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Biology and fishery of pilchard, *Sardinops sagax* (Clupeidae), within a large south-eastern Australian bay

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Abstract. Length–frequency and maturity data of pilchards (*Sardinops sagax*) are described from monthly purse-seine commercial catch samples obtained in Port Phillip Bay (Victoria) between December 1994 and January 1997. These data, together with findings of a 12-month ichthyoplankton bay survey from September 1995 to August 1996, were used to determine the size at which pilchards recruit to the bay fishery and whether they spawn within this system. Monthly pilchard catch rates between January 1990 and June 1996 are also described and analysed in terms of environmental variables during that period. Results show that pilchards do not generally attain sexual maturity or spawn within the bay but use it as a nursery area, entering this system mostly as 0+ to 1+ year-old juveniles (4–12 cm fork length, FL) in late spring–early summer and returning to sea the following winter. This migration is supported by the marked seasonality in catch rates, which each year peak in March–May and are lowest in August–October. The seasonality was adequately explained by temperature lagged 2 months in a multivariate time-series model. Port Phillip Bay appears to be the only semi-enclosed, shallow marine embayment in temperate Australia that supports a substantial pilchard fishery that, in addition, is based predominantly on juveniles.

Introduction

The Australian pilchard, *Sardinops sagax* (Clupeidae) is commonly found in bays and inlets, and in shelf waters across southern Australia from 24°S in Western Australia to 25°S in Queensland, including northern Tasmania (Paxton and Hanley 1989). Major purse-seine pilchard fisheries currently operate in southern Western Australia (WA), South Australia (SA) and Victoria (Vic.), with total catches of up to 17 000 t per year (Fletcher 1991, 1992; Neira *et al.* 1997*a*). Unlike the WA and SA fisheries, which operate mostly in coastal waters, over 60% of the annual pilchard catch in Victoria is taken in Port Phillip Bay, a large, semi-enclosed and relatively shallow temperate marine embayment in south-eastern Australia (Neira *et al.* 1997*a*, 1997*b*). The pilchard fishery in Port Phillip Bay produces the bay's largest commercial catch by weight. Catches between 1990–91 and 1995–96 averaged 1622 t, accounting for 74% and 62% of the total bay and statewide scalefish catch during that period, respectively (Neira *et al.* 1997*a*, 1997*b*).

Despite the commercial importance of pilchards in Victorian waters, little is known about the fishery and relationships with stocks from adjacent states, or aspects of their life cycle, such as spawning and juvenile nursery areas. Much of the biological and fishery data for pilchards in Victoria are scattered in several studies that also include other clupeoids (e.g. Blackburn 1950; Blackburn and Tubb 1950; Hobday 1992; Hoedt and Dimmlich 1995; Hoedt *et al.* 1995; Neira *et al.* 1997*a*, 1997*b*). This contrasts with the situation in Western Australia and New South Wales, where a great deal is known about their biology and fisheries (e.g. Blackburn 1949, 1950; Rapson 1953; Joseph 1981; Stevens *et al.* 1984; Fletcher 1992, 1995; Fletcher and Tregonning 1992; Fletcher *et al.* 1994, 1996*a*, 1996*b*).

This paper presents data obtained during a three-year study of the biology and fishery dynamics of pilchards in Port Phillip Bay. Length–frequency data were obtained from pilchard commercial catch samples in Port Phillip Bay (December 1994–January 1997) to determine the size at which this species enters the bay's purse-seine fishery. In addition, reproductive data obtained during this period, together with the results of a 12-month ichthyoplankton survey in the bay (September 1995–August 1996), were employed to determine whether pilchards spawn within this system. Earlier studies in Port Phillip Bay have reported maturing and spent pilchards from October to May, with the greatest percentage of nearly mature fish occurring in January (Blackburn 1950). Moreover, pilchard eggs and larvae have been found in the bay between September and February, although in very low numbers (Blackburn 1950; Jenkins 1986). This paper also describes seasonal changes in pilchard catch rates in Port Phillip Bay, and investigates whether there is any relationship between monthly pilchard catch rates and the bay's environmental conditions (1990–96). Initially, standard correlation and stepwise regression techniques are used to explore the relationships between monthly catch rates and mean monthly water temperature, salinity, chlorophyll *a* concentration, ammonium in sewage discharge and total river discharge. Time-series tech-

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niques are then used to model monthly catch rates with the above variables. Monthly data on total phytoplankton productivity throughout the bay between September 1993 and March 1995 are also used to ascertain to what extent pilchard catch rates were related to productivity over that period.

Materials and methods

Study area

Port Phillip Bay has a surface area of approximately 1930 km^2, a mean depth of 13.6 m, and is joined to Bass Strait through a narrow, 3 km-wide channel between Point Nepean and Point Lonsdale (Fig. 1). Most river flow originates from the Yarra River and eastern creeks, although net freshwater input is minimal since evaporation almost equals rainfall and river flow over the year. The bay is vertically well-mixed most of the time due to its relatively shallow depth. Tides through the entrance are semi-diurnal, comprising one large and one small tide each day (Harris *et al.* 1996).

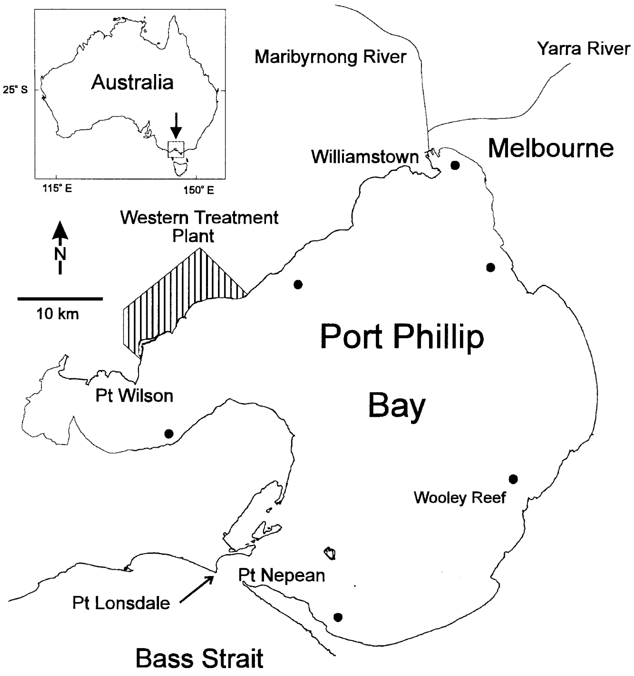

Fig 1. Map of Port Phillip Bay showing the six sites routinely sampled for environmental variables between January 1990 and June 1996 (•).

Length–frequency and reproductive data

Monthly random samples of 162–1240 pilchards were obtained from commercial catches in Port Phillip Bay between December 1994 and January 1997 and measured (fork length, FL, unless stated otherwise) to the nearest 0.1 cm to obtain length–frequency data (n = 11 872). Monthly subsamples of these pilchards were weighed to the nearest 0.1 g, and dissected to identify sex and stage of maturity (n = 1623). Gonadal stages were macroscopically classified from I to V following the method of Laevastu (1965) for batch (partial) spawners (I, virgin; II, maturing and recovering spent; III, maturing; IV, running ripe; V, spent), and the data plotted by month for both sexes. Pilchards for which sex could not be determined through gonadal identification, i.e. fish generally <10 cm FL, were regarded as immature. The gonads of fish that could be sexed were removed from the body cavity and weighed to the nearest 0.01 g. These data were used to calculate the gonadosomatic index (GSI) using the formula GSI = $(W_g/W_f) \times 100$, where W_g is the weight of the gonad (g) and W_f is the whole weight of the fish (g). The GSI values were then averaged by month and plotted for each sex.

