

CSIRO
Division of Fisheries and Oceanography

REPORT 113

***In vivo* Chlorophyll *a* Fluorescence
in the Vicinity of Warm-core Eddies
off the Coast of New South Wales
4. December 1978**

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and D. J. Vaudrey

1980

COMMONWEALTH SCIENTIFIC AND INDUSTRIAL RESEARCH ORGANIZATION
DIVISION OF FISHERIES AND OCEANOGRAPHY
P. O. BOX 21, CRONULLA, NSW 2230

National Library of Australia Cataloguing-in-Publication Entry

Tranter, D.J.

In vivo chlorophyll *a* fluorescence in the vicinity of warm-core eddies off the coast of New South Wales. 4. December 1978.

(Division of Fisheries and Oceanography report; 113)

Bibliography

ISBN 0 643 02512 X

1. Marine biology - New South Wales. 2. Chlorophyll.
3. Fluorescence. I. Parker, R.R., joint author. II. Vaudrey, D.J., joint author. III. Title. (Series: Commonwealth Scientific and Industrial Research Organization. Division of Fisheries and Oceanography. Report; 113)

574.92'5'78

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Printed by CSIRO, Melbourne

IN VIVO CHLOROPHYLL *a* FLUORESCENCE IN THE VICINITY OF WARM-CORE EDDIES OFF THE COAST OF NEW SOUTH WALES
4. DECEMBER 1978.

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CSIRO Aust. Div. Fish. Oceanogr. Rep. 113 (1979)

Abstract

This is the last of a series of reports describing the natural history of a warm-core eddy in the southwest Tasman Sea as it developed from the well mixed isothermal state to the stratified summer state in the latter part of 1978. During this period, the eddy (eddy "F"), making approximately one rotation per week, and moving through a broad anticlockwise arc between Jervis Bay and Eden, retained the same body of water, as judged by its Temperature-Salinity properties and conservative buoy trajectories.

This water body developed a bloom of phytoplankton about a month later than the surrounding sea. This bloom reached a peak in November, and by December it was concentrated at the centre of the eddy, subsurface, near the summer thermocline (depth, approx. 50 m). Estimates based on nitrate uptake suggest that, over this period, eddy "F" was about one-fifth as productive as the Peru upwelling. The basis of this production appears to be vigorous and prolonged convective overturn in winter and in spring. This mixes nutrients from as deep as 300 m throughout the euphotic water column.

As on earlier cruises, there was evidence in December of a diel cycle in 'photosynthetic efficiency' (ϕ_p). Evidence was obtained that, in line with expectation, ϕ_p was correlated with ^{14}C uptake under constant light.

INTRODUCTION

In early 1978 a large warm-core eddy formed out in the Tasman Sea, probably from a meander of the East Australian Current observed by Cresswell in February 1978 (Fig. 1). This large eddy divided into two smaller eddies designated "E" and "F" sometime between May and September 1978 (Boland personal communication). In September 1978, "E" and "F" were surveyed by means of *in vivo* chlorophyll *a* fluorescence (Lorenzen 1965; Tranter *et al.* 1979a, b), and "F" was monitored again in October and November 1978 (Tranter *et al.* 1979b,c). This is the

latest report of the autotrophic natural history of eddy "F". The observations span the period from late winter, through spring, to early summer.

In September, when biological observations began, eddy "F" lay to the east of "E". At that time, "E" and "F" were closely associated, both spatially, and in their physical and biological properties (Tranter *et al.* 1979a). "F" was in the characteristic winter state with a deep mixed layer (> 200 m) through which nutrients, for example, were well distributed. Surface nitrate exceeded $2 \mu\text{g-at l}^{-1}$, a concentration typical of some

coastal upwellings (Rochford 1972). This was the first indication we had that our concept of warm-core eddies as water bodies drawn from 'nutrient impoverished' parent water masses might need to be modified.

There was less phytoplankton in the eddy in September compared with that in the surrounding sea, and we concluded that this was probably the consequence of light limitation. Whereas in this part of the ocean the depth of the euphotic layer ($> 1\%$ ambient surface light) is 70-100 m (Jitts 1959), the isothermal layer in eddy "F" extended to at least twice this depth. Under such circumstances, phytoplankton from surface waters is carried to depths where photosynthetic gains within this mixed layer are cancelled out by respiration losses. Beyond a certain critical depth (Sverdrup 1953; Murphy 1962), no net growth of a phytoplankton population can take place. We found the phytoplankton crop outside the eddy ($F_M > 200$ TU) to be higher than that inside ($F_M < 150$ TU), probably because of earlier water column stability.

The October cruise did not cross the centre of eddy "F" but entered far enough for us to recognize that changes had occurred since September. From its September position east of Eden, it had moved northwest towards Jarvis Bay (Fig. 2) (Cresswell unpublished data). The surface standing crop within the eddy ($F_M > 400$ TU) was now greater than in the sea outside (200-300 TU), the reverse of the September situation. The nitrate content of the euphotic layer ($< 1 \mu\text{g-at N } \ell^{-1}$) had substantially decreased since September, apparently as a consequence of a phytoplankton bloom. XBT traces in the area and data from Nansen stations inside the eddy showed that a summer thermocline had not yet formed.

* F_M = maximized fluorescence,
TU = "Turner Units".

In November, Cresswell (Cruise Summary SP15/79) observed that eddy "F" had advanced along its anticlockwise path and was now located east of Eden. The standing crop inside the eddy ($F_M > 400$ TU) was greater than in the sea outside ($F_M < 200$ TU). A summer cap had established, extending to a depth of about 50 m. There was more nitrate at the centre of the eddy than had been observed (offcentre) in October. November concentrations (c. $1 \mu\text{g-at } \ell^{-1}$), while barely half that observed in September, were higher than would have been expected from the computed depletion rate between September and October. There appeared at first sight to have been some further enrichment between October and November from a source and/or mechanism not yet identified.

This was the situation prior to the December cruise. The following questions were of immediate interest -

- How much exchange took place across the boundaries of the eddy?
- Was there enough nitrate present within the eddy to account for the spring phytoplankton bloom?
- What was the turnover rate of nitrate-N in the water column?
- Was surface phytoplankton production limited in December by nutrients or by grazing?
- What is the likely sequence of events the following year?

