoceros* or *Dictyocha* were found in the gills of affected fish. No mortalities in wild fish have been attributed to *Chaetoceros* or *Dictyocha* and a causal relationship appears highly unlikely in the present case. A similar conclusion was reached by Mackenzie and Todd (1995) investigating the cause of pilchard mortalities in New Zealand.

Hypothesis 2: An exotic pathogen dispersed through the population

Here we consider the possibility that an exotic pathogen was introduced near the outbreak area and was dispersed by various potential vectors through the population. One potential source of an introduced pathogen is the imported frozen pilchard fed to caged tuna at Port Lincoln.

Migration and fish-to-fish contact

This vector is unlikely because the combined effect of the limited sustained swimming speed of pilchard (0.06 to 0.24 m s⁻¹), known stock boundaries (Blackburn 1950, 1960; Parrish *et al.* 1989; Syahailatua 1992; Dixon *et al.* 1993), and the typical incubation periods of infectious diseases (days to weeks) leads to a dispersal rate of only 0.04 to 0.2 m s⁻¹, somewhat less than the observed rate of up to 0.7 m s⁻¹.

Ocean currents

The Leeuwin and East Australian currents were flowing generally southwards (Anon. 1995c) on the west and east coasts, respectively, at the time that mortalities were spreading northwards (Plate II); this suggests that dispersal by ocean surface currents could not have been a vector.

In situ observations of current velocity contemporaneous with the spread support the above and are as follows.

In Bass Strait at Kingfish B (mortalities sighted 7 May), the subtidal current at 8 m was weak and in the opposing direction; the net current run for 1–7 May was less than 60 km westwards; during the second half of April it was mostly eastwards, but at only 0.1–0.15 m s⁻¹ (Lawson and Treloar Pty Ltd, personal communication for Esso–BHP). At Sydney (mortalities sighted 15 May), the subtidal current over the previous month, 3 km offshore from Bondi at 10 m and 50 m, was mostly southwards at 0.2–0.6 m s⁻¹ and 0–0.4 m s⁻¹, respectively (P. Tate, AWT Ensight, personal communication). The only northward flow, of 0.4 m s⁻¹ at 10 m and 0.2 m s⁻¹ at 50 m, occurred on 6 and 7 May in response to a southerly wind. At Coffs Harbour on 30 May 1995, CSIRO drifters released at the 40 m and 65 m isobaths were carried southwards on the shelf initially at about 0.6 m s⁻¹ in EAC waters (G. Cresswell, personal communication).

Off the west coast (Fig. 5), the currents measured underway by Acoustic Doppler Current Profiler on *Franklin* were generally southward, reaching 1 m s⁻¹ near the shelf break, but only 0.1 m s⁻¹ over the shelf off Dongara and Geraldton and up to 0.3 m s⁻¹ over the shelf en route to the Dongara line. Strong northwesterly winds blew during the week before the cruise so the currents then would have been even more strongly counter to the progress of mortalities than those observed during the cruise.

Much less is known about deeper ocean currents at the time of mortalities, but during the September 1983 to March 1984 Australian Coastal Experiment (Huyer *et al.* 1988) strong (greater than 0.5 m s⁻¹) and persistent (more than 5 days) northward currents occurred over the upper slope off Newcastle, but not off Sydney and Cape Howe. Deep currents could therefore have been at the speed and direction of the spread of mortalities along limited stretches of coastline, but almost certainly not along most of the 6000 km of the spread.

Ballast water

In 1991 an estimated 39 million tonnes of ballast water was transported along the Australian coast by domestic shipping (Kerr 1994); there were 138 passages between South Australian and other Australian ports in 1991. However, the one-way movement of the kills up the coasts with no further mortalities once the front had passed is not consistent with an un-ordered sequence of port-to-port visits in 1995.