Ichthyoplankton sampling

Fish eggs and larvae were sampled fortnightly at 12 sites throughout Port Phillip Bay between September 1995 and August 1996. All sites were randomly selected before each sampling trip. Samples were obtained with a bongo sampler equipped with two, 3-m long, 0.6-m diameter cylindrical–conical nets of 500- and 300-μm Nytal mesh. All samples were taken at night in oblique tows from bottom to surface. Tows lasted for 5 min and were carried out at speeds of 1.0–1.5 knots. Digital flowmeters (General Oceanics) attached to the mouths of both nets were used to calculate the volume of water filtered by each net during each tow. Nets were washed after each tow, and the samples fixed in 4% formaldehyde in seawater and later preserved in 70% ethanol. All larval clupeoids were removed from samples under a dissecting microscope, identified to species by using Neira *et al.* (1998), and counted. Clupeoid fish eggs in subsamples of 100 mL were identified and counted.

Commercial catch and effort data

Monthly commercial catch and effort data for pilchards in Port Phillip Bay between January 1990 and June 1996 were obtained from the Catch and Effort (CandE) database archived at the Marine and Freshwater Resources Institute (MAFRI). Fishing returns containing daily fishing entries are provided each month by commercial pilchard fishers and these data are then routinely incorporated into the CandE database. As nearly all of the commercial pilchard catch in the bay is taken with purse seines (300–400 × 35–50 m, 10–12 mm mesh-bunt) (Neira *et al.* 1997*a*), monthly catch rates used in this study (kg day^{-1}) were calculated only for purse seines by dividing total monthly catch by number of days fished. Based on preliminary analyses of monthly bay catches from 1986 that show a distinct annual pattern of highest catches being taken in March–May (average 54%), followed by a marked decline through to September–October (Neira *et al.* 1997*a*), hyperstability of catch rates was assumed to be non existent (Hilborn and Walters 1992) and catch rates were therefore used as an index of pilchard abundance in the bay.

Sampling and analysis of environmental data

Environmental data were collected at six near-shore sites in Port Phillip Bay fortnightly between February 1990 and June 1996 (Fig. 1). Salinity and temperature were measured at various depths at each site with a YEO-KAL SDL sensor, and the data averaged by month. Daily river discharge from the Yarra and Maribyrnong rivers into the bay was obtained from Melbourne Water, summed over a month and multiplied by 1.4 to account for inflows downstream of the gauging sites (Sokolov 1996). These data were $\log_{10}(x+1)$ transformed for the analysis to improve the variance constancy across time.

Chlorophyll *a* concentration was used in this study as an indicator of phytoplankton biomass. Chlorophyll samples were collected fortnightly at each of the six sites by gravity filtration through Whatman GF/C glass fibre filters. Samples were stored frozen, the chlorophyll extracted by ultrasonication in ice-cold 90% acetone and the concentrations (μg L^{-1}) determined by polychromatic spectrophotometry (Strickland and Parsons 1972) with the equations of Jeffrey and Humphrey (1975). Comparison between chlorophyll collected with GF/C filters and on 0.2-μm membrane filters indicated that the concentrations reported herein may underestimate the true chlorophyll concentration by 10–40%, representing the fraction of plankton which passes through GF/C filters with a nominal pore size of 1 μm. Data were averaged over month and depth. Since preliminary analysis indicated that mean chlorophyll *a* concentrations at the mid-eastern site (Wooley Reef, Fig. 1) during 1990–96 were almost identical to those in the central basin of

Port Phillip Bay, which accounts for 76% of the bay's volume (Harris *et al.* 1996), this site was chosen to represent the bay as a whole. As with river flow, chlorophyll data were also log transformed for the analysis to improve the variance constancy across time. Ammonium (NH_4) concentration from the Western Treatment Plant (WTP; Fig. 1), which is the largest point source of nutrients to Port Phillip Bay (Harris *et al.* 1996), was obtained weekly during the study period, multiplied by discharge volume and summed for each month to obtain a total monthly discharge. Total monthly bay-wide phytoplankton productivity data (carbon fixation) between September 1993 and May 1995 were obtained from Beardall *et al.* (1996) and are provided in mg of carbon (C) per m^2 per day (see Beardall *et al.* 1996 for details).

Statistical methods

Initially, linear-modelling techniques were employed to analyse the data, because no evidence of non-linearity had been found in scatterplots of catch rates against environmental variables. After Pearson correlations were performed, data of environmental variables up to a 12-month lag and catch rates were subjected to stepwise regression (Forward Selection Method) using partial correlations as an exploratory tool to ascertain which variable(s) were significant ($P \leq 0.05$). A lag time of up to 12 months was considered adequate since we were only interested in possible short-term relationships between the seasonal changes in the bay's environmental conditions and pilchard catch rates. Stepwise regressions were also used to test for multicolinearity between significant environmental variables, while Principal Component Analysis (PCA) was employed to remove multicolinearity between highly correlated variables if present.

A multivariate time series model that used the prewhitening method (Pankratz 1991) was then employed to incorporate the response (catch rates), significant environmental variables and the autocorrelated error structure, if present. A cross-correlation function was used to determine the appropriate lag time for the respective environmental variables and catch rate data. The data were also checked for possible artificial statistical feedback that occurs when past values of a response affect current values of an environmental variable (Pankratz 1991). Plots of both the autocorrelation function (ACF) and the partial autocorrelation function (PACF) were used to help identify both significant residual autocorrelations and white noise residuals. Various diagnostic tests, such as the F-test, Durbin–Watson (D–W) test (first-order autocorrelation check), standard error, square root mean squared error (MSE) and Akaike's Information Criterion (AIC), were used to test the validity of the model assumptions and goodness of fit.

Total monthly phytoplankton productivity data (carbon fixation) from Port Phillip Bay between September 1993 and May 1995 (Beardall *et al.* 1996) were regressed with catch rates and environmental variables to ascertain whether there were any significant relationships between these variables during that period. Regression diagnostics, such as R^2, D–W and Shapiro–Wilk (S–W) tests, were also performed and the data plotted for each of the analyses with their respective studentized residuals.

Results

Length frequencies

Pilchards sampled from purse-seine commercial catches in Port Phillip Bay between December 1994 and January 1997 ranged between 4.4 and 22.3 cm FL (mean, 12.8 cm), with 77.6% of the fish between 10.5 and 15.5 cm. Pilchards between December 1994 and February 1995 (10.5–17.0 cm; mean, 13.8 cm) showed a unimodal length distribution, with an increasing mean size due an increasing proportion of fish >14.0 cm (Fig. 2). A second mode of smaller fish between 9.0 and 11.0 cm (mean, 10.5 cm) appeared from March to May 1995, with fewer fish >14.0 cm being present. No fish were caught between June and September 1995, and no samples were obtained in October 1995. In November 1995, the length distribution was again unimodal, corresponding to fish between 4.8 and 9.5 cm (mean, 6.8 cm). Length distributions remained unimodal from November 1995 through to July 1996 except for a small secondary mode between 8.0 and 9.0 cm in January 1996, and another smaller mode between 18.5 and 22.0 cm in July 1996, the latter corresponding to fish caught at the southern end of the bay. The mean length of pilchards increased from 6.8 cm in November 1995 to 14.6 cm in July 1996, with fish from August 1996 to January 1997 showing a continuation of this modal progression except for fish >18.0 cm caught in September through to December 1996 (Fig. 2).

