Zooplankton in a marine bay. I. Horizontal distributions used to estimate net population growth rates

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ABSTRACT: The zooplankton of Westernport Bay, Australia, is dominated numerically by a population of the copepod *Acartia tranteri* (medium sized form), while the copepods *Paracalanus indicus* and *A. tranteri* (large form) are invaders from the adjacent waters of Bass Strait. In this paper we estimate the rates of gain or loss of populations of these species within the bay from horizontal distributions and information on water exchange rates. Over the long term, these rates of loss or gain must be balanced by positive or negative net population growth rates. The basis for the analysis is a simple steady-state 2-box mixing model with boxes representing the inner, east arm of the bay and the outer bay or western entrance. We estimated the exchange rate between these sectors by a computer fit of the model to published salinity data for 1973–1975. The mean turnover rate of water in the eastern arm of the bay was $0.009 \, d^{-1}$, corresponding to a residence time of 114 d. The resident population of *A. tranteri* (medium) was subjected to a median loss to washout of $0.8 \% \, d^{-1}$, which accounts for about 40 % of total mortality estimated for late nauplii and copepodites. The net population growth rate of $0.8 \% \, d^{-1}$ needed to offset this loss is easily achievable by this species. The 2 Bass Strait species had median rates of gain within the bay, corresponding to negative net population growth or net mortality rates, of $1.5 \% \, d^{-1}$ for *A. tranteri* (large) and $3.2 \% \, d^{-1}$ for *P. indicus*. Confidence limits were wide, but all except 3 values were smaller in absolute magnitude than $5 \% \, d^{-1}$. The small differences between the average net population growth rates of resident and non-resident species point out the subtlety of the differences in growth and mortality rates of bay and neritic populations that suffice to keep them separate.

INTRODUCTION

The zooplankton of bays and estuaries usually differs from that of adjacent coastal waters in both total abundance and species compositon. Estuarine zooplankton, like other estuarine fauna, is usually more abundant and less diverse than neritic zooplankton (Riley 1967). The reduced diversity is often attributed to the reduced and fluctuating salinity, to which relatively few species can become adapted (Cronin et al. 1962, Riley 1967). Marine bays and estuaries of low river flow have greatly reduced physical barriers to immigration of oceanic species, yet the diversity of zooplankton can be as low as in estuaries (Newbury & Bartholomew 1976, Landry 1978, Kimmerer & McKinnon 1985).

The typical pattern of distribution of zooplankton in bays is that one or a few species are numerically dominant, often at high abundance. The more diverse fauna from the adjacent ocean becomes reduced in absolute as well as relative abundance within the bay. Thus the dominant bay species maintain their dominance not only by their own high abundance, but also by the reduced abundances of other species.

A gradient in abundance of a species from the ocean to inner bay waters can arise either through behavioral mechanisms or through differential population growth and mortality rates. Numerous instances have been noted in which zooplankton species maintain themselves within a bay by means of vertical positioning or migration (e.g. Bosch & Taylor 1973, Wooldridge & Erasmus 1980, Kimmerer & McKinnon 1987a [following article]). The reverse case, in which species avoid being transported into a bay, has not been recorded to our knowledge (Kimmerer & McKinnon 1987a).

Although behavioral mechanisms such as those cited above can be important, they are by no means universal, even among bay resident species. In the absence of

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such mechanisms, a bay resident population must have a sufficiently large positive net population growth rate to offset losses to mixing and flushing out of the bay (Rogers 1940, Ketchum 1954, Barlow 1955). The flushing action of estuarine circulation can prevent non-residents from entering an estuary. In a marine bay, however, non-residents can enter through tidally driven mixing. A non-resident invader species must suffer a negative net population growth rate (i.e. net mortality) to offset mixing into the bay, if over the long term its abundance within the bay does not increase. The numerical dominance of the bay resident species is a consequence of the difference in average net population growth rates between it and oceanic invaders.

The purpose of this paper is to estimate the sizes of the net population growth rates needed to offset mixing of common zooplankton species into or out of Westernport Bay, Australia. The basis for the estimate is a simple box model using exchange between an inner and an outer sector of the bay and mean abundances within each sector to provide an estimate of the fluxes of animals due to mixing and advection. These fluxes can then be equated to an excess or deficit in the net population growth rates needed to maintain the populations. The differences between these rates for bay resident and neritic species can indicate the magnitudes of the population processes causing spatial separation of the residents from the non-residents.

An alternative means of measuring fluxes would be to sample intensively in the channel over one or more tidal cycles and to estimate the net flux from the hysteresis in abundance with the tide. We estimate that several tens of thousands of samples would be required for even one such estimate in Westernport Bay, if copepods were randomly distributed within the water column, which they are not. The only way to estimate these rates is to use differences in abundance and exchange rates and to correct as necessary for behavioral effects.