MATERIALS AND METHODS

Two ships were involved in this summer exercise, R.V. "Sprightly" and F.R.V. "Courageous". Both provided opportunity for observations on *in vivo* chlorophyll fluorescence. "Courageous" started earlier than "Sprightly" and finished later, the observations being separated into two periods by an intervening southerly storm. The first set of observations extended from 28 November to 4 December, the second set from 8 December to 13 December. "Sprightly" worked in the vicinity of the eddy from 1 December to 7 December.

In general, observations on "Sprightly" were carried out in a similar way to that reported earlier (Tranter *et al.* 1979c). Surface *in vivo* fluorescence (F_A) was measured along the ship's track using a flow-through Turner Design fluorometer. Periodically the pumped stream was dosed with DCMU (Diuron) to measure maximum fluorescence (F_M) which estimates autotrophic biomass (Slovacek and Hannan 1977). We are presently forced to ignore the fluorescence contribution of free photopigment and estimate photosynthetic efficiency (ϕ_p) as $(F_M - F_A)/F_M$ (Samuelsson and Oquist 1977). The Turner Design fluorometer was also used in batch mode to measure fluorescence of water samples obtained with Niskin bottles. An *in situ* fluorometer (Variosens II) was used for continuous vertical profiles of F_A , to 200 m.

The water samples for analysis of *in vivo* chlorophyll fluorescence were aliquots from the same Niskin bottle samples from which colleagues drew aliquots for measuring nutrients, primary productivity, detritus content and muramic acid. The samples were stored in dark brown bottles, at room temperature, until measured, usually about an hour after collection. The same aliquot was used for determining both F_A and F_M . Samples were drawn periodically for chlorophyll extraction and phytoplankton preservation, from the Turner fluorometer effluent. In addition, some chlorophyll extractions were made on samples from the Niskin bottle casts. Extra Niskin samples were taken at points where the Variosens profile showed a peak of *in vivo* chlorophyll fluorescence.

The system for measuring *in vivo* chlorophyll fluorescence used on "Courageous" was different and less sensitive than that used on "Sprightly". The Variosens I (Früangel and Koch 1976), not previously used in this series of cruises, and designed for observations *in situ*, was modified

for laboratory on-stream analysis as in the Turner. A Turner cuvette and plumbing attachments were used on line with the ship's seawater supply to provide an excitation chamber for the Variosens. This fluorometer rarely came on scale with surface water except in port and in the region of the eddy. Its main usefulness was as a qualitative indicator of high autotrophic biomass in surface water and as a measure of *in vivo* chlorophyll fluorescence at depth, using water samples from Nansen bottle casts. For the latter purpose, only F_M was measured. Samples from Nansen bottle casts were stored in dark brown bottles dosed with DCMU. The use of Variosens I, for recording surface fluorescence underway, was based solely on F_A . The noise to signal ratio was too great for reliable underway measurements of F_M to be made.

Satellite tracking data were not available for buoys released in the vicinity of eddy "F". Its location and movements during the study period were determined from XBT casts.

RESULTS

Figure 3 shows the isotherm topography at 250 m, an indication of the location and boundaries of the eddy. The centre lay at about $36^{\circ}30'S$, $151^{\circ}40'E$. Its diameter, as defined by the 15° (T_{250}) isotherm, was about 120 km. The eddy moved anticlockwise towards the coast during the course of the study, possibly as a consequence of the heavy storm between 5 December and 12 December. For this reason the isotherm topography is presented for two periods: before and after the storm (Fig. 3a, 3b).

Figure 4 shows the track of "Sprightly" superimposed on the isotherm topography, and Fig. 5 the track of "Courageous" similarly superimposed.

The underway records of surface *in vivo* chlorophyll fluorescence from

R.V. "Sprightly" are shown in contour form in Fig. 6. The "Courageous" observations (F_A) are not presented because of their relatively low sensitivity but they are consistent with those from "Sprightly". For the first time since our observations began in September, surface fluorescence did not closely follow the T_{250} contours of the eddy. Instead, high values (> 200 TU) were aggregated towards the southern sector of the eddy, the highest (> 400 TU) lying south of the eddy centre. Some of the lowest values that were recorded (< 100 TU) formed a band, running E-W at about $36^{\circ}24'S$, crossing the T_{250} $17^{\circ}C$ isotherm. North of the eddy the standing crop was lower to the west of $151^{\circ}E$ than to the east, but the records are too sparse to say how far this low extended across the continental shelf.

In September, before the summer cap had formed, phytoplankton in the eddy were distributed through the upper layers, such that surface values of F_M were a good predictor of the subsurface water column mean. This was no longer the case in December (Fig. 7). Frequently there were high values at depth when surface values were relatively low.

The distribution of chlorophyll fluorescence with depth at a number of "Sprightly" stations is shown in Fig. 8. These profiles were determined in two entirely different ways: *in situ* with the Variosens; and on board, with the Turner, from the Niskin samples (F_M). Although profiles by the two methods show a close correspondence, Variosens and Turner results are not strictly comparable. Variosens F_A is useful, as shown in Fig. 8, for indicating the approximate distribution of the standing crop, e.g. where to sample, but not to estimate standing crop *per se*. With our present techniques, this must be done with either bottled or pumped samples. However, the relative positions of the peaks were generally located by each method

at about 50 m, sometimes higher (stations 291, 292), sometimes lower (297, 298).

Four sections across eddy "F" were selected (Fig. 9) to examine the vertical patterns of distribution of phytoplankton, temperature and nitrate: (1) the N-S "Sprightly" section from station 297 (beyond the northern edge of the eddy) to station 302 (close to the eddy's centre); (2) the W-E "Sprightly" section from station 290 (inside the eddy near the western boundary) to station 296 (well outside and east of the eddy); (3) the S-N "Courageous" section from station 11 (close to the eddy's centre) to station 18 (outside the eddy, to the north); and (4) the E-W "Courageous" section from station 19 (near the centre) to station 26 (outside the eddy to the west).

Figure 10 shows the first section (297/302). The maximum phytoplankton concentration was found in the centre of the eddy at about 50 m (> 400 TU). At the surface, the phytoplankton was very sparse. At the edge of the eddy (station 299) the plankton was distributed rather uniformly to about 75 m ($F_M \approx 225$ TU).