Gonadal stages and gonadosomatic indices

Most male (99.6%) and female (98.7%) pilchards sampled from commercial catches in Port Phillip Bay between December 1994 and January 1997 were virgin and maturing (stages I–III), while the remaining small proportion were spent (stage V) (Fig. 3). None of the fish were in spawning condition (stage IV). Pilchards sampled between November 1995 and January 1996 (4.4–12.4 cm; mean, 8.7 cm) were all juveniles for which sex could not be determined, while all male and female pilchards examined between February and June 1996 (8.5–16.8 cm; mean, 12.3 cm) had gonads in stages I–II of development. Mean monthly GSIs between December 1994 and January 1997 ranged from <0.5 between February and June 1996, to a maximum of 2.7 (females) and 2.3 (males) in October 1996 (Fig. 4). Maximum GSI values recorded in that month were 6.2 in a 19.7 cm (85.9 g) female and 5.8 in a 19.8 cm (90.1 g) male. The large proportion (>80%) of maturing (stage III) male (15.5–21.2 cm; mean, 18.1 cm) and female (15.5–21.2 cm; mean, 17.6 cm) pilchards recorded in October 1996 (Fig. 3) accounted for the comparatively high mean GSI values obtained in that month (Fig. 4).

Larval fish assemblage

In total, 17 162 fish larvae belonging to 35 teleost fish families were caught during the ichthyoplankton survey carried out in Port Phillip Bay fortnightly between September 1995 and August 1996. Neither pilchard eggs nor larvae were found in the 264 samples analysed. *Engraulis australis* larvae were the second most abundant taxa (18.1%) after gobiid larvae (51.4%).

Environmental conditions 1990–96

The study period included two years that were among the wettest (1993) and driest (1994) in the Port Phillip Bay catchment area for the past 25 years. There was a significant intra-annual variation but no inter-annual variation in river flow during the study period (Table 1). Peak river flow usually occurred in winter–spring. Monthly river flow varied by a factor of 50 during the study period, from a minimum of 11

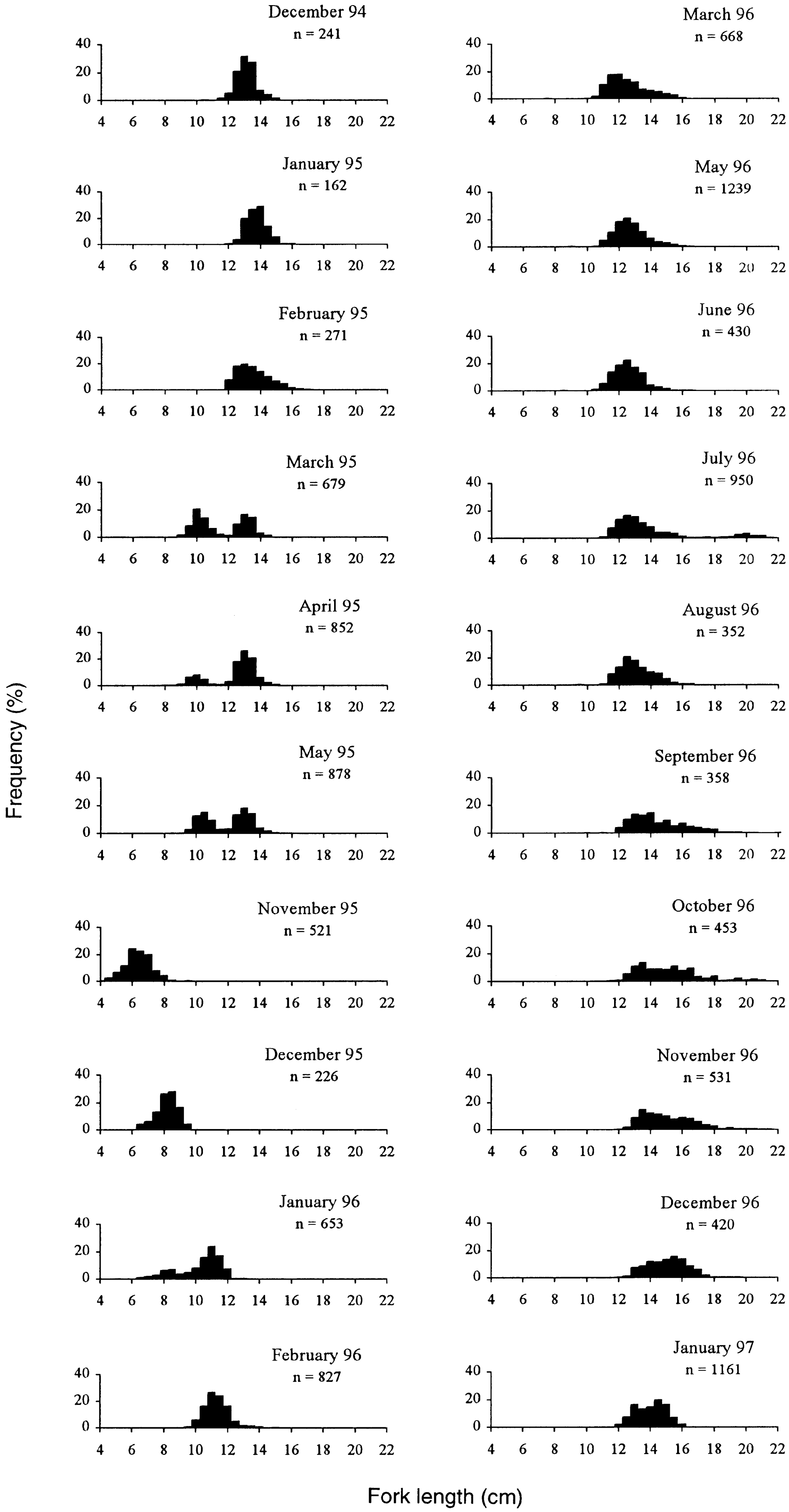

Fig 2. Length–frequency distributions (FL, cm) of pilchards caught in commercial catches in Port Phillip Bay between December 1994 and January 1997. No fish were caught between June and September 1995, and no samples were obtained in October 1995.