Predators

Spread of a disease could have been as observed if the pathogen were carried by a fast-moving predator. Fish-eating birds are known to carry microbial diseases, and the short-tailed shearwater (*Puffinus tenuirostris*) is reported to carry the influenza virus and Type A viruses (Warham 1990). Huge numbers of the shearwater breed in colonies from NSW to SA. Naarding (1980) estimated that there were 5.6 million breeding pairs around Tasmania, and the fledglings and adults depart for wintering grounds in the North Pacific in April and May (Harrison 1983). Shearwaters also eat pilchard (Montague *et al.* 1986), as does the little penguin *Eudyptula minor* (Klomp and Wooller 1988; Gales and Pemberton 1990b; Cullen *et al.* 1992), which occurs around temperate Australia.

Mammals and fish can carry identical viruses. The opaleye (*Girella nigricans*) carries the opaleye calicivirus and is the intermediate host to a nematode lungworm that parasitizes the California sea lion (Wolf 1982). Pilchard were reported to constitute 1.6% of the total diet of Australian fur seal (*Arctocephalus pusillus doriferus*) in Bass Strait (Gales and Pemberton 1990a). Other recorded predators of pilchard are tuna (J. Young, CSIRO, personal communication), western Australian salmon (Malcolm 1966), Gould's squid (O'Sullivan and Cullen 1983) and dolphin (F. J. Neira, personal communication).

Although a fast-moving predator of pilchards could perhaps account for the rapid spread of mortalities we have no evidence for any pilchard predator carrying an infectious agent through the population.

Hypothesis 3: Exotic pathogen triggered by normal seasonal variability

A test of this hypothesis by correlative analysis requires the demonstration of a consistent relationship between the local change in ocean conditions and the outbreak of mortalities; this requires many comparable time-series of ocean data, and these are not available (except for SST, but cloud cover is a problem). There is a fairly consistent relationship of mortalities with cooling of surface waters, due either to upwelling or simply to the onset of winter. For example, the Sydney Water data show that mortalities occurred 10 days after the first recording of 16°C water for

40 days. The temperature dropped 2°C over two days, which is normal for Sydney (Griffin and Middleton 1992). However, although the temperature at Kingfish B was also 16°C for the 10 days before sightings of mortalities, it had been 17°C for the 3 previous weeks (from 1 April). The data are insufficient to examine Hypothesis 3 in any detail.

Comparison with mass mortalities elsewhere

Mass mortalities of fish in crowded aquaculture conditions are relatively common and can often be directly attributed to microbial diseases. Mass fish mortalities in the open ocean, however, are less frequently observed. Möller (1988) speculated that neither disease nor starvation caused mass mortalities in the marine environment unless associated with an acute environmental catastrophe.

In addition to the Walvis Bay mortalities discussed above (Hypothesis 1), mass mortalities among marine fish have been attributed to environmental conditions in Kiel Bay, Germany (Kils et al. 1989), and in Concepcion Bay, Chile, and New York Bight (Sinderman and Swanson 1979). These mass mortalities have common features that distinguish them from the 1995 Australian pilchard mortality: there were definite, readily observed changes in the physical environment of the fish; more than one species was affected; the mass mortalities were periodic not singular; and the scale of their impact was in 10s or 100s not 1000s of kilometres. These environmentally induced outbreaks bear little resemblance to the Australian and New Zealand pilchard deaths.

Disease has been associated with several mass mortalities in the marine environment (Sinderman 1990), and clupeids (such as the pilchard) are a family of fish often susceptible to disease. Their widespread distribution and schooling behaviour might further the rapid transmission of diseases or alternatively make the kills more visible. Epizootics caused by the protist *Ichthyophonus hoferi*, affecting organs including the heart, have been recorded in western North Atlantic herring (*Clupea harengus*) since 1898 (Sinderman 1990) and may have killed almost half of affected stocks of western North Atlantic herring in the 1950s. It was first recorded in the eastern North Atlantic in 1940, as an epizootic of mackerel, but not until 1991 as an epizootic of herring (Anon. 1995b). Each epizootic takes several years to run its course. *Ichthyophonus* has been observed in eastern North Pacific herring (*Clupea harengus pallasii*) since at least 1989, sometimes occurring with viral haemorrhagic septicaemia virus (Meyers et al. 1986). Only two disease-related population declines have been identified for Pacific herring, one where *Ichthyophonus* appears to have been the dominant cause of mortality and the other where the clinical and pathology findings are consistent with mortalities due to viral haemorrhagic septicaemia virus.