The "Sprightly" W-E section (290/296) (Fig. 11) traversed the whole eddy just north of centre, along the 'corridor' of low F_M surface values shown in Fig. 6. A subsurface (50-75 m) peak of higher standing crop (> 400 TU) was evident just east of centre. At about the same depth, a second peak was evident beyond the eastern edge of the eddy (station 296), associated with shoaling of the isotherms and nitrate isopleths. At the centre surface phytoplankton was sparse.

The two "Courageous" sections are shown in Fig. 12 and 13. The same general pattern was observed, viz. subsurface peaks at the eddy centre and just beyond the eddy edge. Both peaks on section 19/26 (E-W) were located at about 50 m (Fig. 13), the outer peak on section 11/18 at 25 m

(Fig. 12). Nitrate data are not available for these sections.

In past reports (Tranter *et al.* 1979a-c) we have described the pattern of photosynthetic efficiency $\left(\frac{F_M - F_A}{F_M}\right)$ in the eddy area, on the assumption that this would prove to be a measure of phytoplankton growth rate as it has been shown to be in the laboratory (Samuelsson and Öquist 1977). On this cruise, we had the opportunity to test this assumption by comparing ^{14}C uptake under constant light with $F_M - F_A$, the increase in fluorescence yield after inhibiting photosynthesis with DCMU. The results are shown in Fig. 14. It is clear that the two parameters are related, the error involved in predicting one parameter from the other being less than 25%; therefore photosynthetic efficiency, measured in this way, represents a rate function which can be used as a measure of phytoplankton growth.

As in our earlier reports, we have first removed the diel effect before considering the surface pattern of photosynthetic efficiency in the eddy area. Figure 15 shows the diel cycle as a faired line through the 3-hour means of all available time/ ϕ_p data ($\phi_p = (F_M - F_A)/F_M$). A multimodal curve is evident similar to those presented in earlier reports. It is characterized by early morning and late evening maxima, a pronounced midday minimum, and a slight minimum during midnight hours. This curve was used to compute coefficients to remove the diel effect by standardizing ϕ_p at 2400 hr ($\hat{\phi}_p$). The surface distribution of $\hat{\phi}_p$ in the eddy area is shown in Fig. 16. This distribution forms a complex pattern. To the north of the eddy, $\hat{\phi}_p$ decreased seaward and increased towards the eddy.

Throughout this series we have reported our results in fluorescence units, either TU (Turner Units) or VU (Variosens Units),

depending on the instrument used, and have distinguished between samples taken underway by pump from surface waters and those taken from depth by water bottles. However, to allow our results to be expressed in terms of chlorophyll concentrations, we have also provided intercalibration data. Figures 17 and 18 show the relationship between extractable chlorophyll *a* and the *in vivo* chlorophyll fluorescence F_M , Fig. 17 being for surface, on-stream samples (pump) and Fig. 18 for samples from depths to 75 m (Niskin bottles). The regression for surface samples is in this case indistinguishable from that for bottle samples from depth. The relationships are relatively close, showing that F_M can satisfactorily estimate the chlorophyll concentrations.

DISCUSSION

How much exchange takes place across the boundaries of the eddy?

The assumption has been made in this series of studies of warm-core eddy "F" that there was little exchange across the boundaries between eddy and adjacent water masses. This assumption can be tested, to some extent, by examining the T-S characteristics of the eddy between September and December (Fig. 19).

For this purpose, stations were selected from each cruise (SP12, 14, 15 and 16/78) which lay at or near the centre of the eddy, as defined by T_{250} symmetry. For comparison, adjacent stations well outside the boundaries of the eddy were also chosen. Finally, the station at the edge of the meander thought to be the origin of the eddy that gave rise (by division) to eddy "F" was also considered. The values shown extend to 200 m; because the eddy is a lens, samples from greater depths could lie outside the boundaries of the eddy. Figure 19 shows that samples from eddy stations formed a tight parcel of T-S values lying

between 17-19°C and 35.55-35.65‰ S. By contrast, stations outside the eddy covered a temperature range of 12-22°C and a salinity range of 35.00-35.60‰.

The T-S properties of the meander station (see Fig. 1) lie in between. However, except for the 200 m sample, they all lie close to the salinity of the eddy samples (viz. 35.5-35.6‰), while their temperatures (18-23°C) are somewhat warmer. Godfrey (personal communication) believes that enough cooling could take place after separation of the meander from the East Australian Current to explain the temperature difference.

In summary, the T-S properties of eddy "F" between September and December 1978 are consistent with the proposition that this eddy was derived from the East Australian Current meander observed by Cresswell on "Sprightly" Cruise 3/78 (February) and that there was little exchange across its boundaries of any other type of water.

Was there enough nitrate present to account for the phytoplankton bloom?

If the waters from which warm-core eddies are derived (mainly west central South Pacific water) are as poor as is commonly believed (Rochford 1959; Jitts 1965), and if there is so little subsequent exchange of new water across the boundaries of the eddy, then what is the explanation for the spring phytoplankton bloom? The answer appears to lie in the internal dynamics of the eddy.

In seeking to explain this phenomenon we have assumed that phytoplankton production is limited by either light or nutrients, and we have chosen nitrate-N for special consideration. Figure 20 shows the distribution of nitrate with depth in eddy "F" between September and December, together with that of the meander from which the eddy was probably derived. There were spectacular changes.

In February, the meander was low in nitrate ($< 0.5 \mu\text{g-at } \ell^{-1}$) above about 75 m, and high in nitrate ($> 4 \mu\text{g-at } \ell^{-1}$) below about 150 m. In September, when the water column was isothermal to nearly 300 m, the nitrate content, as would be expected, was relatively uniform with depth and concentrations of the order of $2-4 \mu\text{g-at } \ell^{-1}$ extended all the way to the surface. During October, November and December the nitrate concentration at depth remained relatively constant but became reduced near the surface to levels as low as in the February meander ($< 0.5 \mu\text{g-at } \ell^{-1}$).