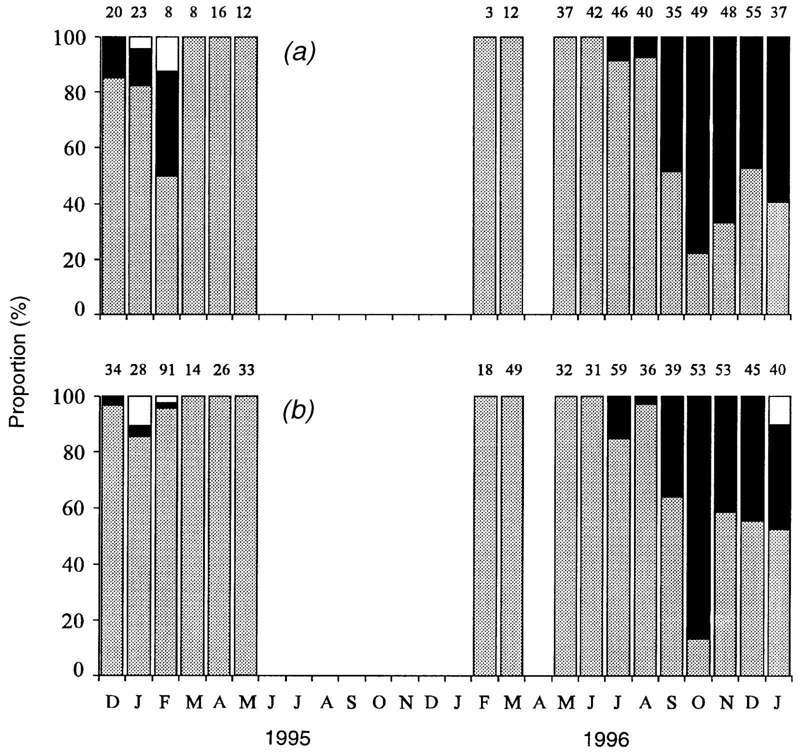

Fig. 3. Proportion of the different gonadal stages (I–V) in *(a)* male and *(b)* female pilchards sampled from commercial catches in Port Phillip Bay between December 1994 and January 1997 (note absence of running-ripe fish stage IV). Values above bars indicate number of fish examined. No fish were caught between June and September 1995, and no samples were obtained in October 1995. All fish examined between November 1995 and January 1996 were juveniles for which sex could not be determined. Hatched bars, stages I–II; black bars, stage III; white bars, stage V.

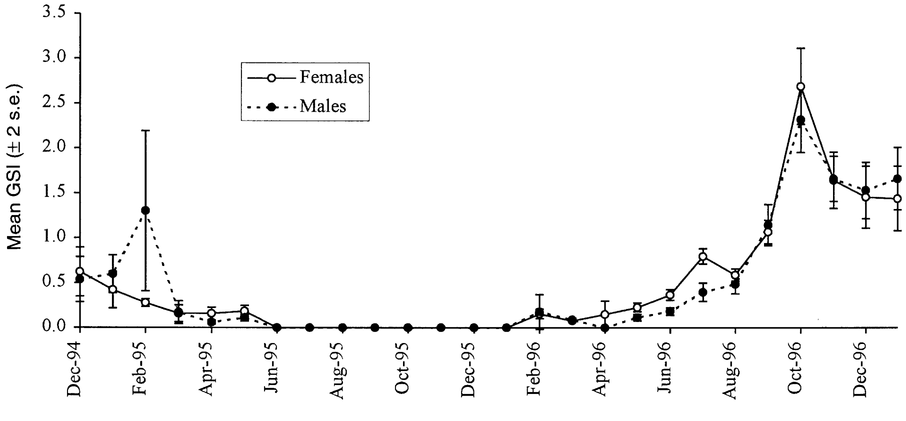

Fig 4. Mean gonadosomatic indices (GSIs ± 2 s.e.) in male (- - •- -) and female (—o—) pilchards sampled from commercial catches in Port Phillip Bay between December 1994 and January 1997 (see Fig. 3 for number of fish examined in each month). No fish were caught between June and September 1995, and no samples were obtained in October 1995. All fish examined between November 1995 and January 1996 were juveniles for which sex could not be determined.

GL month^{-1} in February 1991 to over 500 GL month^{-1} in September 1993. In 1994, monthly flow never exceeded 75 GL month^{-1} (Fig. 5*a*).

Maximum and minimum mean monthly salinities in Port Phillip Bay during 1990–96 were recorded in April and May 1991 (35.5), and October 1992 (32.7), respectively (Fig. 5*b*).

Table 1. *F*-values and levels of significance of regressions of intra- and inter-annual variation of environmental variables and pilchard catch rates (kg day^{-1}) in Port Phillip Bay between January 1990 and June 1996

dfe, error degrees of freedom. *$P \leq 0.05$; **$P \leq 0.001$; ***$P \leq 0.0001$

Source/dfe	River flow	Salinity	Temperature	Ammonium	Chlorophyll *a*	Catch rates
Month	14.115***	12.723***	25.756**	34.375***	0.194	21.595***
Year	1.036	8.815**	0.863	3.478	5.968*	2.068
dfe	74	75	75	69	73	75

