

Advection, dispersion and mortality of a patch of southern bluefin tuna larvae *Thunnus maccoyii* in the East Indian Ocean

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ABSTRACT: Mortality rate of southern bluefin tuna larvae *Thunnus maccoyii* was determined from measurements of a large, high density patch of larvae in the East Indian Ocean made in January–February 1987. An advection-diffusion-mortality model that improves on elliptical spread models was used to model changes in the patch over a period of 6 d. The patch at the start of sampling consisted of a distinct cohort of larvae 7 to 8 d old. Diffusion in subsequent 2 d intervals was slow (1.02 to $1.5\text{ m}^2\text{ s}^{-1}$) but within the bounds observed for patch scales in the order of a few kilometres wide. Intensifying southwesterly winds were opposed by advection with a southwestward drift of about 6 cm s^{-1} . The original intention of using a free-drifting drogue to track the centre of the patch, and thereby account for the advective process, was not successful because of the relative drift of buoy and larval patch. Instantaneous mortality (Z) was estimated to be 0.66 d^{-1} (a daily survival rate of 52 %). This is the first time the mortality of tuna larvae has been directly estimated in the open ocean.

INTRODUCTION

Southern bluefin tuna *Thunnus maccoyii* is an important commercial species fished by Australia, Japan, New Zealand and other countries. Adults have an almost circumpolar distribution between latitudes 30 and 50° S (Shingu 1981), although the only known spawning ground is south of Java in the East Indian Ocean within the latitudes 7 to 20° S and longitudes 102 to 124° E (Nishikawa et al. 1985). The species is thought to be substantially overexploited (Caton & Majkowski 1987). However, little is known of its early life history and nothing is known of the patterns of dispersal and rates of mortality of the larvae, although it is believed that larval mortality is an important component of recruitment variability (Cushing 1975, Rothschild et al. 1989). It is also considered that the most important source of bias in estimating egg production is likely to be mortality during the period from spawning to the stage on which the estimate is based (Saville & Schnack 1981). As it is not yet possible to identify tuna eggs or larvae < 3.0 mm (SL) to species (Nishikawa & Rimmer 1987), surveys to estimate abundance must be based on the larger larvae.

There are no estimates of larval mortality rates for

any species of tuna in the open ocean. Tuna larvae are generally thought to occur in low densities and have a patchy distribution (Wade 1951, Strasburg, 1960, Klawe 1963, Richards & Simmons 1971), and while isolated tows have produced moderately large catches of tuna larvae – presumably because they intersected a patch (Richards & Potthoff 1980, Yukinawa 1987) – patches have not been reported in the literature. During a study to determine the optimal sampling procedure for estimating tuna larval abundance in the Indian Ocean (Davis et al. 1990a, b), we found a large patch of *Thunnus maccoyii* larvae, which we were able to sample intensively over 6 d. This provided us with an opportunity to study the processes of advection, dispersion and mortality of tuna larvae in the open ocean.

In the open ocean, the transport and distortion of larval distributions produced by the physical processes of advection and diffusion must be accounted for before estimates of mortality are possible. Theoretically, population mortality could be estimated by intensively and regularly sampling an isolated patch of larvae and the area to which they could have spread in order to estimate temporal changes in population numbers. In practice, apart from the problem of tracking the patch, it is difficult to sample an area that is wide enough, or to

sample sufficiently intensively, to produce accurate estimates of population sizes and hence mortality (Harding & Talbot 1973, Henderson et al. 1984, Leak & Houde 1987, Kiørboe et al. 1988, Chenoweth et al. 1989, Incze et al. 1989). An alternative approach is to examine the successive changes in larval densities, but this requires modelling changes in larval abundance due to the physical processes of advection and diffusion. Fortier & Leggett (1985) studied the decline in densities of capelin larvae around a free-drifting drogue by assuming that the dilution of larvae, presumed to be primarily due to vertical mixing, was reflected in salinity changes. In an advective-diffusive environment, an isolated larval patch from a single instantaneous spawning would produce a characteristic elliptical spread. Mortality rates have been estimated by forcibly fitting ellipses to observed distributions by statistical regression or optimization (Talbot 1977, Munk et al. 1986, Heath & MacLachlan 1987, McGurk 1989). In this paper, we present results from a novel method that uses a model of advection, diffusion and mortality to optimize predictions from one period to the next.

MATERIALS AND METHODS

Field sampling. Sampling was carried out in the southern part of the spawning grounds (Nishikawa et al. 1985) in the North Australia Basin, which has a bottom depth of ca 5000 m (Fig. 1). The station at 16° 30.2' S, 115° 50.4' E was selected after large numbers of *Thunnus maccoyii* larvae (> 4 larvae m^{-3}) were caught in a trial oblique tow. A satellite-tracked buoy drogued at 20 m depth with a parachute (Cresswell et

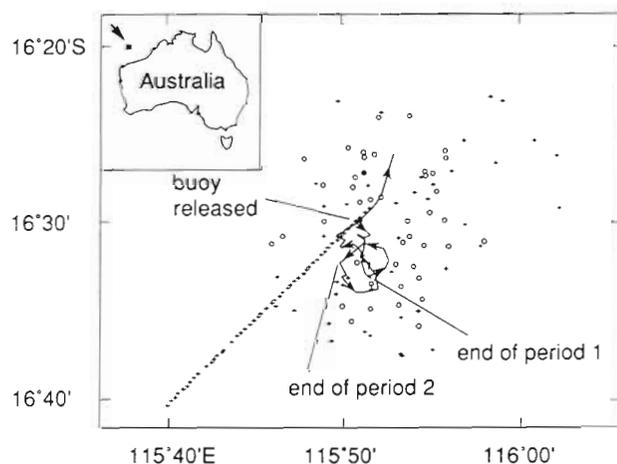


Fig. 1. Ichthyoplankton stations in the Indian Ocean northwest of Australia taken on 28 January to 2 February 1987 (periods 1 to 3). Arrow and line indicate the drift trajectory of satellite-tracked buoy no. 6128 during the period of sampling; station locations (o: day, +: night) were chosen randomly to lie within 20 km of the buoy's position

al. 1978) was deployed at this station on 28 January 1987 at 17:40 h (local time) to flag the patch of larvae.