The zooplankton of Westernport Bay, a marine bay on the southeast coast of Australia (Fig. 1), is dominated for much of the year by a medium sized form of the copepod *Acartia tranteri*, with *Paracalanus crassirostris* and *Bestiola similis* very abundant in summer (Kimmerer & McKinnon 1985). In the adjacent neritic waters of Bass Strait, *P. indicus*, *Oithona similis*, and a larger form of a *A. tranteri* are the most abundant, and several other species are common (Kimmerer & McKinnon 1985, G. F. Watson unpubl.). We refer to the size classes of *A. tranteri* (including an uncommon small form in Bass Strait) by appending the suffixes S (small), M (medium), or L (large) to the species name, although these may be separate species (A. D. McKinnon unpubl. data). *Acartia tranteri* (M) adults can migrate vertically within the western entrance

channel of Westernport Bay to avoid mixing out of the bay, but this behavioral mechanism is apparently not used by juveniles or by the other species considered here (Kimmerer & McKinnon 1987a). Other behavioral mechanisms that would favor retention are possible (e.g. lateral migration: Wooldridge & Erasmus 1980) but unlikely given the size of the channel and the strength of currents there (Kimmerer & McKinnon 1987a).

Westernport Bay is only nominally estuarine: salinity varies seasonally slightly above and below that of Bass Strait (Harris & Robinson 1979). The bay consists of a broad western entrance, a narrow eastern entrance, and two branches extending around French Island. Much of the bay area, particularly north of French Island, is shallow seagrass beds or mud flats, which are drained by a network of channels. Strong currents in these channels produce easily visible eddies, minimize stratification (Hinwood 1979), and maintain high turbidity.

METHODS

Plankton sampling. Horizontal distributions of zooplankton and related variables were determined on 9 occasions by sampling along a transect from Bass Strait up the eastern arm of the bay (Fig. 1; Table 1). The time interval between transects was chosen to be long relative to estimated generation times of the species, so that short-term variations in abundance would be aver-
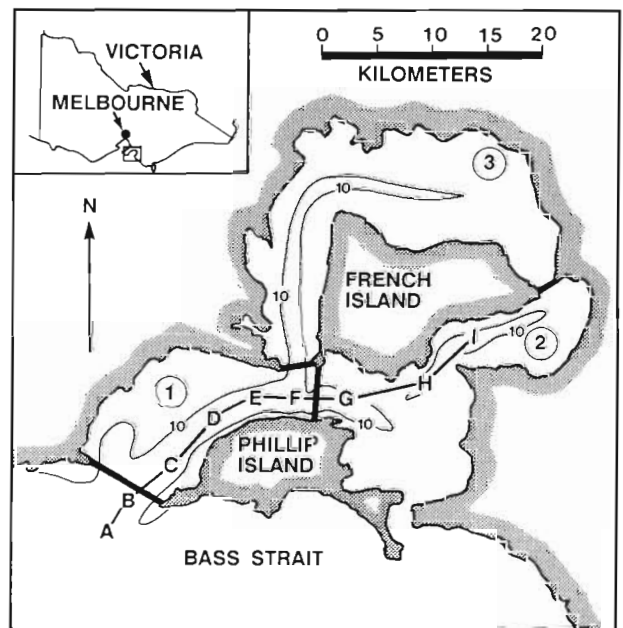

Fig. 1. Map of Westernport Bay, Victoria, Australia, showing the 10 m depth contour, transect stations (A to I), and sectors used in the box model (numbers in circles)

Table 1. Transect information. Dates, numbers of stations sampled, times of day samples were taken, plankton mesh size used, and times of high and low tides closest to the sampling period

Transect	Date	No. of stations	Sampling times (h)	Mesh size (μm)	Time of nearest tides (h) High	Low
I	21 Jul 1982	5	1009–1520	200	1303	1842
II	22 Sep 1982	9	1045–1520	200	1620	0956
III	24 Nov 1982	6	1418–1640	200	1905	1301
IV	16 Feb 1983	7	1250–1640	200	1624	1012
V	28 Sep 1983	6	0910–1235	50	1645	1028
VI	29 Nov 1983	8	0905–1159	50	0810	1348
VII	5 Jan 1984	6	1350–1548	50	1506	0913
VIII	17 Apr 1984	8	1405–1621	50	1415	1959
IX	21 Jun 1984	7	1520–1722	50	1819	1130

aged out. Samples were taken by day only, since previous sampling had indicated that the species of interest were not demersal (Fancett & Kimmerer 1985, Kimmerer & McKinnon 1987a). At each station we collected plankton by single vertical hauls to the surface from 1 m off the bottom, or at most 20 m depth, using a 200 μm mesh, 0.5 m conical net (Transects I to IV), or a 50 μm mesh, 35 cm net with a 0.5 m reducing cone (Transects V to IX). Zooplankton samples were preserved in 2 to 4 % formaldehyde in seawater. Vertical profiles of temperature and salinity were taken with a Beckman RS5-3 field salinometer on Transects IV to IX. On some transects we also collected water samples for seston dry weight and chlorophyll.