Table 1 establishes a quantitative basis for comparison. Here, integrated values are presented for 0-75 m (the 'euphotic column') and for 0-300 m (the 'mixing column'). General observations in the southwest Tasman Sea by Jitts (1959) and observations on Cruise SP16/78 by Scott (personal communication) indicate that the 1% light level is located at about 75 m. The mixing column estimate is based on the maximum observed depth of the isothermal layer in the centre of the eddy in September.

Table 1 shows, not only the mean nitrate-N values for euphotic column and mixing column, but also, where available, the mean concentration of 'phytoplankton nitrogen' based on N:chlorophyll *a* ratios determined by Newell and Bulleid (1975). Other forms of nitrogen are not considered.

Although the euphotic column of the meander was low in nitrate, computation showed that there was enough in the mixing column as a whole to explain the high values observed throughout the isothermal layer the following September. Likewise, there was enough in the euphotic part of the September water column to explain the subsequent October bloom; it does not need to be explained in terms of nutrient input from outside the boundaries of the eddy.

What was the turnover rate of nitrate-N in the euphotic column?

Assuming a constant rate of phytoplankton production between September and October, nitrate-N in the euphotic column was used up at the rate of about $6 \text{ mg-at m}^{-1} \text{ day}^{-1}$ (Fig. 21). At this rate nitrate would disappear within a week or so. However, in November we found more nitrate, not less, than the previous month. To account for this in the context of a continuing rate of usage of $6 \text{ mg-at N m}^{-2} \text{ day}^{-1}$, a total amount of about 225 mg-at m^{-2} would have had to be present in the euphotic column at the eddy centre at the end of October. This is exactly the same as the September level at the eddy centre when the water column was isothermal.

Perhaps the bloom that we encountered off-centre in October was progressing from periphery to centre; that is, there had been no significant nutrient uptake yet at the eddy centre.

A turnover rate of $6 \text{ mg-at N m}^{-2} \text{ day}^{-1}$ is four times as high as previously recorded in the Eastern Tropical Pacific and about one-fifth that of the Peru Upwelling (Dugdale 1976).

Was surface phytoplankton production limited in December by nutrients or by grazing?

Figure 20 shows that surface nitrate concentration had been reduced by December to levels of the same order as found in the February (1978) meander from which the eddy is assumed to have been derived. There were only $35 \text{ mg-at NO}_3\text{-N m}^{-2}$ in the euphotic column compared with $225 \text{ mg-at NO}_3\text{-N m}^{-2}$ the previous September. By December, the standing crop of phytoplankton was concentrated near the summer thermocline (Fig. 8, 10-13) which marked the boundary between the upper nitrate-poorer waters and the lower nitrate-richer waters.

The most conspicuous grazing components observed in December were swarms of salps, particularly the large species *Thetys vagina* (Fig. 22). Midwater trawls (Brandt, personal communication) frequently took huge catches of this species near the subsurface phytoplankton peak, their stomachs green with phytoplankton. Salp aggregations appeared to be so large relative to phytoplankton and nitrate levels above the thermocline, that the availability of nutrients within the euphotic column may well have been determined by nutrient recycling associated with the grazing process.

What is the likely sequence of events in late summer and the following year?

It seems likely that the standing crop will continue to diminish within the summer cap and that the subsurface peak will accompany the thermocline as it deepens, progressively diminishing with decreasing light. Next winter the surface waters will be enriched once again, followed by a second spring bloom. This second bloom will probably be of lower intensity than the first, and this annual cycle of events will continue year by year until the eddy dissipates. To test this hypothesis adequately, it would be necessary to make annual observations of the intensity of the spring bloom on eddies whose positions are continuously tracked. Perhaps the best opportunity to do this would be by means of remote sensing of ocean color using the Coastal Zone Color Scanner. Alternatively, the total amount of N in the water column could be monitored. Since distributions within water columns are complex and 3-dimensional, this would be a formidable task. Comparison of eddies of different ages might yield greater dividends.

ACKNOWLEDGMENTS

We are indebted to Mr B. Scott for the opportunity to compare our measure of photosynthetic efficiency with his measure of productivity by way of ^{14}C uptake under constant light. Discussions with colleagues in Physical Oceanography were a frequent source of stimulus.

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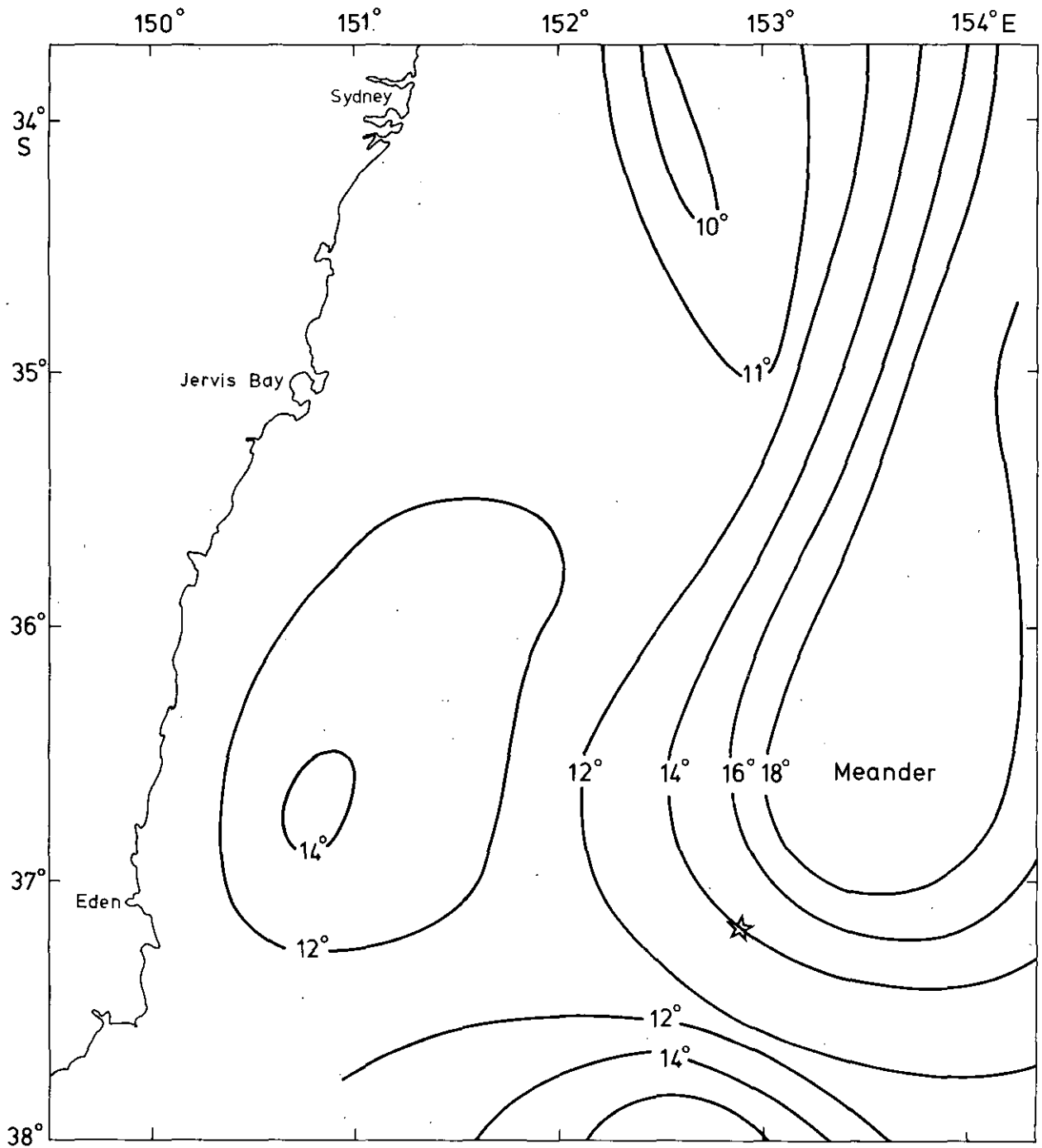