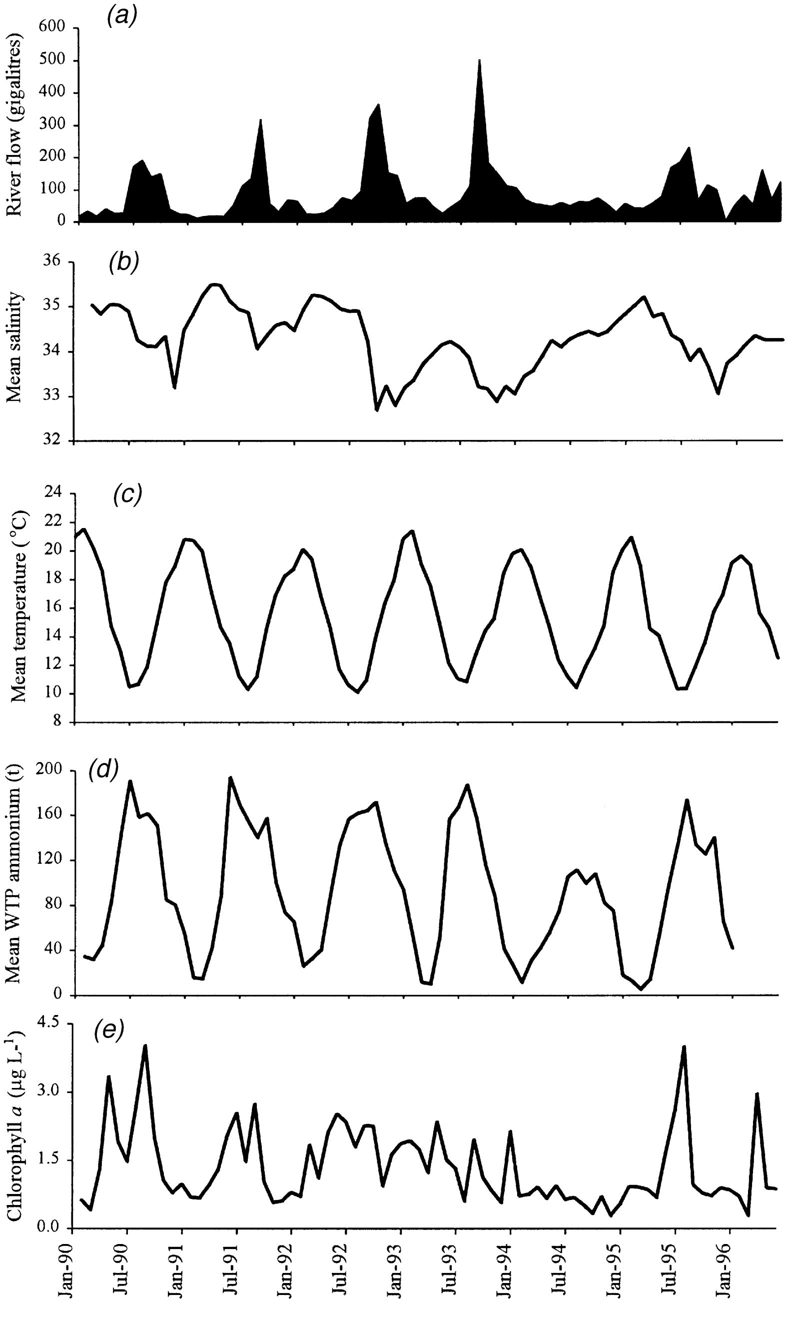

Fig 5. (*a*) Monthly fluctuations in total river flow (gigalitres, GL) into Port Phillip Bay, and (*b*) monthly mean salinity, (*c*) temperature (°C), (*d*) ammonium discharge (t) and (*e*) chlorophyll *a* concentrations (µg L^{-1}) in the bay between January 1990 and June 1996.

Mean monthly salinities during this period showed significant intra-annual and inter-annual variation (Table 1). The annual pattern, however, shows maximum salinity in autumn–early winter (March–May) due to high evaporation over summer, followed by a minimum in late spring–early summer (October–December) after high winter river flow (Fig. 5*a*). Minimum salinity lagged peak river flow by 1–3 months due to slow mixing within the bay in all years except 1994, when salinity increased throughout the year from 33.1 to 34.7 due to a relatively low river flow.

Mean monthly water temperatures in Port Phillip Bay during 1990–96 were markedly seasonal, with the highest temperatures between January and March (average, 19.3–20.6°C) and the lowest in July and August (average, 10.4–10.8°C) of each year (Fig. 5*c*). Maximum and minimum mean temperatures were recorded in February 1990 (21.6°C) and August 1992 (10.1°C), respectively. There was a significant intra-annual variation but no significant inter-annual variation in the mean monthly temperatures during this period (Table 1). Monthly averages varied by 0.9–4.0°C between years, with the summer of 1989–90 being the warmest, and the spring–summer of 1995 the coldest.

Monthly ammonium discharge from the WTP during 1990–96 ranged from around 20 t in summer to 160–200 t in winter of each year except 1994 (the driest year), when the maximum winter discharge was <120 t (Fig. 5*d*). There was a significant intra-annual variation but no significant inter-annual variation in the total monthly ammonium discharged during this period (Table 1).

Maximum and minimum mean monthly chlorophyll *a* concentrations at the Wooley Reef site during 1990–96 were recorded in September 1990 (4.0 μg L^{-1}) and in both December 1994 and March 1996 (0.2 μg L^{-1}), respectively (Fig. 5*e*). There was a weak but significant inter-annual variation but no intra-annual variation in the mean monthly chlorophyll *a* concentration during this period (Table 1). Although peak concentrations varied between years and were observed in all seasons, mean chlorophyll *a* concentrations were usually highest in winter and lowest in summer (Fig. 5*e*).

Catch rates 1990–96

Monthly pilchard catch rates from Port Phillip Bay between January 1990 and June 1996 showed a significant intra-annual variation but not a significant inter-annual variation (Table 1). Catch rates followed a similar pattern to that of monthly catches (Fig. 6*a*), and were usually highest during mid-summer to late autumn and lowest during winter to early spring (Fig. 6*b*). Peak catch rates during the high season, i.e. January to May, ranged between 3620 and 6160 kg day^{-1}. There were no catches between June and September 1995 despite the substantial effort (273 h of search time) recorded during that period (CandE database, MAFRI).

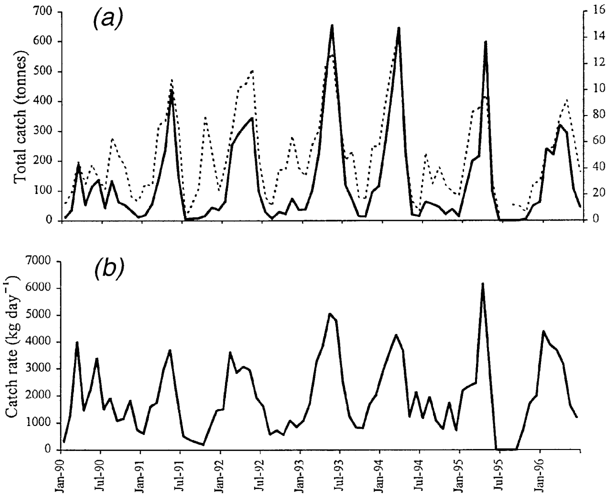

Fig 6. Pilchards caught in Port Phillip Bay between January 1990 and June 1996: *(a)* — total monthly catches (t) and - - - - effort (no. days), and *(b)* monthly catch rates (kg day^{-1}). No fish were caught between June and September 1995.

Analysis of catch rates and environmental variables

Monthly pilchard catch rates between January 1990 and July 1996 followed a similar trend to that of mean monthly water temperature in the bay during that period, whereas the opposite was true for total monthly river flow (Figs 5*a*, 5*c*, 6*a*). Stepwise regression showed that monthly catch rates during this period were significantly correlated with temperature lagged 2 months ($F_{1,56} = 77.004$; $P \leq 0.0001$). Moreover, the intra-annual variation in catch rates was adequately explained by temperature lagged 2 months, since this variation was found to be non-significant after accounting for temperature ($F_{1,55} = 0.52$; $P > 0.05$). Catch rates were also found to be significantly correlated with salinity lagged 5 months ($F_{1,56} = 13.204$; $P \leq 0.0001$). However, salinity was excluded from the model after salinity lagged 5 months was found to be significantly negatively correlated with temperature lagged 2 months ($r = -0.56$; $P \leq 0.0001$), and after PCA further supported the presence of multicolinearity given that these two variables could be explained by the negative of each other. In addition, no significant inter-annual variation in catch rates was found after accounting for temperature lagged 2 months ($F_{1,55} = 2.20$; $P > 0.05$), and none of the three remaining variables, i.e. total river and ammonium discharge, and mean chlorophyll *a* concentration, was found to be significant.

The cross-correlation between monthly catch rates and mean monthly temperatures after use of the prewhitening method of transfer function modelling also showed a significant correlation at lag 2 months (Table 2). Moreover, there was no evidence of statistical feedback as the cross-correlations between catch rates and temperature for lags of –1 to –12 months were non-significant, thereby supporting the use of this modelling technique (Pankratz 1991). None of the other

Table 2. Cross-correlations between mean monthly temperatures (°C) and monthly pilchard catch rates (kg day^{-1}) in Port Phillip Bay between January 1990 and June 1996

*, statistically significant. Blank spaces indicate absence of cross-correlation

Lag for variable temperature	Sign of correlation at lag for temperature	Lag for variable temperature	Sign of correlation at lag for temperature
–12	+	1	–
–11	+	2	+*
–10		3	+
–9	–	4	+
–8	–	5	
–7	+	6	
–6	+	7	+
–5	+	8	–
–4	+	9	–
–3	+	10	–
–2		11	+
–1	+	12	–
0	–		

environmental variables tested was found to be significantly cross-correlated with pilchard catch rates.