Zooplankton samples were subsampled with a Folsom splitter or Stempel pipette to give an aliquot containing 300 to 600 individuals. Copepods, normally the only common taxon, were identified to species and gross life stage: nauplius, copepodite, and adult. When more than one species of the same family were present their nauplii were grouped together. Abundances of copepods refer to post-naupliar stages only, except where otherwise noted. One hundred adult females of *Acartia tranteri*, or all those in a sample, were identified to size class, and the proportions of females in each size class were used to calculate the numbers of males and juveniles in the size class.

Particulate matter in the water samples was filtered onto tared, pre-combusted 45 mm GF/C filters, which were then rinsed with a few ml of distilled water, dried at 60 °C for 48 h, and weighed. Samples for chlorophyll analysis were filtered onto 25 mm GF/C filters and extracted in 90 % acetone for later analysis by fluorometry using a Turner Model 110 fluorometer.

Box model. The purpose of the model was to estimate the net growth rates of populations of abundant species that would be required to offset gains and losses due to mixing and advection. Assumptions used in constructing the model were: (1) Changes in abundance of populations within the bay average to 0 over a time scale of years; (2) the contents of each box can be approximated by using the mean value from all stations within the box; (3) vertical stratification is negligible; (4) plankton behave as passive tracers of water movement; and (5) mixing between Sectors 2 and 3 northeast of French Island can be neglected. The validity and consequences of these assumptions are addressed in the 'Discussion'.

The model, based on the estuarine box models of Officer (1980), describes the mass balance of a substance of concentration Q. Using the symbols listed in Table 2, the rate of change of Q in sector j, connected to sector i only, is:

$$\frac{dQ_j}{dt} = W + Y \tag{1}$$

The mixing and advective rate of gain of Q_j is:

$$W = x_{ij} (Q_i - Q_j) + [F (P_i Q_i + P_j Q_j)] \tag{2}$$

The advective term in brackets on the right side of Eq. (2) depends on the volume flux produced by net evaporation or net rainfall,

$$F = \frac{(e-r)}{z_j} - \frac{R}{V_j} \tag{3}$$

and the step function P is determined by the direction of the freshwater flow,

$$P_i = 1, \; P_j = 0 \; \text{if} \; F \geq 0 \; \text{(net evaporation)},$$
$$P_i = 0, \; P_j = 1 \; \text{if} \; F \leq 0 \; \text{(net rainfall and runoff).} \tag{4}$$

The W term in Eq. (1) can be calculated from data on abundance (Q_i, Q_j), the exchange or mixing coefficient x_{ij}, and the freshwater flux F. Methods for determining Q_i, Q_j, and x_{ij} are described below. Briefly, abundance data were obtained from the transects and x_{ij} was determined from historical data on salinity and temper-

Table 2. Meanings and dimensions of symbols used in the box model

Symbol	Meaning	Dimensions
e	Evaporation rate	LT^{-1}
F	Freshwater flux from sector i to j, divided by the volume of sector j	T^{-1}
μ	Specific rate of net population growth of zooplankton in sector j, $= Y/Q_j$	T^{-1}
m	Net population growth rate needed to offset mixing and advection	T^{-1}
P_1	Step function defining whether freshwater flux is positive or negative	–
Q_i	Concentration of plankton or any substance in sector i	ML^{-3}
q_i	Ratio of Q_i/Q_j	–
R	Runoff to sector j	L^3T^{-1}
r	Rainfall	LT^{-1}
S_i	Salinity in sector i	L^{-3}
V_j	Volume of sector j	L^3
W	Rate of loss or gain of Q per unit time due to mixing and advection	$ML^{-3}T^{-1}$
x_{ij}	Exchange rate between sectors i and j, equal to the effective mixing volume of sector j. For the plankton flux model, i is 1 and j is 2	T^{-1}
Y	Rate of production of Q per unit time and volume	$ML^{-3}T^{-1}$
z_j	Depth in sector j	L

ature in the bay. F was calculated from x_{ij} and salinity by inserting S for Q in Eq. (2), inserting Eq. (2) into (1), and setting Y to 0, since S is conservative. The rate of change of S was considered to be slow relative to that of plankton abundance, so Eq. (1) was solved for F in steady state by setting the derivative to 0. This value for F was then reinserted into Eqs. (2) and (1), and the equation was divided by Q_j, to give:

$$\frac{d(\ln Q_j)}{dt} = x_{ij}[q_i - 1 + (S_j - S_i)(q_i P_i/S_i + P_j/S_i)] + \mu \quad (5)$$

where $\mu = Y/Q_j$ is the specific *in situ* rate of increase of Q, or the net population growth rate. The part of μ that offsets mixing and advection to or from the bay population is:

$$m = \mu - \frac{d(\ln Q_j)}{dt} =$$
$$x_{ij}[1 - q_i + (S_i - S_j)(q_i P_i/S_i + P_j/S_j)] \quad (6)$$

Averaged over the long term, $m = \mu$, so m is the mean rate of net population growth required to offset mixing and advective losses and gains. The model was used to calculate m from Eq. (6), using x_{ij} and Q values as

defined below. For the first 3 transects we had no salinity data; however calculations for the last 6 transects revealed that the median absolute error in Eq. (6) that resulted from eliminating the advective term on the right of Eq. (6) was only 3 %, and the maximum was only 12 %. Therefore the m values for the first 3 transects were computed assuming F was 0, i.e. $S_i = S_j$.