The larvae were sampled with a 70 cm diameter ring net made of plain weave Estal monofilament with a mesh aperture of 0.5 mm and open area ratio of 5:1 (Davis et al. 1989) fitted with a calibrated mechanical General Oceanics flowmeter which was towed at speeds of 1.0 to 1.3 $m s^{-1}$. A transect of surface tows, each about 390 m long and separated by about 200 m, was made starting 2 km NE of the buoy and heading in a SW direction into the wind for 30 km. These were completed at night between 21:05 h on 28 January and 03:09 h on 29 January. The surface tows were deployed from a boom on the port side amidships, clear of the wake of the vessel about 0.5 m under the surface, oscillating between 0 and 2 m. A total of 88 oblique tows was then made at random positions within a 20 km radius of the buoy, starting at 08:40 h on 29 January and finishing at 23:30 h on 2 February. Oblique tows, guided by real-time depth data, were made from the surface to the top of the thermocline (about 50 m depth) and back to the surface to cover the known depth range of the tuna larvae (Davis et al. 1990a). Ichthyoplankton sampling was not carried out during transitional light periods of dawn and dusk.

The temperature and salinity of the water pumped from about 2 m depth were recorded continuously by a thermosalinograph (Grundy Environmental Systems Inc. Model no. 6620). Casts were made at random positions to a depth of either 150 or 500 m at dawn and dusk each day with a Neil Brown Mark 3B CTD probe with a 1150 deck unit and General Oceanics rosette sampler fitted with 8 l Niskin bottles. Due to calibration problems with the CTD sensors only the raw temperature-salinity data were obtained. Wind speed measurements were made using the ship's anemometer. Full details of ichthyoplankton and hydrographic data collected on this cruise are presented in Davis & Clementson (1989).

Treatment of samples. Ichthyoplankton samples were preserved in 95 % ethanol. Tuna larvae were sorted from the plankton using a rotatable sorting ring under a dissecting microscope with dark-field illumination. *Thunnus maccoyii* were identified using the criteria of Nishikawa (1985) and Nishikawa & Rimmer (1987). Identification was only attempted on larvae > 3.5 mm as the diagnostic pattern of melanophore distribution may not have developed in smaller larvae. Some confusion exists in distinguishing between *T. maccoyii* and *T. obesus* either because the dorsal body pigments cannot be detected in some *T. maccoyii* larvae, or, rarely, when *T. obesus* has a caudal fin pigment spot dorsal to the notochord (Nishikawa & Rimmer 1987). As only one *T. obesus* larvae was identified with the usual pattern of pigment distribution in this study

confusion of the 2 species was not a problem. Tuna larval densities were expressed as number per m² sea surface calculated from the volume filtered and the depth reached by the net. The age composition of *T. maccoyii* in each sample along the surface transect was determined from the criteria of Jenkins & Davis (1990). Where more than 20 larvae were present, a random subsample of 20 larvae was aged. The abundance data were grouped into 3 periods (Table 1). The grouping of stations into ca 2 d periods was necessary to provide sufficient sampling coverage to define changes in the spatial distribution of *T. maccoyii* larvae with time, although it does not represent a true synoptic pattern. The start of each day was taken as 18:00 h to coincide with the approximate onset of daily otolith increment formation (Jenkins & Davis 1990). Period 1 included data from the surface transect after surface catches (*S*) were adjusted to oblique tow equivalents (*O*) using the regression equation ($O = 0.86S + 29.23$, $R^2 = 0.83$, $p < 0.001$) determined from paired surface and oblique tows taken over the 6 d period (Davis et al. 1990a). In an attempt to reduce the variation in catches in oblique tows due to day/night differences in avoidance, day catches were divided by the mean day/night catch ratio of 0.27 (SE = 0.07) determined from oblique tows taken over the 6 d period (Davis et al. 1990a). Ichthyoplankton and station data are presented in detail in Davis & Clementson (1989).

Advection-diffusion-mortality modelling. Parameters for advection-diffusion and mortality are optimized from a model which predicts the evolution of a given initial larval distribution. This involves calculating larval densities corresponding to the initial distribution on a uniform grid encompassing an area larger than the measured distribution. Larval densities at each of the grid points are considered to be seed populations. The predicted concentration at any one of the stations for the next period is obtained by summing the contributions from the seed populations, each of which spreads as an ellipse under the influence of advection, diffusion and mortality. The model makes no assumptions about the nature of the drift of the larvae; whether it is passive or active. It simply fits the parameters to best describe the change in the observed distribution.

The evolution of the larval distribution is described by the standard linear equation for advection, diffusion and mortality:

$$\frac{\partial N}{\partial t} = K_x \frac{\partial^2 N}{\partial x^2} + K_y \frac{\partial^2 N}{\partial y^2} - U \frac{\partial N}{\partial x} - V \frac{\partial N}{\partial y} - ZN, \quad (1)$$

where N = larval density (no. m⁻²); U = advection in the east-west direction (x), positive to the east (m s⁻¹); V = advection in the north-south direction (y), positive to the north (m s⁻¹); t = time (s); K_x , K_y = diffusion coefficients in the x and y directions, respectively (m² s⁻¹); and Z = instantaneous mortality (s⁻¹).