The restriction of these disease-induced mass mortalities to one or several species more closely resembles the single-

species impact of the Australian and New Zealand pilchard kills than do the environmentally induced mass mortalities. However, the multi-year time scale of these events and their recurrence at the same locality over time differs from the multi-month time scale and lack of repeated mortalities that characterized the pilchard event.

More similar to the pilchard event is the mass mortality of four marine catfish species off the south coast of Brazil (M. Costa, Companhia de Tecnologia de Saneamento Ambiental, Sao Paulo, Brazil, personal communication, July 1995). Mortalities of mainly adult catfish began in February 1994, the end of the spawning season, near a port in Babitonga Bay and spread both northwards (with prevailing currents) and southwards as a front of kills at an average rate of 2.5 to 3 km per day, finally covering 1700 km of coastline. Phytoplankton blooms or toxicants were not observed. The ultimate cause of mortalities is unknown, although virus-like particles (20–32 nm in size, therefore not Herpes virus) were seen in kidney tissue. *Aeromonas hydrophilla*, a common bacterium in stressed fishes, was also observed. Since the spread of mortalities was consistent with an epizootic spread in a non-resistant population by fish-to-fish contact, M. Costa raises the possibility that the mortalities began following the transport in ballast water of the same disease organism that caused a similar catfish mortality off Sierra Leone, West Africa, in 1992–93.

There are marked similarities between the Brazilian and Australian events, although the fish species are not closely related. The sudden appearance of mortalities that passed as a front of kills in both directions, and against prevailing currents, to cover 1000s of kilometres of coastline are common to both events. The pilchard kill front, however, travelled about ten times faster than the catfish kill front, and covered a greater distance. Mortalities in both instances first occurred close to an area of marine traffic, raising the possibility of an exotic infectious agent entering and spreading through a non-resistant population. There were scattered mortalities of marine catfishes off Brazil in 1995, the year following the first observations. We are unaware of any pilchard mortalities in Australia or New Zealand in early 1996.

Conclusion

The paucity of routinely collected data around Australia, especially subsurface data (pilchard are found to depths of 200 m (Fletcher 1990)) leads to the possibility that an environmental anomaly occurred but went unrecorded or was unresolved from normal variability. Hence, we cannot completely rule out the possibility that Hypothesis 1 is correct, even though it seems highly unlikely since no support for it could be found in the bulk of the data examined here. The only significant environmental anomaly found was the elevated nitrate concentration at the Rottneest Island station, and that is only relevant to the pilchard

mortalities if phytoplankton can be implicated in some way. Sampling off Western Australia revealed the low-biomass phytoplankton assemblage typical of low-nutrient waters. Nearly one-quarter of cells were *Chaetoceros* sp., but gill-damaging species were identified in neither the water nor fish gills. Normal blooms of various species were found in the east, including mucilage-forming *Thalassiosira*, but these were not found in the gills of affected fish. Locally toxic dinoflagellate blooms of *Gymnodinium mikimotoi* and *G. pulchellum* were found in SA and Victoria, but not in all areas where pilchard mortalities occurred. Phytoplankton is unlikely to have been a contributing factor because of the greatly differing phytoplankton species' identities at the different locations where pilchard mortalities occurred. Similarly, Smith *et al.* (1995) found no evidence of environmental stress associated with the pilchard mortalities in New Zealand.

Hypothesis 2 is more plausible because the epidemiology is consistent with the introduction of an exotic pathogen into a non-resistant population. However, the source and vector of an introduced pathogen remain unknown. Hyatt *et al.* (1996) show that the aetiological agent is most likely the Herpes-type virus consistently associated with moribund fish. We have discounted the likelihood that fish-to-fish contact, ocean currents or ballast water were vectors, leaving predators as remaining candidates. Whittington *et al.* (1996) come to a similar conclusion.