The exchange rate x_{ij} was determined by fitting Eq. (1) to a large set of salinity data from 1973–75, summarized by Harris & Robinson (1979), their Table II. The data are averages over sectors and over 10 approximately 2 mo time periods. Eq. (2) to (4) were inserted into Eq. (1), Y was set to 0, and Q was replaced by S. Estimates of x_{ij} were made for each of the 10 time periods by simulating the time course of salinity in Eq. (1) using a series of assumed values of x_{ij}. Starting from an initial low value, assumed values of x_{ij} were increased at intervals of 0.001 d^{-1} and the time course of salinity was generated for 1973 to 1975 with a 1 d time step. The value of x_{ij} resulting in the correct prediction of S for each of the 10 time periods was determined by a linear interpolation. An overall mean value of x_{ij} was then calculated from the values for each time period. This overall mean was within 0.001 d^{-1} of the value that minimized the sum of squares. The mean values of x_{ij} estimated by this simulation were used to calculate residence times for the entire bay, for the upper bay (Sectors 2 and 3 combined), and for Sector 2 alone.

The simulation was run for data from 1973 to January 1975, using daily rainfall values and estimates of evaporation, and monthly runoff values divided by the number of days per month. Runoff from the major streams was obtained as monthly totals from the Victoria State Rivers Commission. Evaporation was determined using the equation of Smith & Jokiel (1975) from water temperature, wet and dry bulb air temperature, and wind speed. The last 3 variables and rainfall were obtained from daily Bureau of Meteorology records taken at a station on the western shore of Westernport Bay. Water temperature was obtained from Harris & Robinson (1974) for 7 of the 10 time periods for which salinity data were available. Average daily water temperature for sector j, used in the evaporation calculations, was estimated by fitting an annual sine curve to that set of summary temperature data ($r^2 = 0.95$). Mean salinities from Harris & Robinson (1979) were assumed to apply at the midpoints of the time periods.

For the plankton flux model (Eq. 6) we used data from Sectors 1 and 2 only, since plankton samples were not routinely collected in Sector 3. The mean value of x_{12} was used in Eq. (6) to calculate values of m for common plankton species in Sector 2. Q_1 values were determined as arithmetic means of data from Stns B, C, D, and E, and Q_2 was similarly determined from Stns G, H, and I.

RESULTS

Transect data

Salinity values on Transects IV to IX always changed monotonically from Bass Strait to inner Westernport Bay (see Table 4). Bay values were higher than those in Bass Strait on Transects IV, VIII, and IX, and lower on the remaining transects. Stratification was not normally great: the median difference between temperature values at 0.5 m and the middle of the water column was 0.06 C° (range −0.02 to 1.29) while that for salinity was −0.09‰ (range −0.62 to 0.05). Stns E and G were usually the most strongly stratified.

Seston dry weight and chlorophyll concentrations were nearly constant at Stns A to E, and always higher at Stns G, H, and I (Table 3). Secchi disk visibility always decreased monotonically from the outer stations into the bay.

The only holoplanktonic species consistently present on all transects were *Acartia tranteri* (M), *A. tranteri* (L), and *Paracalanus indicus*. The abundance of *A. tranteri* (M) increased with distance into the bay on every transect, and the trend was significant on all 9 transects (rank correlation coefficient, $p < 0.05$; Fig. 2). Abundances of *A. tranteri* (L) and *P. indicus* generally decreased with distance into the bay, and these trends were significant ($p < 0.05$) on all transects for *A. tranteri* (L) and on all but 3 for *P. indicus*. Other species found on some transects included several with higher abundances outside: the copepods *Calanus australis*, *Oithona similis*, and *O. rigida*, ctenophores, and the larvacean *Oikopleura dioica*. The copepods *Bestiola similis* and *Pseudodiaptomus cornutus* were more abundant inside the bay, and *Euterpina acutifrons* had no consistent spatial pattern of abundance.

Samples on Transects V to IX were taken with a 50 μm mesh net, which retains the naupliar stages. The proportions of *Acartia tranteri* nauplii relative to total postnaupliar stages were significantly lower in Sector 2 than Sector 1 on 4 of the 5 transects (Chi-square test on pooled counts from all stations in each sector; $p < 0.05$), but significantly higher in Sector 2 on Transect VI. The ratios of adult to copepodite abundance from all transects showed no trend with distance into the bay.

Paracalanus indicus nauplii were too rare at inner bay stations to permit the use of Chi-square tests, but the proportions of nauplii were uncorrelated with distance into the bay on Transects V, VI, and VII. On Transects VIII and IX other paracalanid species were present whose nauplii could not be distinguished from those of *P. indicus*. The median life stage among copepodites and adults of *P. indicus* was never correlated with distance into the bay.