The initial distribution was interpolated onto a uniform grid by computing the weighted average of the densities around the neighborhood of each grid point. A 30 × 30 grid with a grid interval of 1.84 km on the x -axis and 1.53 km on the y -axis was centered at the initial distribution. For the interpolation, the search radius in each of the horizontal directions was set at one-tenth of the respective model domain lengths. Inverse distance-squared weighting was used for the interpolation. One difficulty with this modelling approach is the need to assign a time to each of the grid points. This is necessary because it takes at least a day to measure the distributions, and the predicted evolution of the seed populations depends on the time difference between the initial distribution and the observations at the next period. The weighting procedure used for the densities was used to assign an average time to each grid point. Given these times and a set of assumed model parameters, the prediction of density (N_i) at each sampling station (i) for the next period is given by summing the contributions of the seed populations which are instantaneously released at each grid point:

$$\hat{N}_i = \sum_{j,k} \hat{N}_{j,k} g_{j,k} \Delta x \Delta y, \quad (2)$$

where

$$g_{j,k} = \frac{1}{4\pi(K_c K_l)^{1/2} \Delta t} \exp \left[\frac{(-x_c^2/K_c - y_l^2/K_l)}{4\Delta t} - Z\Delta t \right] \quad (3)$$

and $\hat{N}_{j,k}$ = larval densities for the first period interpolated onto a grid with n_x nodes in the j direction (E–W) and n_y nodes in the k direction (N–S); (x_c, y_l) = the

Table 1 Details of samples used to estimate the distribution and abundance (no. m⁻²) of *Thunnus maccoyii* larvae in the 3 time periods. The number of stations sampled during the day or night is indicated by D or N, respectively. TS: surface tows along the transect

Period	Sampling method	Start (local time)	Finish (local time)	No. of stations	Maximum density	Mean density	Standard error
1	TS & random	21:05 h, 28 Jan	16:01 h, 30 Jan	16 D, 60 N	754	53.3	18.3
2	Random	20:35 h, 30 Jan	16:24 h, 1 Feb	20 D, 20 N	64	9.0	2.3
3	Random	20:28 h, 1 Feb	23:31 h, 2 Feb	8 D, 15 N	10	2.2	0.7

distances $(x_i - \hat{x}_{j,k} - U\Delta t)$, $(y_i - \hat{y}_{j,k} - V\Delta t)$ rotated into the direction of the principal diffusion axes; $\Delta t = t_i - t_{i,k}$ is the time difference between the time of sampling for the next period (t_i) and the time computed at the grid point ($t_{i,k}$); $g_{j,k}$ corresponds to the Green's function for advection, dispersion and mortality; and Δx and $\Delta y =$ the grid spacing in the x and y directions respectively. A similar but simpler formulation was used by Hill (1990) to examine potential limits to recruitment in *Nephrops norvegicus* by advection, diffusion and mortality.

The sum of squares error computed from these fitted distributions is used in an optimization procedure (modified Levenberg-Marquardt method subject to simple bounds – routine BCLSF in the IMSL library) to estimate optimal model parameters. Manual guidance and tuning were often required to arrive at satisfactory 'optimal' estimates. The optimization was done in 3 stages. Crude estimates of the advection parameters were first obtained by contouring the measured distributions (by interpolating densities onto a grid and then using the subroutine CONREC from the NCAR suite of programs) and calculating the advection required to shift the centres of the patch from one period to the next. These estimates were optimized whilst keeping the diffusion and mortality parameters fixed at some reasonable value (usually determined a posteriori). The diffusion coefficients and mortality were optimized next whilst keeping the diffusion tensor angle (ϕ) fixed at some arbitrary value. The diffusion tensor angle was optimized last. After another iteration of the optimizations, the resulting predictions were contoured and compared with observations to fine tune the parameters.

A similar approach was used to estimate the advection-diffusion parameters from the salinity distributions, but in this case only the deviations from the mean were advected and diffused. The mean value was made equal to the mean calculated from the measured stations for the first period.

RESULTS

Drift of the satellite buoy

The buoy drifted initially against the wind, which later intensified from the southwest and, by the end of the third period, had reversed the drift of the buoy (Fig. 2). During period 2 and for much of period 3, the buoy drifted anticlockwise for about 2 cycles before accelerating rapidly to the north at the end of period 3. The wind increased from 42 km h^{-1} in period 1 to 58 km h^{-1} by the end of period 3. Without knowing how the buoy responded to wind drag, we could not

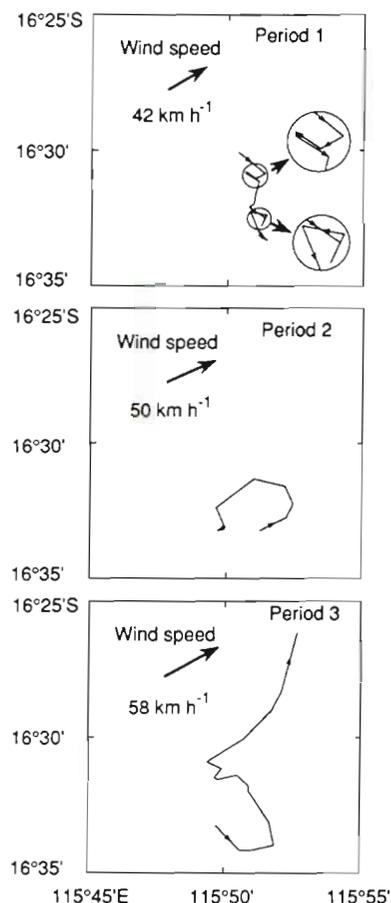


Fig. 2. Wind speed and direction and drift trajectory of the drogue buoy during each sampling period. Arrows indicate the direction to which the wind is blowing and the buoy is drifting

use the buoy track to account for advection of the larvae.

Distribution and abundance of larvae along the transect

Of the tuna larvae caught in the transect that intersected the patch at the beginning of period 1, 43% were $< 3.5 \text{ mm}$ and thus identification was not attempted. As almost all larvae $> 3.5 \text{ mm}$ were identified as *Thunnus maccoyii* (7390 *T. maccoyii* and 7 *T. alalunga* larvae), we assumed that the smaller larvae were also *T. maccoyii*. The density of *T. maccoyii* larvae in contiguous stations along the surface transect showed a Gaussian distribution, starting at a peak density of 754 m^{-2} and declining to 4 m^{-2} at the 11th station, a distance of about 6.5 km (Fig. 3). It can be judged from the shape of the density distribution that the transect probably passed close to the patch centre but traversed no more than the radius of the patch. *T. maccoyii* larvae