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Appendix 1. West-coast cruise data

Methods

Phytoplankton pigment by high-performance liquid chromatography (HPLC)

Niskin bottle samples were taken at three depths (surface, 25–50 m, 50–140 m) at all except Station 6, and 5 L were filtered through Whatman GF/F glass-fibre filters then preserved in liquid nitrogen. Samples were extracted in 90% acetone and analysed with a Waters HPLC unit comprising a 600 controller, 717+ refrigerated autosampler and a 996-photodiode array detector. Pigments were separated on a stainless-steel 25 cm × 4.6 mm i.d. column packed with ODS2 of 5 µm particle size (SGE) with gradient elution as described by Wright *et al.* (1991). The separated pigments were detected at 436 nm and identified against standard spectra by using Waters Millennium software. Chlorophyll-*a* and -*b* peaks in the sample chromatograms were quantitated against standard solutions (Sigma).

Phytoplankton composition and density by visual counting

Ten-litre Niskin bottle samples, taken as above, were concentrated to 30 mL through 10 µm mesh and preserved in Lugol's solution. In the laboratory, a minimum of 500 cells was counted from each sample at 400× magnification in a Palmer Counting Cell.

Microzooplankton biomass

A drop net (Heron 1982) of 100-µm mesh and 0.25-m² mouth area was deployed twice at each station to 100 m or 10 m off the bottom. Samples were fixed in 4% seawater formaldehyde buffered with sodium acetate. In the laboratory, samples were split and one half was dried at 60°C for approximately 48 h then weighed. The other half was retained for qualitative assessment of the phytoplankton component.

Macrozooplankton biomass and composition

Paired 500-µm, 0.4-m² bongo nets were towed obliquely from the surface to 200 m depth or near the bottom and back over 20 min at approximately 1.5 m s⁻¹ at two offshore stations (Stations 2 and 9, 135 m and 300 m) and at two inshore stations (Stations 5 and 8, each 50 m). A 500-µm, 1-m² surface net was towed concurrently for 10 min. Mechanical flowmeters recorded the water volume filtered by the nets. Samples were preserved, split, dried and weighed as above.

Results

The composition of the phytoplankton assemblage is listed in Table A1. Comparative data for the region are unpublished, but the community

structure is typical of similar environments. Diatoms (Bacillariophyceae) account for 87% of the total cell numbers, with species diversity being relatively high. Two genera, *Thalassionema* and *Chaetoceros* constituted nearly 50% of the total cell numbers. The only marked spatial heterogeneities in the data were that (1) the average cell count at Station 8 (mid shelf, northern line) was three times the average of other stations, (2) *Chaetoceros* and silicoflagellates were much less abundant at Station 5 (inner mid shelf, southern line) than elsewhere and (3) there were no cyanobacteria at Station 1 (offshore, southern line).

Pigment composition and concentrations were consistent with a low-biomass, diatom-dominated community (Table A2). The low degree of spatial heterogeneity in pigment distribution was also consistent with the lack of a phytoplankton bloom (Denman 1977). If variance normalized by the mean is used as a measure of 'patchiness', the value of 0.038 for the eight stations sampled indicates a low-to-intermediate degree of spatial heterogeneity relative to other values for the Indian Ocean (Piontkovski *et al.* 1995). The low frequency with which peaks of alloxanthin (Table A2) were detected suggests the virtual absence of the algal group Cryptophyceae (Gieskes and Kraay 1983). The frequency with which chlorophyll-*c*₂, fucoxanthin and diadinoxanthin were detected is consistent with the evidence from the cell counts that the community was dominated by diatoms (Stauber and Jeffrey 1988). The frequent occurrence of the fucoxanthin derivative, 19'-hexanoyl-oxyfucoxanthin suggests the presence of Prymnesiophyceae, perhaps the ubiquitous *Emiliania huxleyi* (Wright and Jeffrey 1987). The latter may have escaped microscopic detection because its small size (Thompson and Calvert 1995) allowed it to pass through the 10-µm mesh used to concentrate field samples prior to microscopic examination. Peridinin was not detected, as is consistent with the low numbers of photosynthetic dinoflagellates counted (Jeffrey *et al.* 1975).

Microzooplankters were unevenly distributed (Fig. A1). Biomass was highest (about 90 mg m⁻³, but perhaps 10% of this was actually *Thalassionema*, *Thalassiothrix* and *Chaetoceros*) at Stations 1 and 2 (southern offshore) and least (about 3 mg m⁻³) at Stations 8 and 9 (northern mid-shelf and offshore). Hence, the station (8) with the most small phytoplankton had the least microzooplankton.