Box model

Exchange rates between Sectors 1 and 2 had a mean value of 0.009 d⁻¹ (± 0.005 SD; median 0.007; range 0.003 to 0.017) for 9 of the 10 time periods over which salinity data were available. For one period of high salinity no value of the exchange rate would allow the model to match the data. The time course of predicted salinity for the mean exchange rate, together with the measured values (Fig. 3), show the degree to which the model fits the data. Similar models gave exchange rates of 0.015 ± 0.006 d⁻¹ for the entire bay and 0.016 ± 0.007 d⁻¹ for the upper bay (Sectors 2 and 3 combined). Residence times corresponding to these exchange rates were 114 d for Sector 2, 62 d for the upper bay, and 64 d for the entire bay.

Table 3. Seston dry weight and chlorophyll a on transects. Top: median and range of values for western entrance Stns C and E. Bottom: medians and ranges of the ratios of individual station values to medians of Stns C and E on sample dates

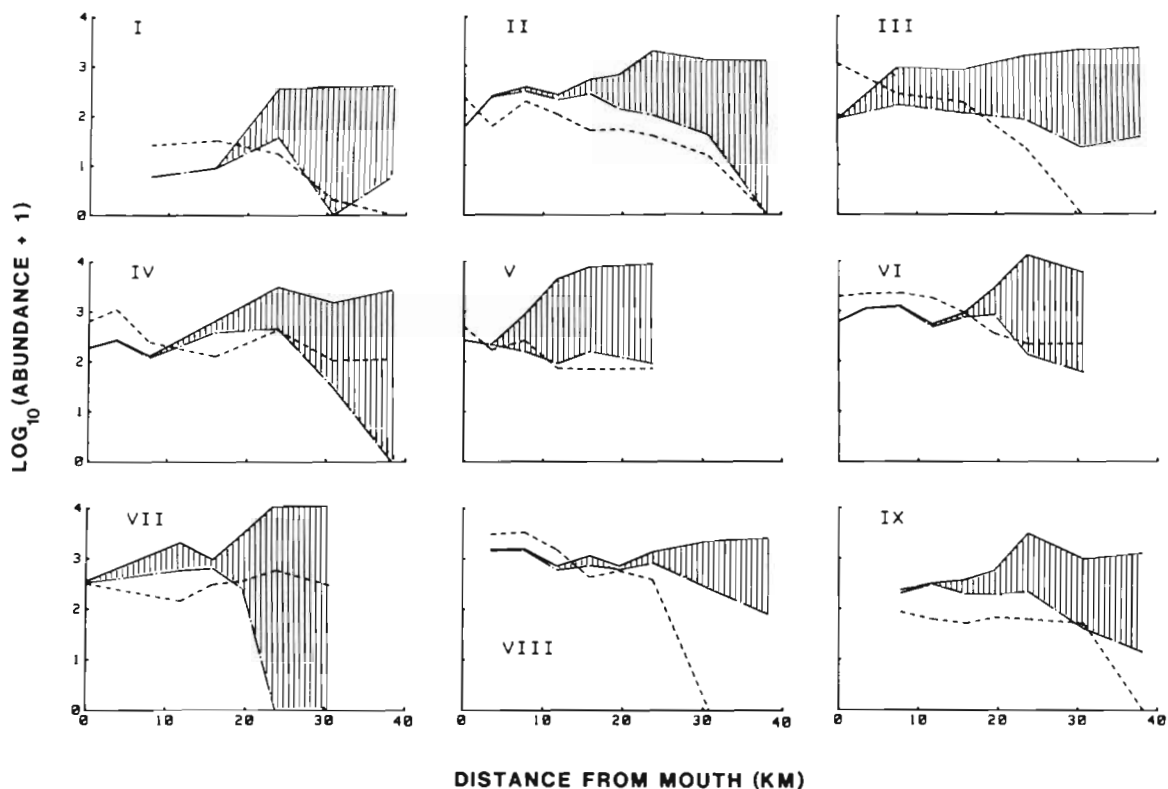|		Seston dry weight (mg l⁻¹)			Chlorophyll a (mg m⁻³)	
	N	Median	Range	N	Median	Range
Median values for C and E	5	3.5	2.3−6.5	6	0.70	0.59−0.92
		Ratio to (C+E)			Ratio to (C+E)	
Transformed values at Stn:	N	Median	Range	N	Median	Range
A	3	1.28	0.99−1.35	4	0.84	0.67−1.05
B	4	1.02	0.89−2.08	5	0.87	0.53−1.15
C	5	0.99	0.93−1.11	6	0.98	0.81−1.16
D	4	1.16	1.01−1.82	5	1.09	0.92−1.31
E	5	1.01	0.89−1.07	6	1.02	0.84−1.19
F	4	1.08	0.86−1.17	4	1.18	1.10−1.67
G	5	1.97	1.37−2.65	6	1.17	1.15−2.64
H	5	3.35	1.68−6.39	5	1.58	1.05−3.66
I	3	3.26	2.85−10.0	4	2.32	1.85−2.37