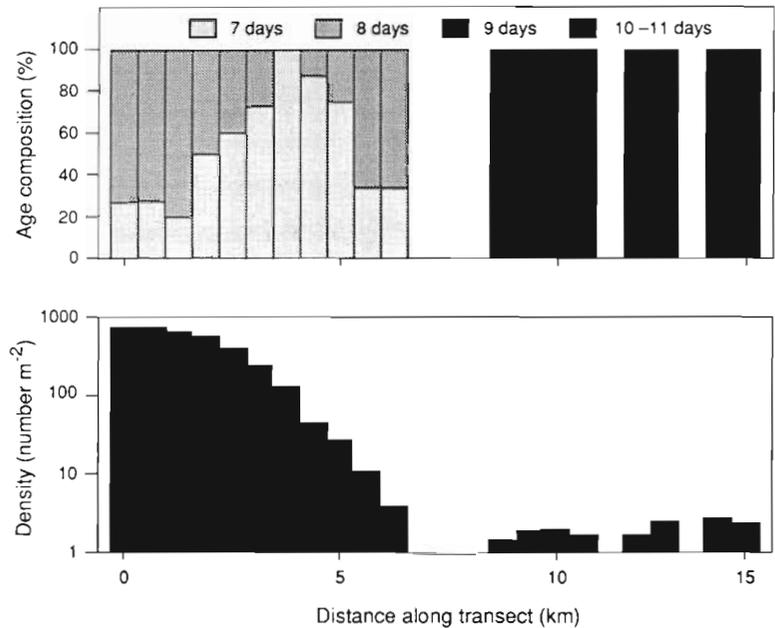


Fig. 3. *Thunnus maccoyii*. Density of larvae and their age composition in the surface transect starting near the estimated patch centre and extending in a southwest direction. Larval density is plotted on a log scale

were absent at Stns 12 to 14, but occurred in low numbers at many stations throughout the remainder of the transect. *T. maccoyii* larvae within the patch were 7 to 8 d old (Fig. 3). All larvae in the smaller patches outside the main patch were older (9 to 11 d). Thus the patch consisted of a single cohort of larvae spawned over a 2 d period, which appeared to be clearly separate from adjacent smaller patches of older larvae. This same cohort dominated random samples taken over the following 5 d (Jenkins & Davis 1990).

Temporal changes in the distribution and abundance of larvae

Random sampling of the larval distributions and salinity was conducted during each of the 3 periods, using the drogued buoy as a marker for the patch. The measured distributions showed the centre of the larval patch gradually drifting southward relative to the buoy (Fig. 4). Consequently, by the third period, it appeared that only the northeastern quadrant of the patch was sampled. Peak measured densities declined from 754 larvae m⁻² in period 1 to 10 larvae m⁻² in period 3. The estimated total number of larvae contained within the 30 × 30 grid (area = 2537 km²) declined from 3.58 × 10¹⁰ in period 1 to 0.921 × 10¹⁰ in period 2, and then to 0.188 × 10¹⁰ in period 3. The centre of the patch was located in waters of about 34.84 ‰ at the southern edge of a fresher pool of water intruding from the northeast (Fig. 4). Mixing and southward advection of the fresher water lowered salinities around the sampled region.

Advection-diffusion-mortality modelling

Our initial aim was to use the measured salinity distributions to estimate the advection-diffusion parameters, which would then be used in the larval model so only the mortality parameter would need to be estimated. We soon realized that this approach was not appropriate (see 'Discussion') and the physical parameters for the larval distribution had to be obtained simultaneously with the mortality parameter.

Two sets of simulations were run (Table 2): one set for the larval distribution and a second set for the salinity distribution. Temperature data were available for estimating the advection and diffusion parameters but were not used as the air-sea heat fluxes would have had to be calculated and there was insufficient information to do this accurately. In each set, model parameters were estimated from the distributions for periods 1 and 2, using period 1 for initialization, and from the distributions for periods 2 and 3, using period 2 for initialization.

The goodness of fit (R^2 in Table 2) was clearly much better for the larval simulations ($R^2 > 0.8$) than for salinity ($R^2 < 0.4$). The fitted larval distributions were in excellent agreement with observations (Figs. 5 & 6) and the fitted peak concentrations were within a few percent of the measurements for both periods (Table 2).

All simulations predict that advection during period 1 to 2 was southwestward, but the larvae simulation predicted a much stronger southward component (5.4 cm s⁻¹) than did the salinity distributions (3 cm s⁻¹). All predictions indicate a primarily westward flow