Model estimates

The multivariate model estimates show that pilchard catch rates are positively related with temperature lagged 2 months (Table 3). Ljung-Box statistics, before accounting for residual autocorrelation, indicate that the residuals are not random (Table 4). Moreover, examination of both the ACF and PACF of residuals suggest fitting an autoregressive model at lag 1 and 4 months. The resulting ACF and PACF plots (Fig. 7) indicate a purely random process that was further supported by the lack of autocorrelated residuals from the Ljung–Box statistics (Table 4). No influential observations were found after tests of the model with a range of measures, indicating that correlations were not dominated by a few values.

Relationship between productivity, temperature and catch rates

Total phytoplankton productivity (carbon fixation) showed a marked seasonality between September 1993 and May 1995 (Fig. 8). Productivity reached a peak of 600–700 mg C m^2 day^{-1} in January–February 1994, declined to <300 mg C m^2 day^{-1} between June and October 1994, and peaked again at 750 mg C m^2 day^{-1} in February 1995. Total productivity (log$_{10}$ transformed) showed a significant positive relationship with mean monthly temperature during the same period (Table 5, Model A). The D–W statistic indicated that the residuals did not contain first order autocorrelation while no higher order autocorrelations were found to be statistically significant ($P > 0.05$). In addition, the S–W test suggested the presence of normally distributed residuals (Table 5), while the plot of studentised residuals and predicted values showed a random scatter and variance homogeneity.

Monthly pilchard catch rates (log$_{10}$ transformed) between September 1993 and March 1995 also showed a significant positive relationship with both temperature lagged 2 months (Table 5, Model B) and total productivity lagged 2 months (Fig. 9*a*; Table 5, Model C). In both regressions, the D–W statistic indicated that the residuals did not contain first order autocorrelation while no higher order autocorrelations were found to be statistically significant ($P > 0.05$). In addition, the S–W test in both cases suggested the presence of normally distributed residuals (Table 5), while the plots of studentised residuals and predicted values showed a random scatter and variance homogeneity (Fig. 9*b*).

Table 3. Maximum likelihood estimation of the multivariate model for monthly pilchard catch rates (kg day^{-1}) and mean monthly temperatures (°C) in Port Phillip Bay between January 1990 and June 1996

Parameter	Estimate	s.e.	T-ratio	Variable	Lag (month)
α	–2088.7	787.6323	–2.65	kg day^{-1}	0
δ	260.1066	50.1335	5.19	temperature	2
$\o_1$	0.41143	1.0043×10^{-4}	4.10	kg day^{-1}	0
$\o_4$	–0.2751	0.10245	–2.69	kg day^{-1}	0

Model diagnostics: AIC statistic, 1245.6676; sample size, 78; s.e., 851.4179. The model may be represented as

$$y_t = \alpha + \delta\, B^2 x_{1,t} + \frac{1}{(1 - \o_1 B - \o_4 B^4)} \varepsilon_t$$

where y_t is catch rates (kg day^{-1}) at time t, α is mean term, δ is coefficient of temperature, $x_{1,t}$ is temperature at time t, ε_t is error at time t, $\o_1$, $\o_4$ are AR coefficients, and B is a back-shift operator, where $Bx_{1,t} = x_{1,t-1}$. Substituting the parameter estimates gives

$$y_t = -2088.7 + 260.1066 B^2 x_{1,t} + \frac{1}{(1 - 0.4114B + 0.2751B^4)} \varepsilon_t$$

Table 4. Ljung–Box statistics estimates for testing residual autocorrelation before modelling ARMA errors (after modelling temperature), and after accounting for residual autocorrelation
$^{**}P < 0.005$

Up to month lag	df	χ^2 (before modelling residual autocorrelation)	χ^2 (after modelling residual autocorrelation)
6	6	10.00**	4.41
12	12	13.41**	9.38
18	18	19.81**	11.78
24	24	24.18**	14.89

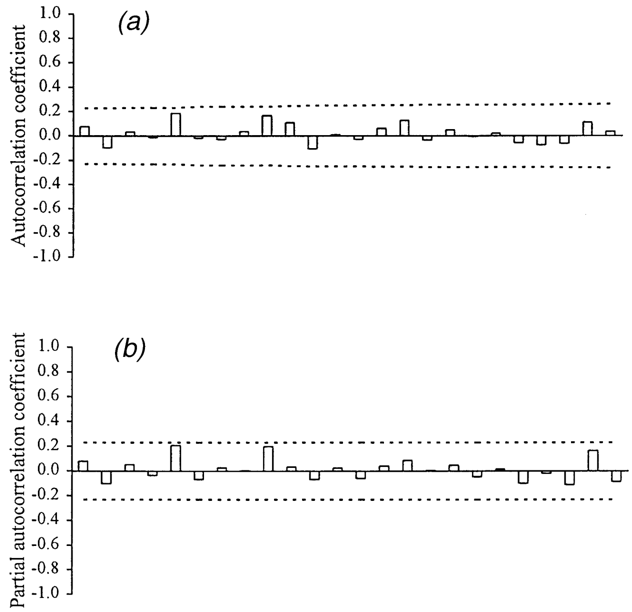

Fig 7. *(a)* Residual ACF and *(b)* PACF plot for the multivariate time series model of catch rates and temperature lagged 2 months.

Discussion

Length frequency and reproductive biology

Length–frequency data for pilchards obtained from commercial catches in Port Phillip Bay between December 1994 and January 1997 showed that over 77% were juveniles and small adults between 10.5 and 15.5 cm, with comparatively fewer fish <10 and >16 cm. Preliminary ageing showed that catches during that period comprised mostly 0+ to 1+ year-old fish, with a small proportion of fish in the 2- to 5-year classes (A. K. Morison, MAFRI, personal communication). These data indicate that pilchards begin to recruit to the bay's purse-seine fishery at a smaller size and younger age than pilchards in Albany (WA), which recruit to the fishery during their second year and are fully recruited by 4 years (~16 cm) (Fletcher 1995). Smaller fish appeared in the catches between March and May 1995, and again in November 1995, the latter after a period of five months in which effort but no catches were recorded. The presence of these mostly juvenile pilchards, particularly the single cohort of mostly 0+ fish caught in November 1995, strongly suggests that they entered the bay in those months. Furthermore, the November 1995 cohort seems to have remained in the bay until at least September 1996, as indicated by its modal length progression through those months. Juvenile pilchards (4.7–6.7 cm) have previously been recorded within Port Phillip Bay between February and May (Blackburn 1950), and within bays elsewhere in south-eastern Australia, such as Westernport Bay (Vic.), Jervis Bay (NSW), and the Hawkesbury River estuary (NSW), in winter through to summer months (Blackburn 1949, 1950; Hoedt *et al.* 1995). Juvenile pilchards (4.5–9.5 cm) have also been recorded in Victoria at the entrance to Westernport Bay and around Phillip Island in February (Hobday 1992). The large adult pilchards recorded in July 1996 were caught just inside the entrance of the bay, which suggests that they moved in from outside. Similar sized fish were again recorded between September and November 1996, although it is not known whether these fish