Fig. 1. Location of the East Australian Current meander (February 1978) from which a large warm-core eddy formed, which later divided to form the smaller eddies "E" and "F", T_{250} isotherms (after Cresswell, Cruise Summary SP3/78). * Position of meander hydro station.

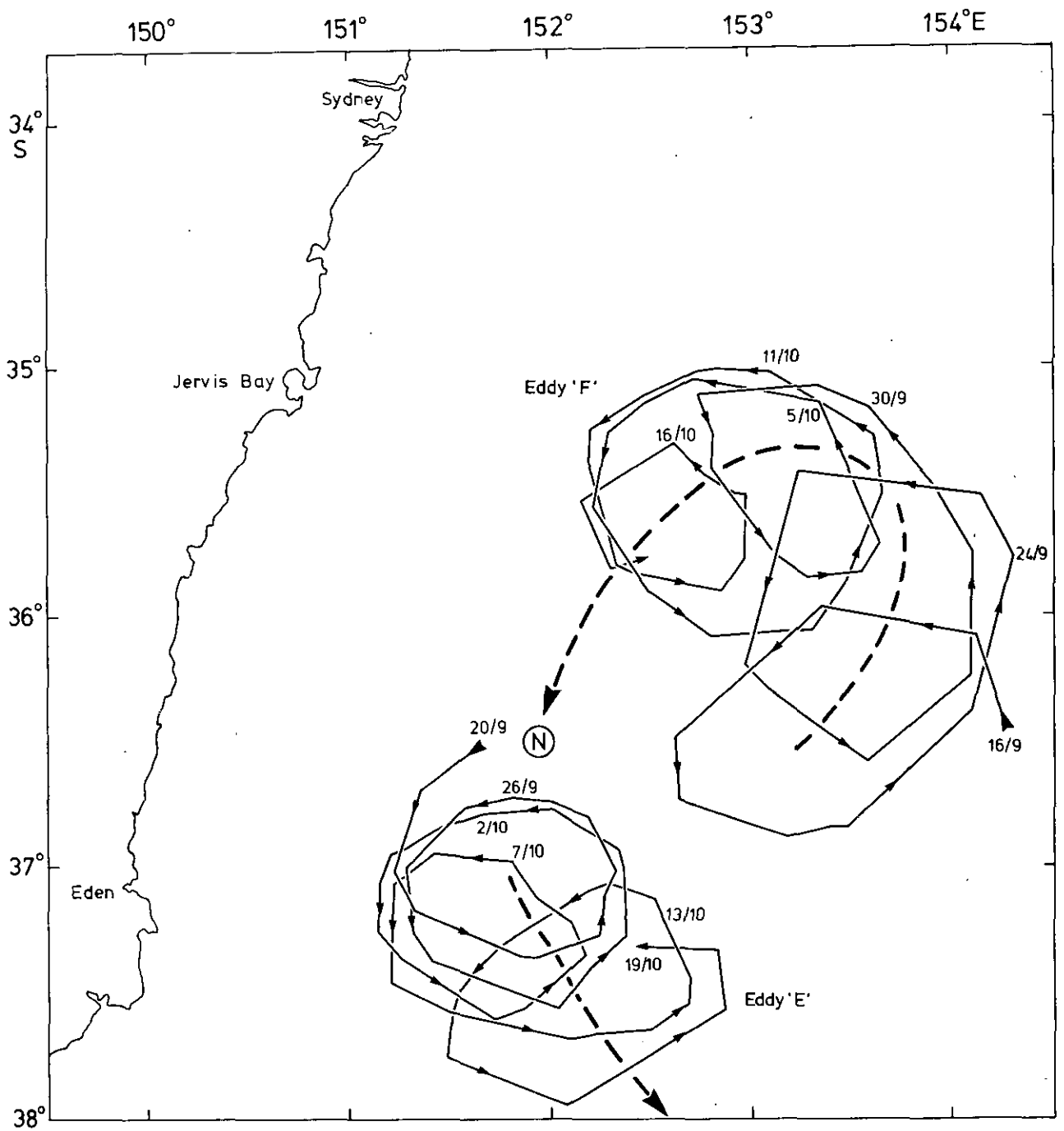


Fig. 2. Paths taken by eddies "E" and "F" between mid-September and mid-October 1978 as indicated by satellite-tracked drifting buoys (After Cresswell, unpublished data). N = November centre of eddy "F".