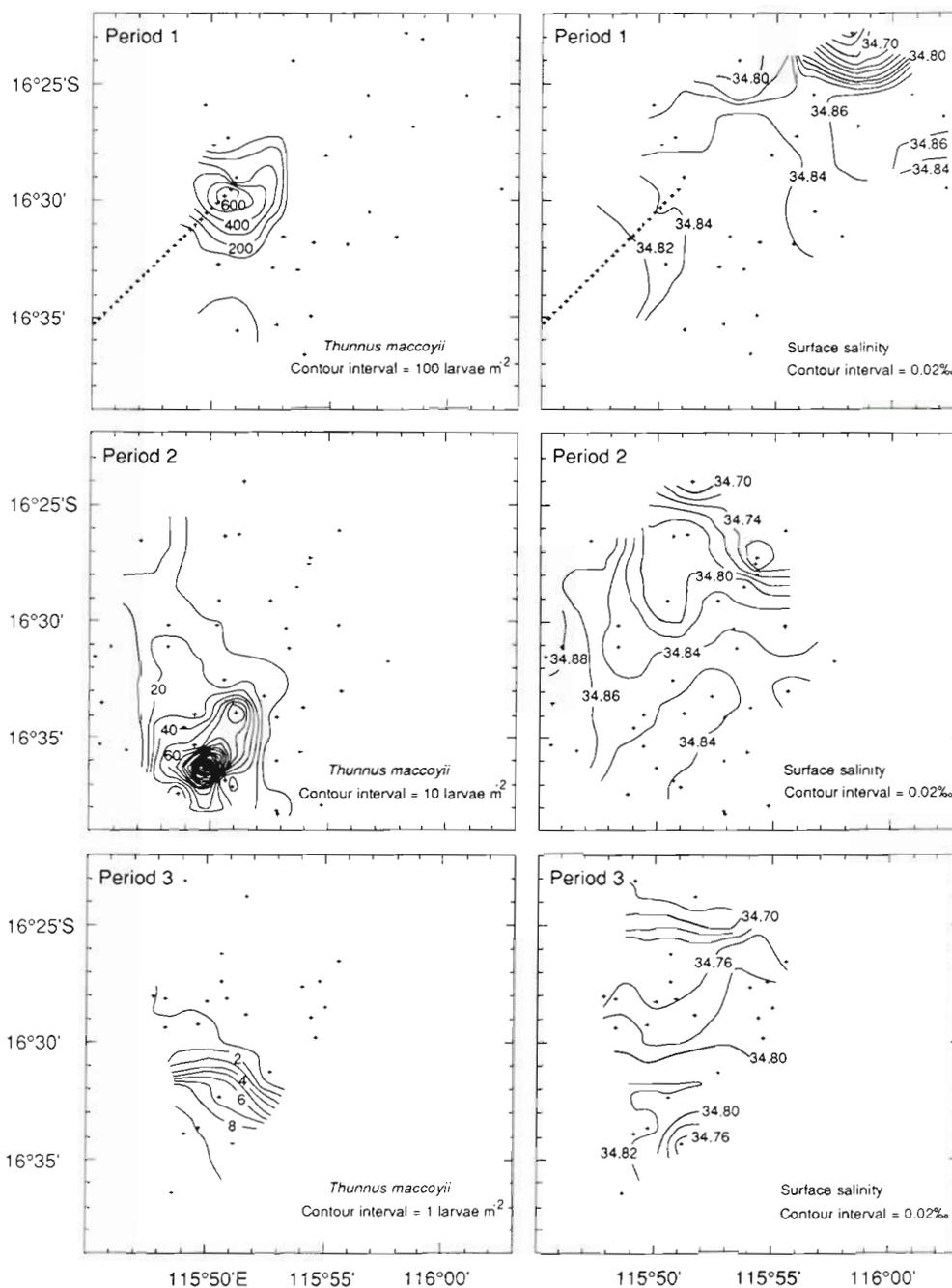


Fig. 4. *Thunnus maccoyii*. Distribution of larvae and surface salinity from observations made in periods 1 to 3. +. station positions. Contour intervals vary between periods as indicated; values of major contours are given

between periods 2 and 3. Diffusion estimates were much larger for salinity than for larvae and optimal angles were also different.

Instantaneous mortality (Z) during periods 1 to 2 was 0.66 d^{-1} which is equivalent to a daily percentage mortality of 48%. An instantaneous mortality of 0.43 d^{-1} (daily percentage mortality of 33%) was estimated for

the period 2 to 3 simulations. For comparison, mortalities were also estimated by examining the decline in the populations within the sampling area (Table 3). Both mortality determined by the model ($Z = 0.66 \text{ d}^{-1}$) and that determined from the decline in the population within the sampling area ($Z = 0.68 \text{ d}^{-1}$) were in good agreement for periods 1 to 2. However, there is a clear

Table 2. Parameters estimated by modelling changes in the distribution of *Thunnus maccoyii* and salinity between periods. ϕ is the angle of the component of the diffusion tensor K_j , measured anticlockwise from the E–W or x-axis. K_c is the component at right angles to K_j . R^2 is the coefficient of determination

Data being modelled	K_c ($\text{m}^2 \text{s}^{-1}$)	Diffusion K_j ($\text{m}^2 \text{s}^{-1}$)	ϕ (deg)	Advection V_x (m s^{-1})		V_y (m s^{-1})	Mortality Z (d^{-1})	R^2	Peak predicted in next period (no. m^{-2})	Peak observed in next period (no. m^{-2})
<i>T. maccoyii</i>										
Period 1 \rightarrow 2	1.50	0.05	70.3	−0.0024	−0.0536	0.66	0.93	244.5	237.1	
Period 2 \rightarrow 3	1.02	0.30	20.0	−0.0226	0.0043	0.43	0.88	10.5	10.1	
Salinity										
Period 1 \rightarrow 2	5.2	0.63	50.0	−0.0300	−0.0291	–	0.32	–	–	
Period 2 \rightarrow 3	10.0	0.10	21.6	−0.0164	−0.0074	–	0.11	–	–	

Table 3. Mortality (Z) between periods determined from the advection-diffusion-mortality model and from the estimated population remaining within the 30×30 grid

	Mortality, Z (d^{-1})	
	From model	From estimated abundance
Period 1 \rightarrow 2	0.66	0.68
Period 2 \rightarrow 3	0.43	0.97

discrepancy in mortality estimated by the model ($Z = 0.43 \text{ d}^{-1}$) and mortality estimated by the decline in the population ($Z = 0.97 \text{ d}^{-1}$) for periods 2 to 3.

Parameters derived from the manual tuning and optimization procedure are not necessarily unique, nor global optima. An indication of the sensitivity of the parameters was calculated from the local Jacobian (gradient of the sum of squares error with respect to each of the parameters) at the chosen optimal point. The Jaco-

bian is a finite difference approximation at the approximate solution. Table 4 presents the change required to be made in each parameter so that each change increases the sum of squares error by 25 % of the value at the chosen optima. This percentage is an arbitrary figure which we use only to provide an indication of the parameter sensitivity. In the larval simulations the advective parameters are well estimated, especially the north-south component. Mortality changes required are about 0.1 d^{-1} but diffusivities changes are larger for periods 2 to 3. Parameters for the salinity distribution appear to be less well estimated. Diffusivities in particular are more variable than those for the larvae and little confidence can be placed in the diffusivities from salinity, with the possible exception of K_j for periods 2 to 3. The angle of the diffusivity tensor appears to be reasonably well estimated only for the period 1 to 2 larval distribution. Advective changes from salinity are over an order of magnitude greater than those from the larval distribution. Table 4 also gives the sensitivity of the