Fig. 2. Distributions of common zooplankton on Transects I to IX. Solid line: total *Acartia tranteri*; broken line: *A. tranteri* (L); shaded area: *A. tranteri* (M); dashed line: *Paracalanus indicus*. Scales are the same on all graphs
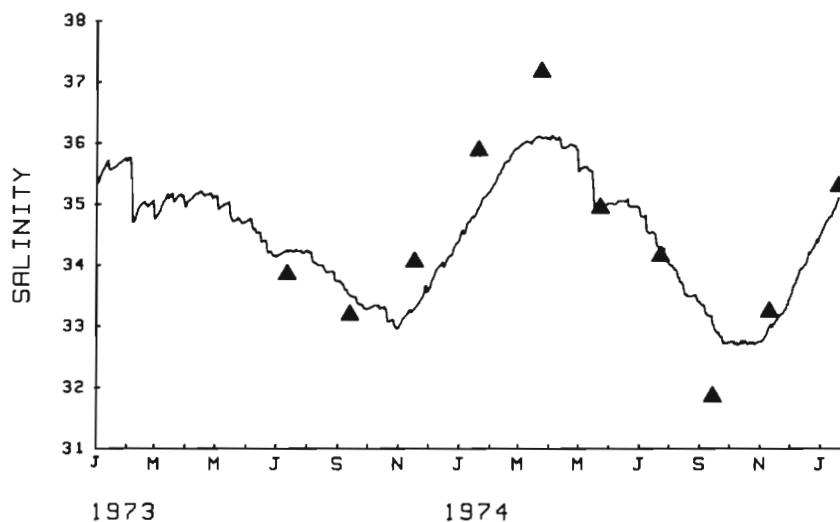

Fig. 3. Time course of salinity in Sector 2 predicted by the mixing model with $x_{12} = 0.009 \; d^{-1}$ (solid line). Actual salinity values (triangles) from Harris & Robinson (1979)

Of the 3 common taxa, adults of *Acartia tranteri* (M) were the only ones that showed a behavioral response to tidal currents (Kimmerer & McKinnon 1987a). Adults of this species were therefore excluded from the analysis. Sector mean abundances of *A. tranteri* (M)

copepodites and *A. tranteri* (L) and *Paracalanus indicus* copepodites and adults, and values of m calculated for Sector 2 with (m_2) and without (m_1) the advective flux term are presented in Table 4. Values of m for *A. tranteri* (M) copepodites were always positive, while

Table 4. Salinities and abundance data (ind m^{-3}) for post-naupliar copepods (copepodite only for *A. tranteri* M). Abundances are means for all stations within each sector. Net rates of loss (d^{-1}) were calculated from Eq. (6) either assuming no advective flux (m_1), or an advective flux term calculated from salinity (m_2). Error caused by neglecting the advective term is given as a percent of m_1 for the last 6 transects. T: transect no.; S: sector no.

| | Salinity | | *Acartia tranteri* M | | | | *Acartia tranteri* L | | | | *Paracalanus indicus* | | | |
| | | | Abundance | | | | Abundance | | | | Abundance | | | |
T	S 1	S 2	S 1	S 2	m_1	m_2	S 1	S 2	m_1	m_2	S 1	S 2	m_1	m_2
I				120	0.009		7	14	0.004		28	6	−0.032	
II			51	849	0.008		254	46	−0.040		100	17	−0.043	
III			257	719	0.006		133	44	−0.018		221	7	−0.269	
IV	35.78	36.97	51	1151	0.008	0.008	255	163	−0.005	−0.005	487	212	−0.011	−0.012
V	35.56	33.97	834	3852	0.007	0.007	152	89	−0.006	−0.006	142	71	−0.009	−0.008
VI	35.38	34.06	70	6891	0.009	0.009	606	94	−0.048	−0.046	1246	217	−0.042	−0.040
VII	35.52	35.03	496	6548	0.008	0.008	621	0	−∞	−∞	229	441	0.004	0.004
VIII	35.70	35.93	105	1256	0.008	0.008	1064	386	−0.015	−0.016	2089	127	−0.136	−0.136
IX	35.20	33.11	53	1184	0.008	0.008	232	89	−0.014	−0.014	65	37	−0.007	−0.007
Median:					0.008	0.008			−0.015	−0.017			−0.032	−0.033
95 % CL of median m_1:			0.006 to 0.009				−0.005 to −0.048				−0.007 to −0.136			
Median % error in m_1:			0.96				4.62				2.96			

those for *A. tranteri* (L) and *P. indicus* were nearly always negative. Differences between values of m calculated with and without the advective term were small (median 3 %) for the 6 transects on which salinity data were available. For all transects, 95 % confidence limits of m calculated without the advective term did not include 0 for any of the 3 species.