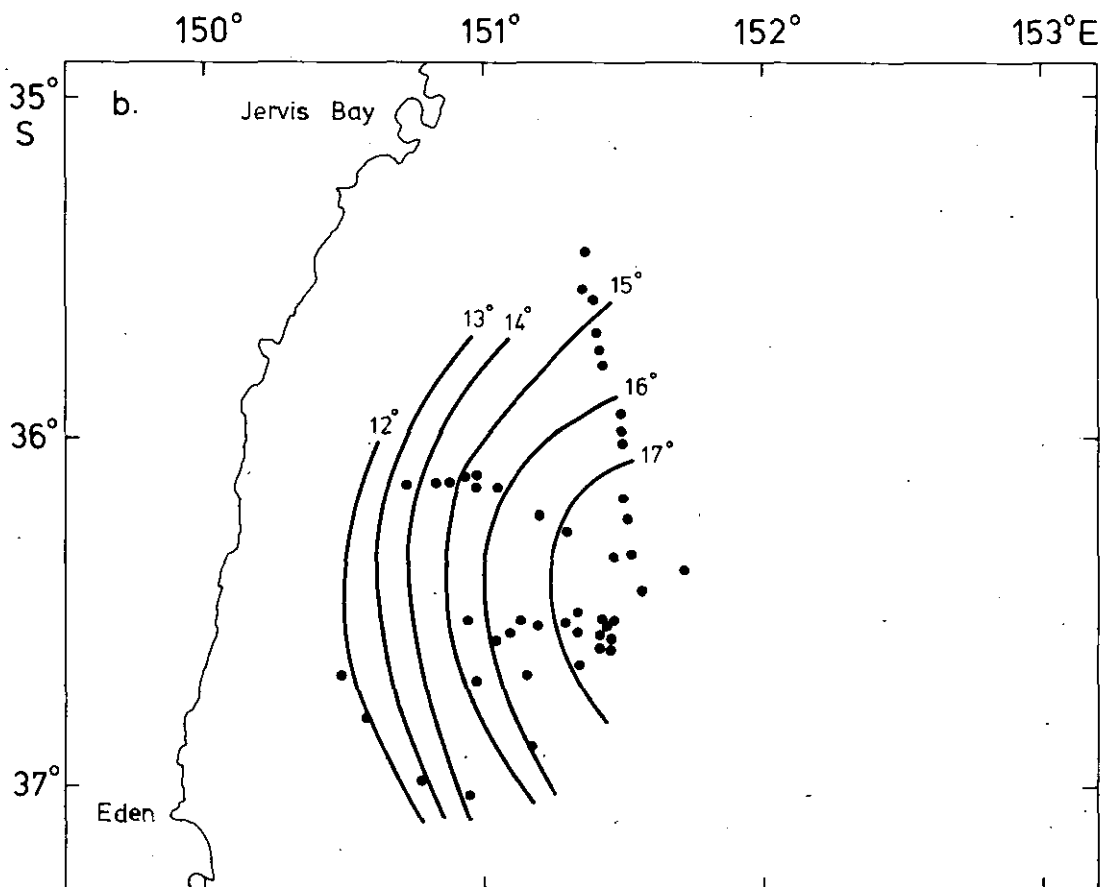
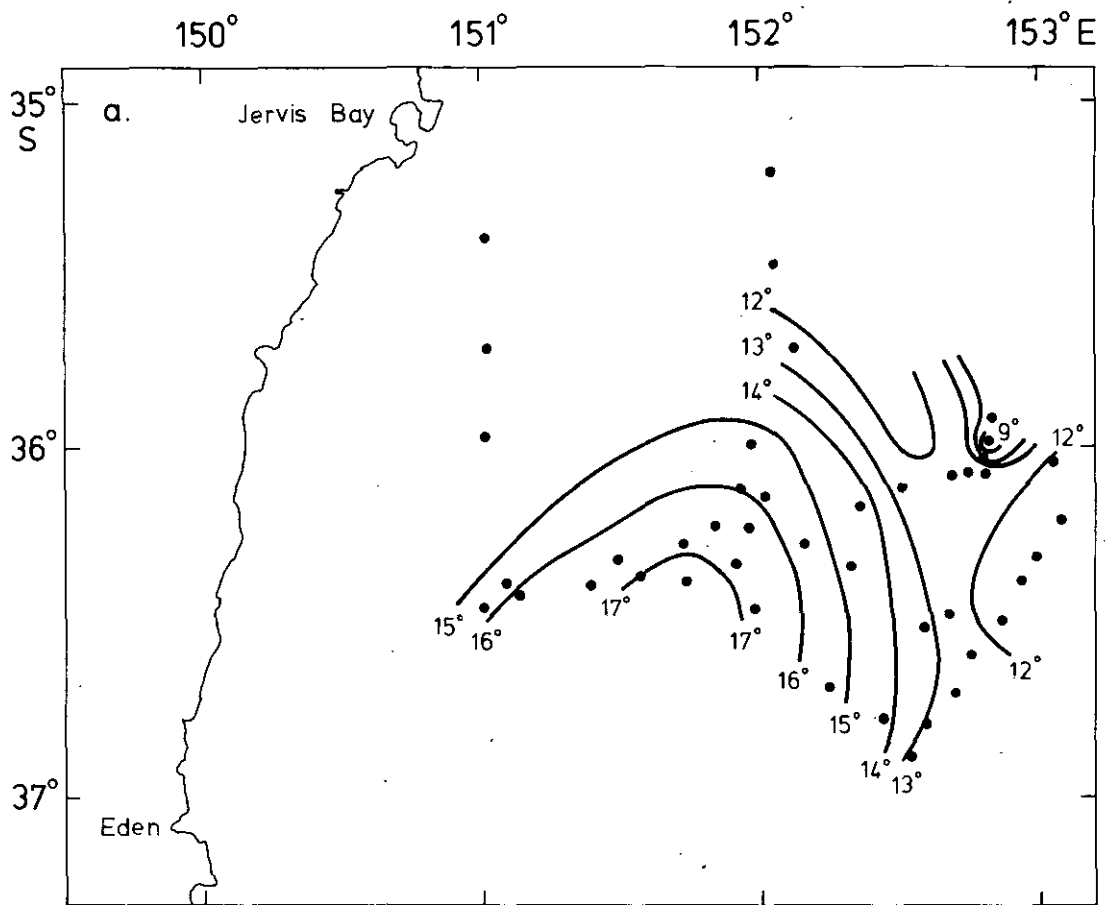


Fig. 3. Location of eddy "F" during the "Courageous" cruise, as indicated by the isotherms at 250 m (T_{250}). The XBT data (positions shown by dots) are contoured for two periods separated by a storm during which the eddy moved appreciably. (a) 28 November-4 December. (b) 8-13 December (1978).