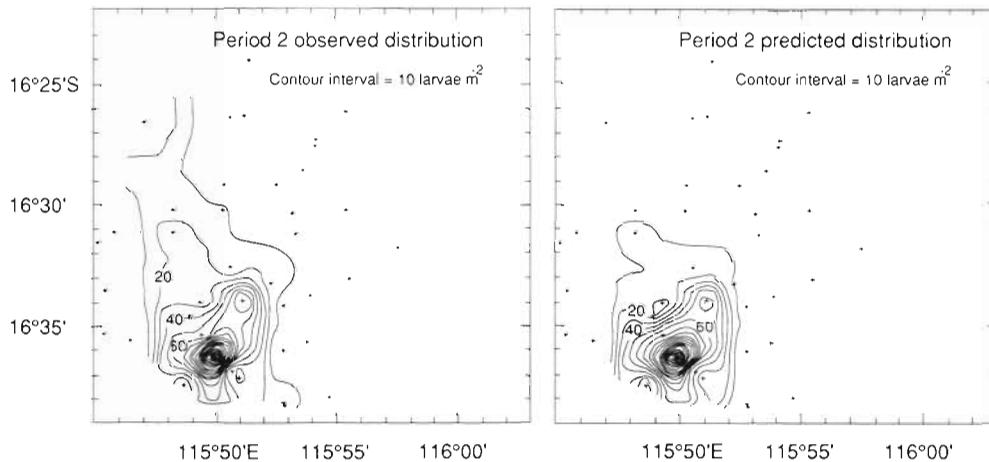


Fig. 5. *Thunnus maccoyii*. Observed distribution and distribution predicted by the advection-diffusion-mortality model in period 2. The model domain corresponds to the boundary of the plotted distribution

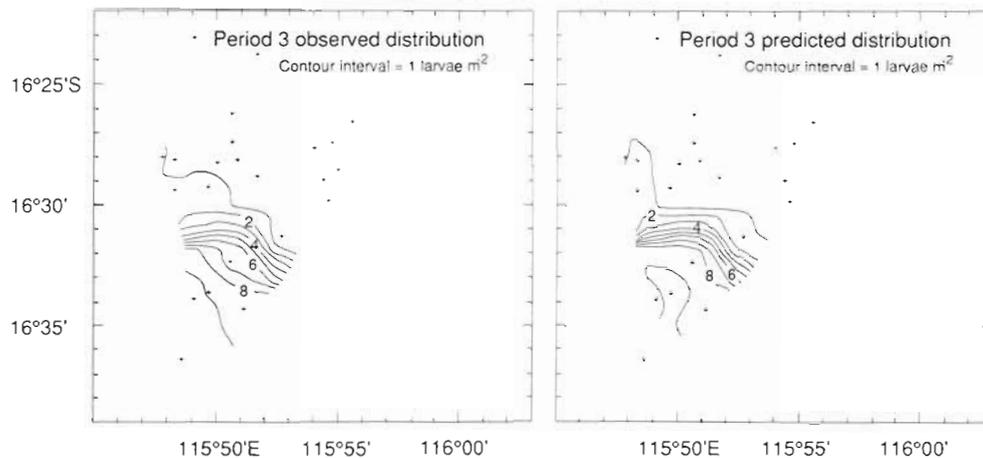


Fig. 6. *Thunnus maccoyii*. Observed distribution and distribution predicted by the advection-diffusion-mortality model in period 3

Table 4. Parameter changes (absolute values) required to increase the sum of squares error by 25% from its value at the optima. For each simulation, parameter changes are calculated from the Jacobian, or the gradient of the sum of squares error with respect to each of the parameters, at the optima. The Jacobian is a finite difference approximation at the optimal solution. These changes serve only as an indication of the parameter sensitivity; changing the parameters by the amount shown will not necessarily change the sum of squares error by 25%

	K_c ($m^2 s^{-1}$)	K_l ($m^2 s^{-1}$)	ϕ (deg)	V_x ($m s^{-1}$)	V_y ($m s^{-1}$)	Z (d^{-1})
Larvae						
1–2	0.53	0.35	8.4	0.0017	0.0003	0.09
2–3	0.90	4.58	51.3	0.0012	0.0004	0.13
Salinity						
1–2	60.8	8.34	229.0	0.0189	0.0153	–
2–3	246.0	0.45	86.3	0.0233	0.0135	–

mortality estimates; the alternate interpretation of the sensitivity analysis is that it provides the change in the mortality parameter required to compensate for a 25% sum of squares error caused by altering one of the other parameters independently

DISCUSSION

Dispersion of larvae in the open ocean imposes stringent requirements on sampling to account for the highly dynamic physical processes, the biological processes of mortality and vertical migration, and the measurement uncertainties, particularly the problem of net avoidance; provided of course that one is near a newly spawned patch of larvae in the first place. Our fortuitous discovery of the large patch of newly hatched *Thunnus maccoyii* larvae presented us with a unique opportunity to study these processes in the open ocean. The principal aim of determining mortality from the change in larval distribution was fraught with difficul-

ties, which we attempted to overcome with a predictive model combined with parameter optimization. The original intention of using the buoy to track the centre of the patch, and thereby account for the advective processes, was not successful because of the relative drift of buoy and larval patch.

Free-drifting drogues have been used to track aggregations of larvae in order to study such processes as vertical distribution, growth, advection, dispersion and mortality (Dragesund & Nakken 1971, Hempel & Schnack 1971, Bjorke 1978, Smith et al. 1978, Conte et al. 1979, Shelton & Hutchings 1982, Henri et al. 1985, Heath & MacLachlan 1987, Heath & Rankine 1988, Röpke 1989). Few of these studies have questioned the efficacy of drogues as Lagrangian reference points. Smith et al. (1978) concluded that their drogue remained within the patch of larvae as there were no significant differences in the size and concentration of larvae over the 3 d of investigations. The lack of significant change in salinity and temperature and zooplankton composition near the drogue was taken as evidence

that it followed the drift of anchovy eggs (Shelton & Hutchings 1982). However, Heath & Rankine (1988) observed discrepancies between the trajectories of patches of larvae and the drogues intended to track them. These discrepancies were reduced by correcting for wind drag. Fortier & Leggett (1985) directly measured the movement of their drogue relative to the surrounding water, using recording current meters and temperature and salinity sensors attached to the drogue. Their drogue failed to remain in the original water mass, which they attributed to water drag on the supporting buoy caused by wind-induced acceleration of the top few meters of the water column.