Macrozooplankton was also unevenly distributed, being more abundant (Fig. A1) at the inshore stations of both lines. The extra biomass is partially explained by the additional presence (Fig. A2) inshore of a sergestid shrimp (subfamily Luciferinae). Copepods were the most abundant group at all stations, accounting for approximately 70% of individuals at the offshore stations.

Table A1. Summary of phytoplankton characteristics at west-coast stations (see Fig. 5), from samples at two or three depths per station ($n = 23$)

Taxon	No. spp.	Cells L ⁻¹	%	Taxon	No. spp.	Cells L ⁻¹	%
Diatoms				<i>Synedra</i>	1	8	0.03
<i>Actinoptychus</i>	1	16	0.06	<i>Thalassionema</i>	2	6847	25.02
<i>Amphora</i>	2	26	0.09	<i>Thalassiosira</i>	1	1515	5.54
<i>Bacteriastrium</i>	2	1426	5.21	<i>Thalassiothrix</i>	1	8	0.03
<i>Biddulphia</i>	1	175	0.64	<i>Trachyneis</i>	1	18	0.06
<i>Cerataulina</i>	1	157	0.58	<i>Trigonium</i>	1	31	0.12
<i>Chaetoceros</i>	48	6104	22.31	Miscellaneous			
<i>Climacodium</i>	1	24	0.09	small centrics		183	0.67
<i>Corethron</i>	2	31	0.12	unknowns		151	0.55
<i>Coscinodiscus</i>	1	31	0.12	Diatoms total		23934	87.47
<i>Cylindriotheca</i>	1	673	2.46	Dinoflagellates			
<i>Detonula</i>	1	673	2.46	<i>Amphidinium</i>	1	8	0.03
<i>Diploneis</i>	2	73	0.27	<i>Ceratium</i>	1	39	0.14
<i>Ditylum</i>	1	399	1.46	<i>Dinophysis</i>	1	8	0.03
<i>Druridgia</i>	1	1284	4.69	<i>Ebria</i>	1	24	0.09
<i>Entomoeoneis</i>	2	16	0.06	<i>Mesoporos</i>	1	39	0.14
<i>Eucampia</i>	2	159	0.58	<i>Oxytoxum</i>	1	8	0.03
<i>Fragilaria</i>	1	8	0.03	<i>Prorocentrum</i>	2	87	0.32
<i>Gossleriella</i>	1	55	0.20	<i>Protoperidinium</i>	7	102	0.37
<i>Gramatophora</i>	1	8	0.03	<i>Pyrocystis</i>	1	8	0.03
<i>Guinardia</i>	1	8	0.03	<i>Scrippsiella</i>	1	24	0.09
<i>Leptocylindrus</i>	1	567	2.07	Miscellaneous	1	8	0.03
<i>Mastogloia</i>	1	8	0.03	Dinoflagellates total		346	1.27
<i>Navicula</i>	1	8	0.03	Silicoflagellates			
<i>Nitzschia</i>	9	2378	8.69	<i>Dictyocha</i>	2	572	2.09
<i>Odontella</i>	1	16	0.06	Cyanobacteria			
<i>Paralia</i>	1	163	0.60	Coccoid (small)	?	2510	9.17
<i>Planktoniella</i>	1	33	0.12	Other			
<i>Pleurosigma</i>	1	26	0.09	Unknown	?	8	0.03
<i>Rhizosolenia</i>	5	502	1.83	Total	27362	100.00	
<i>Skeletonema</i>	1	31	0.12				
<i>Stephanodiscus</i>	1	47	0.17				
<i>Streptotheca</i>	1	39	0.14				
<i>Striatella</i>	1	8	0.03				

Table A2. Pigment composition and biomass at nine west-coast stations (see Fig. 5)

Only chlorophyll *a* and *b* were quantified. ++Strong peak clearly identifiable in chromatogram; +weak peak but identifiable in chromatogram; nd, not detected