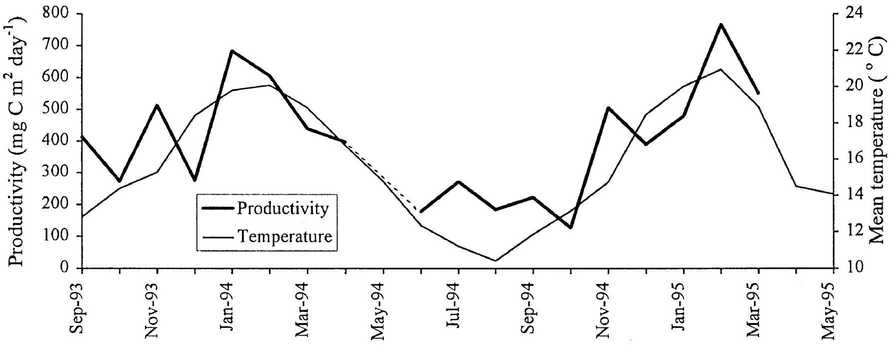

Fig 8. Total monthly phytoplankton productivity (mg C m^2 day^{-1}) and mean monthly temperature (°C) in Port Phillip Bay between September 1993 and May 1995. Productivity data were not available for May 1994 (data from Beardall *et al.* 1996).

Table 5. Regressions of phytoplankton productivity and mean monthly temperature (Model A), monthly pilchard catch rates and mean monthly temperature lagged 2 months (Model B), and monthly pilchard catch rates and phytoplankton productivity lagged 2 months (Model C) in Port Phillip Bay between September 1993 and May 1995

D–W, Durbin–Watson statistic; S–W, Shapiro–Wilk statistic. $^{**}P \leq 0.001$

Variable	Estimate	F-value
Model A: $R^2 = 0.58$; dfe = 16; root MSE = 0.34; D–W = 2.88; S–W = 0.96		
Intercept	4.14	117.29**
Temperature	0.11	21.97**
Model B: $R^2 = 0.64$; dfe = 19; root MSE = 0.38; D–W = 2.29; S–W = 0.93		
Intercept	5.44	210.86**
Temperature lagged 2 months	0.14	33.17**
Model C: $R^2 = 0.61$; dfe = 16; root MSE = 0.37; D–W = 2.17; S–W = 0.97		
Intercept	6.67	949.63**
Productivity lagged 2 months	2.45×10^{-3}	25.00**

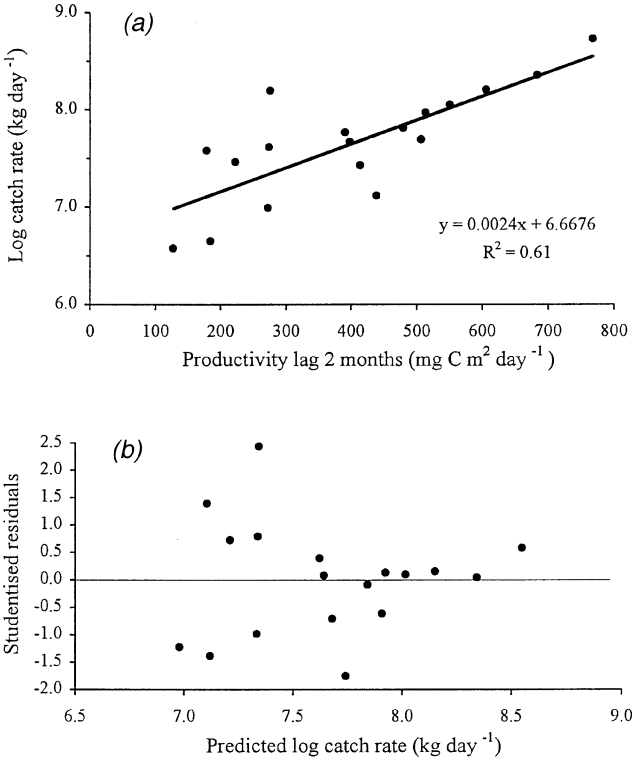

Fig 9. (*a*) Linear regression of monthly catch rate ($\log_{10}$ transformed) and productivity lagged 2 months between September 1993 and May 1995 and (*b*) scatterplot of studentized residuals versus fitted catch rates.

belonged to the July 1996 cohort or were part of a new group that entered the bay in that period.

Both gonadal maturity and GSI data for pilchards in Port Phillip Bay from December 1994 to January 1997 demonstrate that these fish did not attain full maturity in the bay. This conclusion is supported by the fact that over 98% of male and female pilchards examined from catches taken during that period had maturing gonads, very few were spent and none in spawning condition, while all pilchards sampled between November 1996 and January 1997 were immature. This is consistent with earlier findings by Blackburn (1950) who reported maturing and spent pilchards in Port Phillip Bay but none in spawning condition. The highest GSI values obtained for female pilchards in the bay (mean, 2.7; October 1996), most of which possessed stage III ovaries, were well below the GSIs obtained for spawning female pilchards in New Zealand (8–10; Baker 1972) and California (mean, 10.9; range, 4.6–27.2; Macewicz *et al.* 1996). In addition, the finding that most pilchards examined during this study were maturing 0+ to 1+ fish between 10.5 and 15.5 cm is consistent with the fact that pilchards in Western Australia attain sexual maturity during their second year, at approximately 12–13 cm (Fletcher 1995). The sharp decline in GSIs in both male and female pilchards sampled in the bay after October 1996 suggests that fish of increasing maturity may have moved back to sea, where they would presumably have attained full sexual maturity and spawned.

The view that pilchards do not spawn within Port Phillip Bay is reinforced by the absence of pilchard eggs and larvae during our intensive 12-month ichthyoplankton survey in the bay from September 1995 to August 1996. Although very low numbers of pilchard eggs, and also larvae, have previously been recorded during two surveys in the bay, i.e. 40 eggs in a 15-minute surface tow (Blackburn 1950) and 2–15 eggs per 100 m^3 (Jenkins 1986), it is possible that these early life stages could have been passively or actively transported from nearby Bass Strait waters at that time. Although the presence of pilchard eggs in Port Phillip Bay led Blackburn (1950) to believe that spawning occurred within the bay, he regarded this situation as ‘obscure’ since no spawning pilchards were ever caught during his bay survey. In contrast, he reported that spawning presumably occurred at sea off the Gippsland Lakes (Vic.), after finding no eggs or larvae within this system despite numerous plankton hauls. The lack of pilchard eggs and larvae during the present survey in Port Phillip Bay is consistent with the fact that, elsewhere in southern Australia, pilchards are known to spawn mainly in shelf waters outside enclosed bays, with eggs occurring from inshore waters to the shelf’s edge (Blackburn 1950; Fletcher and Tregonning 1992; Fletcher *et al.* 1994; Hoedt and Dimmlich 1995; Hoedt *et al.* 1995). In addition, pilchards are known to spawn in shelf waters in other areas of the world including New Zealand (Baker 1972), California (Ahlstrom 1959), South Africa (Beckley and Hewiston 1994) and Japan (Nakai and Hattori 1962).