Including nauplii in the abundance data resulted in only a slight alteration of the calculated values of m (Table 5).

DISCUSSION

Estimates of exchange rates between sectors gave residence times that agree well with previous estimates of about 2 mo for the entire bay (Harris & Robinson 1979, based on silica distributions; Kimmerer & McKinnon 1985, based on measured salinities). The exchange rates were determined by fitting the model to salinity data from periods of both net evaporation and

Table 5. Values of m (d^{-1}) including nauplii for cruises when 50 μm net was used. Values are not presented for *Paracalanus indicus* for the last 2 transects since there were other members of that family present in abundance

Transect	*Acartia tranteri* M	*Paracalanus indicus*
I	0.007	−0.010
VI	0.009	−0.045
VII	0.008	+0.004
VIII	0.008	−
IX	0.008	−

net freshwater input. The high measured values of salinity relative to predicted values during dry seasons, and the inability of the model to predict the highest salinity value for Sector 2 with any value of the exchange rate, suggest that evaporation rates may have been underestimated. Temperature values used were sector means, and the mudflats that occupy a large part of the area of the bay would have been substantially warmer than the mean during hot, dry weather, especially at low tide. The use of higher summer evaporation in the model would have improved the fit (Fig. 3) by increasing the rate of rise of salinity in the summer, but would not have appreciably altered the estimated exchange rates.

The residence time of the whole bay is close to that of the upper bay, implying that the residence time of the western entrance is short. This is confirmed by studies that show clockwise residual circulation in the western entrance (Hinwood & Jones 1979), presumably due to the Coriolis effect. This circulation explains the break in salinity, seston concentrations, and sometimes plankton abundance near the boundary between Sectors 1, 2, and 3, 20 km from the mouth of the bay (Stn F). Salinity did not vary with distance in the western entrance. Chlorophyll and seston dry weight were consistently higher at Stns G to I than at Stns A to E, which had similar concentrations. Abundances of the common Bass Strait and Westernport Bay zooplankton species also often showed a sharp break within 10 km, less than 1 tidal excursion, of Stn F. These patterns support our division of the bay at the confluence of the 2 arms (Fig. 1).

We now address the assumptions used in the model. Assumption (1), that changes in abundance of the

populations average to 0, is borne out by the data presented here and available from related studies (Kimmerer & McKinnon 1985, 1987a, b) and from an earlier study of plankton in Westernport Bay (Macreadie 1972). A 2-fold increase in a population from one year to the next would require a net population growth rate of only $0.002\ d^{-1}$, but such a net change in abundance has not been observed over the several years of this program, or the 15 yr since the previous study (Macreadie 1972). Variation in abundances from one sampling period to the next would require a net population growth rate μ different from m; however we were attempting to measure only m, the excess or deficit in net population growth rates necessary to maintain the separation of the species. Thus the temporal variation of μ is of no concern here.

Assumption (2) says essentially that the mean value of abundance of a species in a box is the best estimate of the value to be used in Eq. (6). Because plankton abundance data are typically log-normally distributed, it is more common to use geometric rather than arithmetic means. However, the mixing processes modeled here are linear, so arithmetic means are the most appropriate. Variation of the sample mean from the population mean would result in error variance in Table 4, which was accounted for by the summary statistics for m. Similarly, departure from a steady-state condition for salinity as required in model development would result in error variance in the advective term in m, but not bias.

Assumption (3), that vertical stratification is negligible, is supported by available data on salinity and temperature distributions and circulation (Harris & Robinson 1979, Hinwood & Jones 1979, Kimmerer & McKinnon 1985). Assumption (4), that plankton act as passive tracers, is difficult to prove, and is apparently not true for adults of *Acartia tranteri* (M). However, we found no evidence for tidally-oriented motion by the other species or life stages, and have seen none in other studies of vertical positioning by copepods in Westernport Bay (Fancett & Kimmerer 1985). This assumption therefore appears justified by the available data.

Studies of circulation in Westernport Bay have shown a clockwise circulation around French Island, i.e. from Sector 3 to Sector 2 (Harris & Robinson 1979, Hinwood 1979, Hinwood & Jones 1979). This circulation has been neglected in the model because data on plankton abundance in Sector 3 were not collected routinely, and because the volume flux is small. The volume transported on a tidal cycle is about 8 to $18 \times 10^6\ m^3$ (Hinwood 1979), or about 1 to 2 % of the sector volume daily. Based on data from 3 sample sets taken in Sectors 2 and 3 (Kimmerer & McKinnon 1985), plankton abundances west of the tidal watershed are close to those in Sector 2. Thus the above flow rate should have little effect on abundances in Sector 2.

The flow of water through the eastern entrance may be more important to bay circulation, since there appears to be a small net outward flux of water through that channel under some weather conditions (Hinwood 1979). However, the influence of that flux on plankton distributions should be the same as on salinity distributions, and we did not assume that all of the plankton and salinity flux went through the western entrance.