Recent studies on the performance of drifting drogues (Niiler et al. 1987, Bitterman & Hansen 1989, Chereskin et al. 1989) have established that slippages of a few cm s^{-1} can be expected, depending on the drifter design, the prevailing wind, surface gravity waves and the structure of the vertical current shear in the water column. Over a period of a few days, this slippage can amount to a distance comparable to the width of a patch of newly hatched larvae (several kilometers). In our case, even though there was slippage of over 10 km during the experiment, we were fortunate to have sampled part of the patch in the third period.

Our modelling results show a south to southwestward drift of about 6 cm s^{-1} of the larvae, whereas the buoy initially drifted south but, in response to an intensifying southwesterly wind, reversed and drifted northward towards the end of the third period. This suggests an initial southward current in the surface mixed layer and a later wind-induced northward current in the top few meters causing increased drag on the buoy. There is also a disparity between the predicted initial southward drift of the larvae and the predicted southwestward movement of salinity (Table 2), which may be due to large-scale horizontal velocity shear. Fig. 3 shows that most of the variance in the initial salinity is in the northeast corner, associated with the intruding low salinity water mass, whereas most of the larvae variance is further west and south. Thus, the predictions may be reflecting a spatial variation in current patterns – southwestward flow in the northeast and southward flow further west and south. Our estimates of current vectors are therefore representative only of the currents associated with the central region of the larval patch.

The model's predictions of the principal diffusivity for the larval data (1.02 to $1.5 \text{ m}^2 \text{ s}^{-1}$) are within the bounds observed for patches a few kilometers wide, according to Okubo's (1971) diagram. While we have much less confidence in the parameters derived from salinity (Tables 2 & 4), the large diffusivity observed for salinity ($> 5 \text{ m}^2 \text{ s}^{-1}$) may be a reflection of the increased scale over which the salinity anomalies are dispersed or

perhaps the enhancement of the horizontal diffusivity by vertical mixing of salinity profiles caused by increasing winds. In any case, the use of diffusivities derived from salinity is clearly not valid for the larval distributions. It should also be noted that we did not take into account the variance in the day/night ratio which would have resulted in increased diffusivities of the larvae. However, we could not find an appropriate method for incorporating this variance in the optimization.

The disparity in mortality estimates for periods 2 to 3 based on the model (0.43 d^{-1}) and the population approach (0.97 d^{-1}) (Table 3) highlights the necessity for stringent sampling when using the population approach to estimate mortality. In period 3, only a portion of the total population was sampled (Fig. 3) and hence the mortality from the population approach was overestimated; in this case by more than twice the value from the model. The model was used to fit parameters to period 2 to 3 data to demonstrate the versatility of the method. Nevertheless, we do not consider there was sufficient sampling coverage of the patch during period 3 to place too much reliability on the model's mortality estimate. Thus, the entire spread of larvae must be properly sampled to apply the population approach to mortality. Results from fixed-grid surveys will also be invalid unless the inter-station distances are less than the width of the typical patch. Unless mortality is low, patchiness of larval distribution is likely to persist because mortality tends to counteract the spreading influence of diffusion (Talbot 1977, Koslow et al. 1985).

The model used here improves on the single elliptical spread model used by previous investigators (Munk et al. 1986, Heath & MacLachlan 1987, Talbot 1977, McGurk 1989). The allure of simplicity offered by the elliptical spread model is, however, at the cost of making the implicit assumptions that spawning is instantaneous and localized at a point, that the advection, diffusion and mortality parameters are constant, and that of course the resulting observed distribution is something like an ellipse. In practice, we have not found a convincing demonstration of an elliptical larval distribution, although the Rhodamine-B dye tracer distributions of Talbot (1977) do resemble ellipses. As Munk et al. (1986) state, it is not always possible to obtain reasonable regressions of ellipses; in many cases, the fitting of ellipses can only be described as gross distortions of observations. Talbot (1977) attempted to account for the irregular distortions to the distributions by calculating the area enclosed between isolines and equating these to equivalent circular areas (Joseph & Sendner 1958). This technique is only valid for isotropic horizontal diffusion. The method proposed here relaxes the assumptions inherent in the elliptical spread model but with the requirement for measure-

ments to be made at 2 periods: one for initialization and the other for comparison with predictions. A parameter for the time of origin is not required with our method. As we demonstrate with our estimations, parameters are allowed to, and do, vary with time and there is no requirement for the measured distribution to be elliptical. Parameters are, however, required to be constant between the initialization and prediction periods.

Day/night differences in catches were observed in this patch of *Thunnus maccoyii* larvae (Davis et al. 1990), which was attributed to avoidance. It is likely that day/night differences in avoidance are only part of the total avoidance problem (Smith & Richardson 1977). As net avoidance is size-dependent (Barkley 1972, Murphy & Clutter 1972), the abundance of the larger, presumably older, larvae will be underestimated, as the larvae's ability to avoid the net will have improved over the period that the estimate was made. We have no information on the change in net avoidance ability with size for any tuna species. We can, however, investigate the sensitivity of estimates of Z to changes in the catchability of the larvae, which in the absence of advection and diffusion is given by:

$$Z = -\frac{1}{t} \ln \left(\frac{\hat{N}_2}{\hat{N}_1 f} \right), \quad (4)$$

where \hat{N}_1 = density (no. m^{-3}) of larvae observed in period 1; \hat{N}_2 = density observed in period 2; f = ratio of catchabilities of the larvae at the 2 time periods, t = time difference (d) between periods; and the unit of Z is d^{-1} .