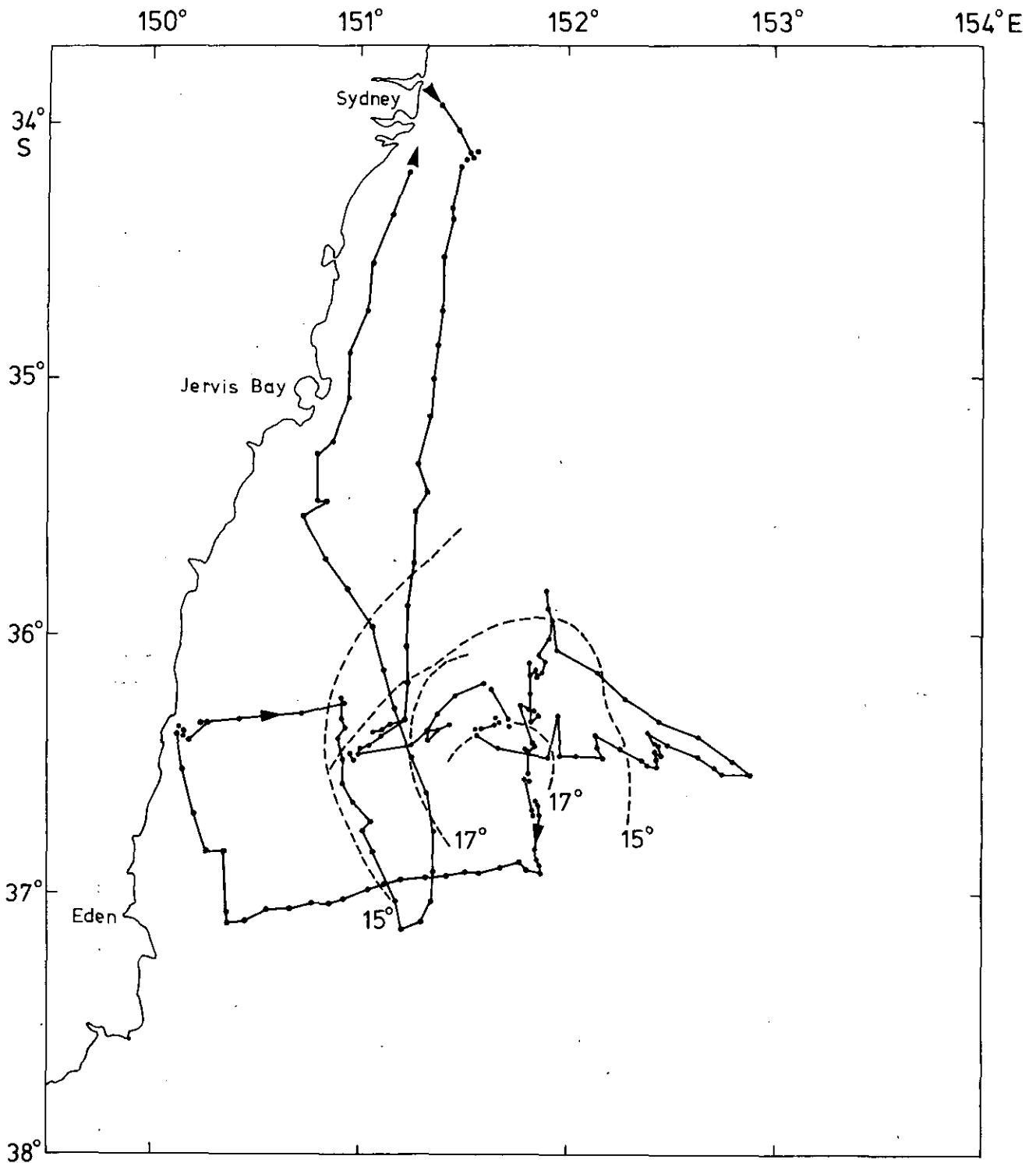


Fig. 4. Track of R.V. "Sprightly" in relation to eddy "F", as defined by T_{250} isotherms ("Courageous" XBT data). The boundaries of the eddy correspond approximately with the 15°C isotherm, and the centre of the eddy with the 17°C isotherm. Dots show the positions where surface F_M was measured.