Net population growth rates of the bay species are constrained over the long term to a maximum equal to the exchange coefficient, i.e. $0.009\ d^{-1}$ for Sector 2; most of the values for *Acartia tranteri* (M) are close to the maximum. As the numerical dominant in Westernport Bay, this is also the species about which the greatest amount of information is available on population dynamics. Adults of this species migrate vertically but juveniles do not (Kimmerer & McKinnon 1987a), so the bulk of the population is subjected to the mixing loss. The required net population growth rate is well within the capabilities of this species. Somatic production of copepodite stages averages 11 % d^{-1} throughout the year (Kimmerer & McKinnon 1987b). The mortality rate of late nauplii and copepodites averages only about 2 % d^{-1} (Kimmerer & McKinnon 1987b), i.e. about 2.5× that due to washout. Mortality rates of adults are about 6 % d^{-1} and of early nauplii, 16 % d^{-1}. The reproductive rate of *A. tranteri* (M) can be as high as 12 eggs female^{-1} d^{-1}, and adults comprise about 7 % of the population (Kimmerer & McKinnon 1987a, b). Thus a loss rate of 0.8 % d^{-1} is not large.

The *Acartia tranteri* (M) population in Westernport Bay maintains itself against only a small loss to washout. A hypothesis for the maintenance of large populations of only a few species of zooplankton in estuaries is that relatively few species have high enough population growth rates to survive rapid washout (Ketchum 1954). For example, *Acartia tonsa* flourished in a small estuary where it needed a population growth rate of about 40 % d^{-1} to overcome flushing (Barlow 1955). On the other hand, Landry (1978) reported that the rate of loss due to mixing of *A. clausi*, the dominant species in Jakle's Lagoon (Washington USA), was only 0.3 to 2 % per tidal cycle, and was significant only during winter when population growth rates were low. Thus a high rate of flushing is not necessary to maintain reduced diversity.

Net population growth rates of natural populations have rarely been determined, especially on populations approximately in long-term steady state. Exceptions include the studies of Barlow (1955) and Landry (1978), which showed very different rates of loss of numerically dominant bay resident populations. The

Acartia population in Barlow's study clearly maintained its dominance by its ability to withstand strong physical forcing, i.e. flushing out of the estuary. The *Acartia* population in Landry's study must have maintained dominance by some biological mechanism, perhaps predation on nauplii of other species. The same is probably true of *A. tranteri* in Westernport Bay.

Since adults of *Acartia tranteri* (M) migrate vertically to maintain themselves inside the bay (Kimmerer & McKinnon 1987a), proportions of adults might have been expected to increase with distance into the bay. The lack of any such correlation can be attributed to the time scale: the residence time of Sector 2 is ca 114 d, while the development time of *A. tranteri* (M) from egg to adult is about 30 d (Kimmerer & McKinnon 1987b). The ratio of adults to total copepods therefore depends more on local processes than on differential mixing. In other words, the loss rate of juveniles due to mixing is so low that its absence cannot be seen in the abundance data for adults.

For the same reasons, the high proportions of *Acartia tranteri* nauplii in lower bay samples on some of the transects are not the result of differential washout. The nauplii were more abundant there because of spatial variation in local processes such as reproductive rates or mortality rates. In general nauplii were most abundant where absolute abundances of adults were low, suggesting that cannibalism may have been an important source of mortality (Lonsdale et al. 1979). The exception to this pattern occurred on Transect VI, when the proportion of nauplii was high in Sector 2 and low in Sector 1. This was the time of highest growth rate of the *A. tranteri* (M) copepodites (Kimmerer & McKinnon 1987b) and presumably also the highest reproductive rates of the adults; thus at this time enhanced reproductive rates within the bay may have offset any cannibalism by adults.

The values of m for *Acartia tranteri* (L) and *Paracalanus indicus* were more variable than those for *A. tranteri* (M) for several reasons. First, there is no lower bound for a negative net population growth rate; values can be anywhere between 0 and $-\infty$. Second, m is more sensitive to variation in Q_2 than in Q_1, and the former is smaller and more variable than the latter. Third, variation of Q_1 is less closely coupled to that of Q_2 in a Bass Strait population than in a bay population because of advection past the bay mouth. That is, the Bass Strait water masses providing zooplankton for entrainment on successive flood tides might be widely separated and therefore contain zooplankton of different abundance, age, and species composition.

Values of m for the Bass Strait species were mostly very small, with medians of -1.5% d^{-1} for *Acartia tranteri* (L) and -3.2% d^{-1} for *Paracalanus indicus*. The confidence intervals of these values were wide, but all

but 3 of the 18 individual values for the 2 species were between 0 and -5% d^{-1}. The overall net mortality of these species is apparently due to a combination of reduced fecundity and increased predation within the bay (Kimmerer & McKinnon 1985), since neither behavior, flushing rate, nor salinity stress can explain it. The large difference in zooplankton species composition between the bay and Bass Strait can arise from such a small difference in net population growth rates because of the long residence time of the bay. The actual sources of these differences will be addressed in a later paper.

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