The relationship between apparent mortality and true mortality has been plotted for changes in catchability of 100 to 50 % for $Z = 0.66 d^{-1}$ determined between periods 1 and 2 (Fig. 7). It seems unlikely there would be a 50 % reduction in catchability between periods 1 and

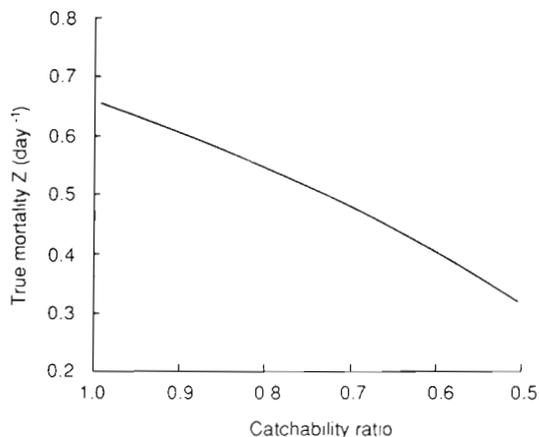


Fig. 7 *Thunnus maccoyii*. Effect of a change in catchability of larvae between survey periods on estimates of instantaneous mortality (Eq. 4). True mortality where there is no change in catchability (catchability ratio = 1.0) is $0.66 d^{-1}$

2, as the larvae would only have grown from about 3.7 mm to 4.5 mm in that time (Jenkins & Davis 1990). If the catchability between periods were reduced by 25 % then Z would still be greater than $0.5 d^{-1}$. It is more likely that changes in catchability between periods 2 and 3 would have a greater effect on apparent mortality than between periods 1 and 2, as the larvae were larger and may have been reaching a size where changes in avoidance ability were more apparent. However, this is not reflected in apparent mortality which was lower between periods 2 and 3 than 2 d earlier. It is nonetheless possible that a decrease in catchability was masked by a true lower mortality.

The value of $Z = 0.66 d^{-1}$ (a daily survival rate of 52 % d^{-1}) determined between periods 1 and 2 would appear to be our most reliable estimate of the upper limit of instantaneous mortality for *Thunnus maccoyii* larvae; the lower limit is probably about $0.5 d^{-1}$ (a daily survival rate of 60 % d^{-1}). These larvae are past the yolk sac stage, having survived the critical period of transition from endogenous to exogenous feeding (Hjort 1914, May 1974). Their survival rate is much lower than the range of 85 to 97 % d^{-1} for marine post-yolk-sac larvae reviewed by Dahlberg (1979), although many of those reviewed were clupeiform species with a much longer larval duration: 50 to 130 d compared to 20 d in *T. maccoyii* larvae (Jenkins & Davis 1990). Our estimate of survival corresponds more closely to estimates of 55 % for *Trachurus symmetricus* larvae (Hewitt et al. 1985) at about the equivalent stage of development. Young & Davis (1990) suggested that a significant reduction in prey populations would have been likely near the centre of the patch of *T. maccoyii* larvae, on the basis of larval abundances, larval feeding rates, and prey abundance, and that competition for food would have been possible. Jenkins et al. (in press) demonstrated the density-dependence of larval growth through competition for food. Under conditions of slower growth, cumulative mortality would be higher because the larvae would remain longer within a predatory field (Shepherd & Cushing 1980). This would not affect the estimation of instantaneous mortality, but it is possible that starvation contributed to the high mortality rate observed in these larvae.

It is useful to consider the origin of this patch of *Thunnus maccoyii* larvae, as it provides us with information on the spawning of the adults. We estimated that 3.58×10^{10} larvae 7 to 8 d old were in the patch in period 1. We do not know the cumulative mortality that had occurred from spawning up until 7 d. Richards et al. (1981) and McGowan & Richards (1986), based on the survival estimates compiled by Dahlberg (1979) for 6 species of marine larvae, used a value of $Z = 0.0996 d^{-1}$ to estimate cumulative mortality in 9 d old *Thunnus thynnus* larvae in the Gulf of Mexico. This

was equivalent to a 40.8 % survival rate from spawning to 9 d. Our findings suggest that such a high survival rate would be unlikely for *T. maccoyii*. We estimated survival of 7 to 8 d larvae over a 2 d period to be 27 % (37 % if there were a 25 % reduction in catchability). One would not expect the daily mortality rate from spawning up until 7 d to be less than that observed in 7 d old larvae as there is evidence that mortality rates decline exponentially with increasing size (Peterson & Wroblewski 1984, McGurk 1986). If instantaneous mortality averaged over the entire period from spawning to 7 d was $Z = 0.66 \text{ d}^{-1}$ then survival would only be about 1 %. Our estimate of the number of eggs spawned over the 2 d using $Z = 0.66 \text{ d}^{-1}$ is 3.63×10^{12} eggs. Kikawa (1964) estimated fecundity to be 15×10^6 eggs in a 158 cm (80 kg) fish. The size range of adults caught on the spawning ground has been reported to be 135 to 180 cm with a sex ratio of 1.2 males : 1 female (Robins 1963). Assuming total spawning and that the average size of fish was 158 cm, then ca 5×10^5 fish (40 000 t) were involved in the spawning event that generated the patch. While this estimate is very crude and subject to unassessed error it seems very high, as the parental biomass is considered to be 120 000 to 240 000 t (W. Hearn pers. comm. 1990). The mortality rate observed during this study may have been higher than normal due to factors such as starvation, as discussed previously. Using this value to estimate cumulative mortality would overestimate the number of eggs produced. Alternatively, parental biomass estimates may be too low. Even if cumulative mortality was half this value ($Z = 0.33 \text{ d}^{-1}$) then 5.3×10^4 fish (4200 t) were involved in this spawning event, indicating that spawning in *T. maccoyii* may take place in very large schools. Acoustic surveys of the spawning grounds usually detect large tuna (species unknown) as individual marks or in small schools rarely exceeding 200 individuals (Yukinawa & Miyabe 1984). No schools of the magnitude estimated in this study have been reported, so it seems likely that adults may come together briefly for spawning and then disperse. It is not known whether this major spawning episode was unique or whether similar spawning events occurred in a number of places within the spawning area, or whether spawning on this scale occurred at other times during a protracted spawning period, as sampling has not yet been carried out at the appropriate temporal and spatial scales. Even if such sampling can be carried out it is imperative that proper account be taken of advection and diffusion in calculations of mortality. The standard paradigm based on a single elliptical model is unacceptable, especially in the open ocean where the physical processes in the near-surface layers change rapidly and sampling is difficult. The method proposed here is an attempt to provide improved estimates of mortality.

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