Although the spawning season of pilchards in Victorian waters could not be inferred from the data collected in this study, the sharp increase in GSIs between August and

October 1996 suggests that spawning may commence in the spring. A spring–summer spawning in Victoria was suggested by Blackburn (1950), based on the small number of pilchard eggs found in Port Phillip Bay between September and late January, and by Hoedt and Dimmlich (1995) after both pilchard eggs and larvae were found in coastal waters off Phillip Island and outside Westernport Bay between November and February. In New South Wales, spawning takes place between late autumn and early spring (Blackburn 1949; Joseph 1981), whereas along the coast of Western Australia there are two main spawning periods depending on locality, April to July and December to March (Fletcher and Tregonning 1992; Fletcher *et al.* 1994, 1996*b*).

Fishery and relationships with environmental variables in the bay

Results showed that pilchard catch rates in Port Phillip Bay between January 1990 and June 1996 were markedly seasonal, with significantly higher rates during mid-summer–late autumn, particularly in March, April and May. Given that pilchards feed on zooplankton and/or phytoplankton depending on availability in the water column (Kawasaki and Kumagai 1984; James 1988), we may expect to find a close relationship between pilchard catch rates and plankton availability. There is little seasonal variation in the total abundance of zooplankton in Port Phillip Bay (Fancett 1988), but considerable variation in phytoplankton abundance. Total phytoplankton productivity (a growth rate) in Port Phillip Bay is highest in spring–summer, and lowest in winter (Beardall *et al.* 1996; Beattie *et al.* 1996). However, phytoplankton biomass (an instantaneous standing stock), which is mainly dominated by diatoms (Magro *et al.* 1996), is greatest in winter and lowest in spring, with seasonal changes driven largely by the change in microphytoplankton (>20 µm) biomass (Beardall *et al.* 1996). Thus, pilchards begin to enter the bay at the time of lowest microphytoplankton biomass while maximum pilchard catch rates are found at times of high productivity but low biomass. Although zooplankton grazing cannot account for the low microphytoplankton biomass in spring, it may account for the low total biomass in summer through selective grazing on smaller (<20 µm) plankters (Beattie *et al.* 1996). Though no stomach contents were analysed in this study, it could then be argued that pilchards are attracted to the bay by the enhanced primary productivity in spring, and remain there through summer, a time of low biomass, because productivity is still high and competition for microphytoplankton is low. Primary productivity may therefore be a better indicator of food availability than phytoplankton biomass (chlorophyll concentration).

Further analyses included time-series modelling of monthly pilchard catch rates with mean monthly water temperature, salinity, chlorophyll *a* concentration, and ammonium and total river discharge in the bay between January 1990 and June 1996. These analyses showed that catch rates were significantly correlated with temperature lagged 2 months. In addition, dynamic regression analyses of catch rates, water temperature and phytoplankton productivity in the bay between September 1993 and May 1995 showed a significant positive correlation between temperature and productivity, and between catch rates and productivity lagged 2 months. Thus, providing phytoplankton productivity in the bay follows the same annual pattern, these results suggest that pilchards may congregate towards productive areas to feed, reaching maximum abundances two months after the productivity and temperature peaks and then returning to sea when bay temperatures and productivity start to decline. An increase in temperature in the bay during early summer could therefore be the trigger for juvenile pilchards to move into the bay, as has been shown to be the case for the juveniles of several marine fishes entering permanently-open estuarine systems in South Africa (Whitfield and Kok 1992).

No pilchards were caught in Port Phillip Bay between June and September 1995, despite the effort (search time) recorded over that period. Although catches were recorded during those months in 1996, the absence of pilchards in 1995 could be attributed to a combination of factors including fishing mortality, emigration and natural mortality. Alternatively, it is also possible that their disappearance could have been associated with the massive mortality that affected pilchards through their entire distributional range in Australia between March and June 1995 (Griffin *et al.* 1997). Although dead pilchards were found washed up in several places within Port Phillip Bay at that time (Neira, unpublished), it is not known whether these had died due to the herpes virus thought to be responsible for the hypoxia that caused the mass mortality (Hyatt *et al.* 1997) or to other unknown cause(s).

Conclusions

The length–frequency, reproductive, ichthyoplankton, catch rate and environmental data provided in this study demonstrate that, in general, pilchards do not spawn within Port Phillip Bay but use the bay as a nursery area, entering the bay mostly as juveniles in late spring–early summer and returning to sea the following mid- to late winter to spawn. They tend to reach maximum abundances in early autumn two months after the highest temperatures, before leaving the bay when both temperature and productivity have declined. Furthermore, the presence of large adult pilchards at the southern end of the bay in some months suggests that they might periodically re-enter the bay and congregate in that area. This behaviour is consistent with the general life-history strategy described for pilchards in New South Wales by Blackburn (1949), with juvenile pilchards being most abundant in bays and inlets in spring and summer and adults remaining mostly at sea although irregularly re-entering bays. This life cycle strategy, however, differs from that in south-western Western Australia (WA), where juvenile pilchards have been caught in neritic regions along the south coast, particularly near Esperance, but rarely in enclosed bays or estuaries despite the large number of such systems in that region (e.g. Potter *et al.* 1990; Fletcher 1991; Valesini *et al.* 1997). For example, large, permanently open systems such as the Swan and Peel–Harvey estuaries in south-western WA are used as nursery areas by the juveniles of several commercially important marine teleosts, and yet pilchards are extremely rare despite being abundant in coastal waters near both systems (Potter *et al.* 1983; Loneragan *et al.* 1989; Fletcher 1991).

Apart from the evidence presented here for Port Phillip Bay, and that provided by Hoedt *et al.* (1995) for Westernport Bay (Vic.) and Blackburn (1949) for coastal embayments in New South Wales, there are no previous records of pilchards using semi-enclosed bays and/or inlets as nursery areas elsewhere in Australia or worldwide. In addition to pilchards, Port Phillip Bay serves as a nursery area for the juveniles of commercially important marine fish species such as *Aldrichetta forsteri* (Mugilidae), *Arripis* spp. (Arripidae) and *Sillaginodes punctata* (Sillaginidae) (Hall and MacDonald 1986; Jenkins and May 1994; Jenkins *et al.* 1997). In this context, Port Phillip Bay is comparable to permanently open estuarine systems in south-western Australia and South Africa, where the majority of the more abundant species are marine teleosts represented predominantly by their juveniles (Day *et al.* 1981; Potter *et al.* 1983, 1990; Loneragan *et al.* 1989; Whitfield and Kok 1992). As with estuaries in both of these temperate regions and elsewhere in the world, major benefits of Port Phillip Bay to juvenile pilchards may include high productivity and favourable temperatures, shelter, low incidence of piscivorous predators and abundant food supply, all of which facilitate their rapid growth (Haedrich 1983; Miller *et al.* 1985). Since Port Phillip Bay is the only semi-enclosed bay in Australia that supports a substantial pilchard fishery, and this fishery is based mostly on 0+ and 1+ juvenile fish (Neira *et al.* 1997*a*, 1997*b*; A. K. Morison, personal communication), further research is required to ascertain *(1)* the overall impact of these catches on the spawning biomass; *(2)* both the recruitment frequency and quantity of pilchards that move into and out the bay; and *(3)* whether these fish originate from one or more stocks in south-eastern Australia. More information is also needed to elucidate further the relationship between pilchard biology and environmental variables within Port Phillip Bay to precisely assess the role played by the bay in the life cycle of pilchards.

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