Station	Depth (m)	Pigment (mg m ⁻³)								
		Chl <i>a</i>	Chl <i>b</i>	Chl <i>c</i> ₂	19'-Butanoyl- oxyfucoxanthin	Fucoxanthin	19'-Hexanoyl- oxyfucoxanthin	Diadinoxanthin	Alloxanthin	Zeaxanthin
1	0	0.43	0.07	++	+	++	++	++	+	+
	50	0.34	+	++	+	+	++	nd	nd	+
	140	0.11	+	+	nd	+	+	nd	nd	+
2	0	0.41	+	++	nd	++	++	+	nd	++
	50	0.38	+	++	nd	++	++	+	nd	++
	100	0.33	+	++	nd	++	++	++	nd	++
3	0	0.28	+	++	nd	++	++	+	nd	++
	35	0.38	0.06	++	nd	++	++	+	nd	+
	50	0.36	+	++	nd	++	++	+	nd	+
4	0	0.31	+	++	nd	++	++	+	+	+
	30	0.52	0.08	++	+	++	++	++	+	++
	50	0.48	+	++	+	++	++	++	nd	+
5	0	0.47	0.08	++	+	++	++	++	++	++
	25	0.49	+	++	+	++	++	+	+	+
	50	0.53	0.09	++	+	++	++	+	+	+
7	0	0.35	+	++	++	++	++	+	+	++
	20	0.42	+	++	++	++	++	+	+	+
	40	0.33	+	++	nd	++	++	nd	nd	nd
8	0	0.40	+	++	nd	++	++	+	nd	++
	25	0.41	+	++	nd	++	++	+	nd	++
	45	0.41	+	++	nd	++	++	+	nd	++
9	0	0.38	0.07	++	+	++	++	+	+	++
	50	0.11	nd	+	nd	nd	nd	nd	nd	nd
	100	0.10	nd	+	nd	nd	nd	nd	nd	nd

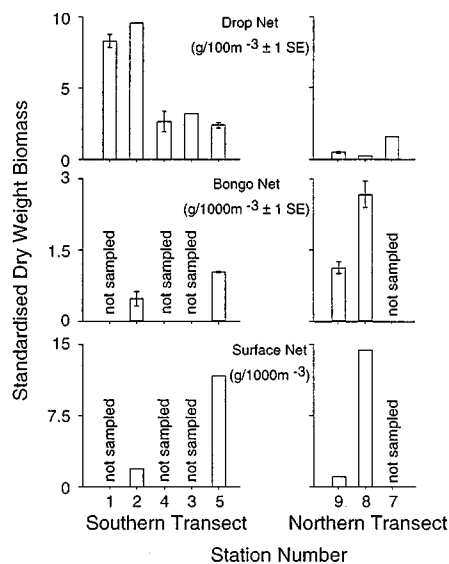


Fig. A1. Standardized dry-weight biomass in the drop-net, bongo-net and surface-net samples. Standard errors ($n = 2$) are shown except for unreplicated samples. Station locations are shown in Fig. 5.

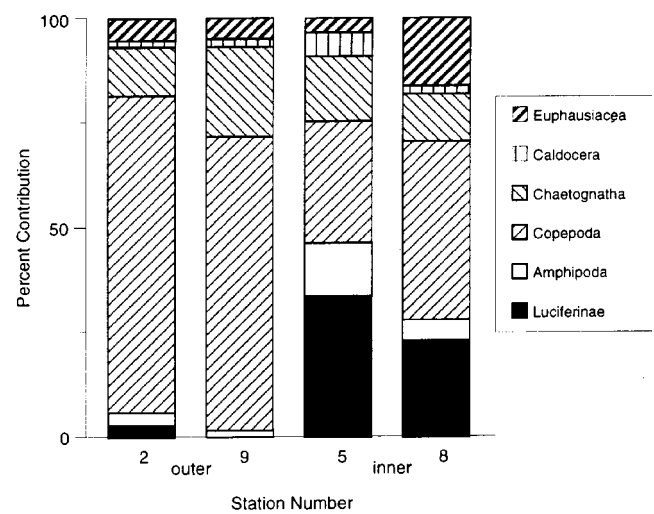


Fig. A2. Contribution of the major zooplankton taxa to the abundance in the codend of the left bongo net. Station locations are shown in Fig. 5.