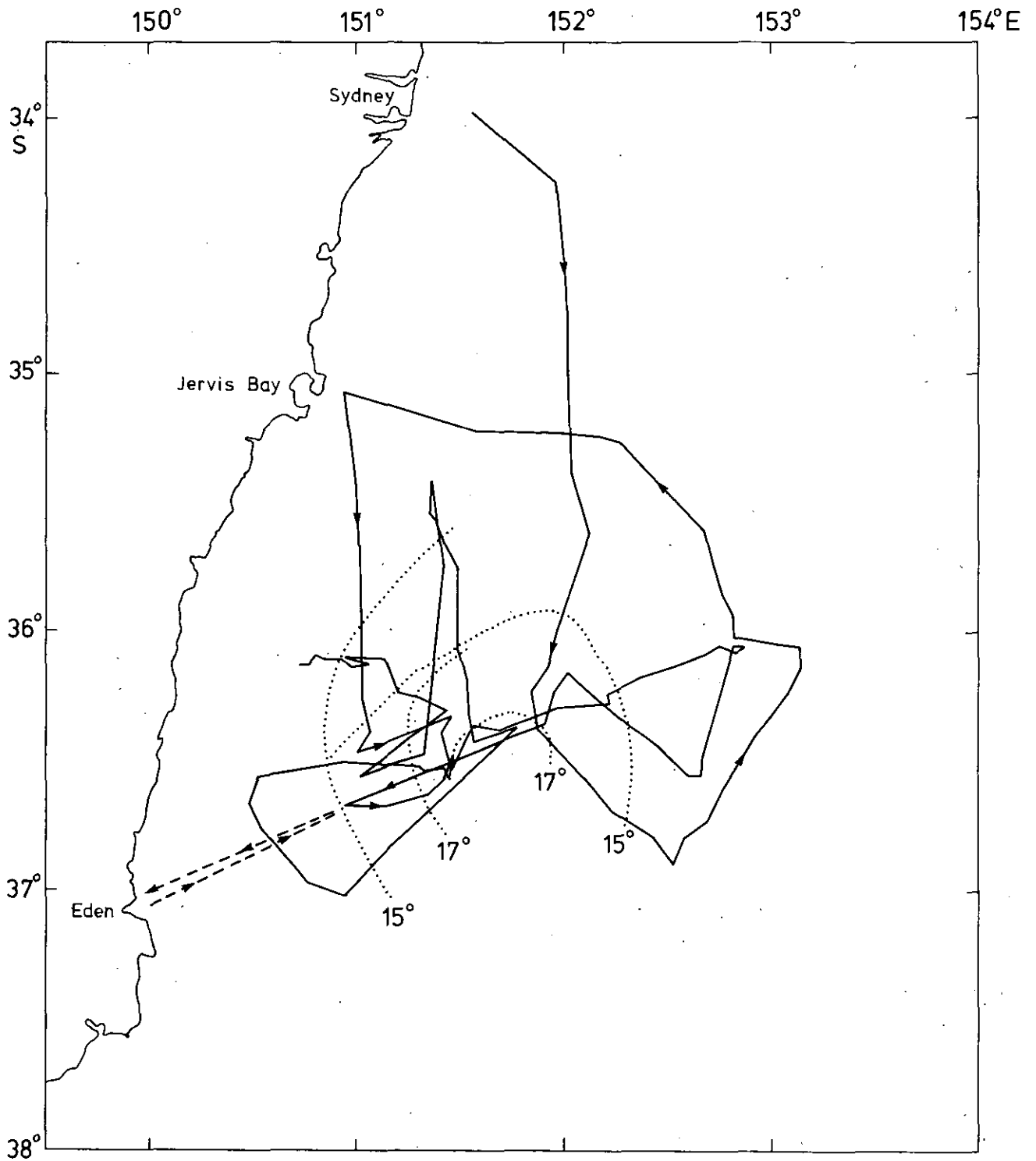


Fig. 5. Track of F.R.V. "Courageous" in relation to eddy "F".

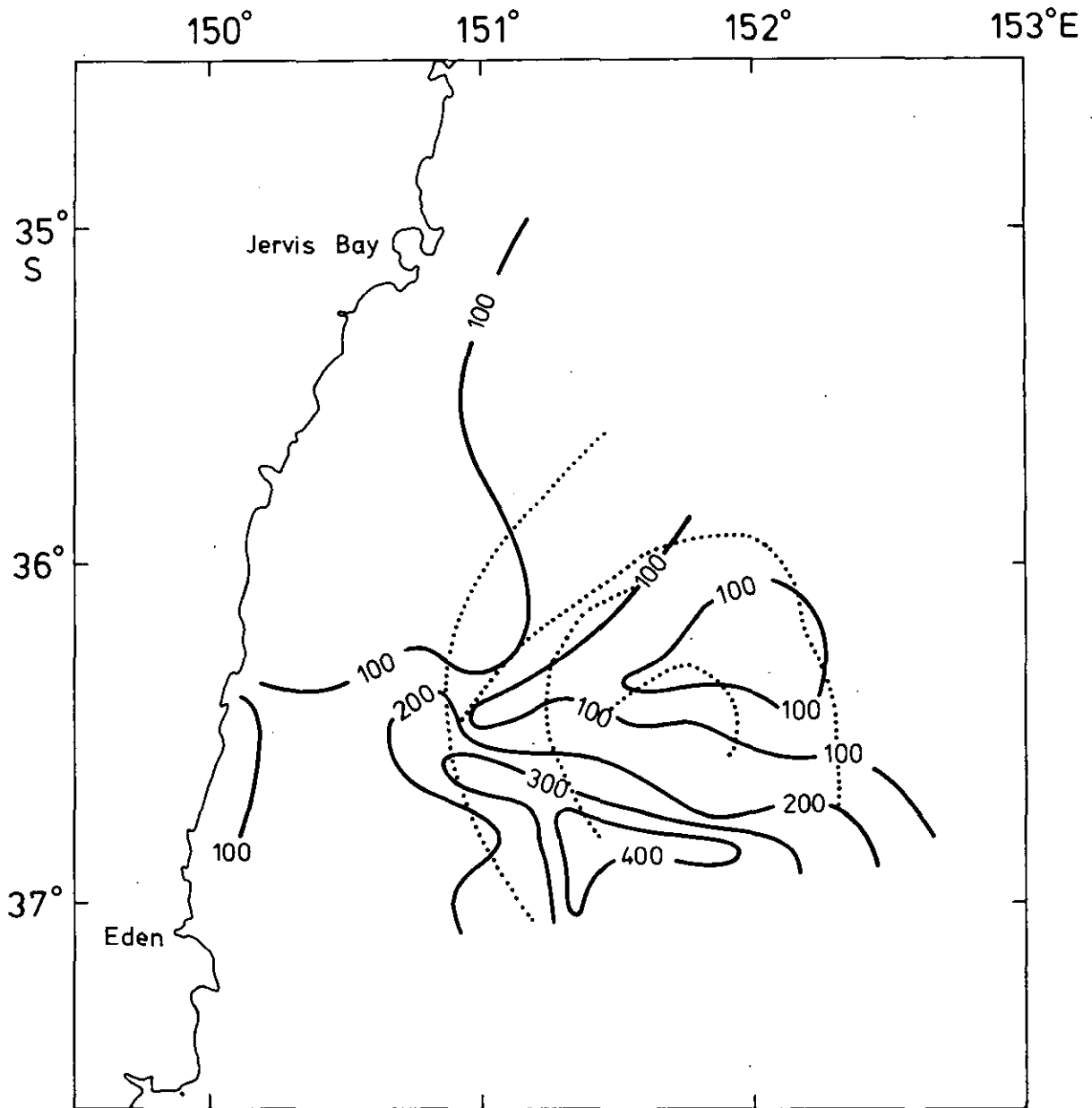


Fig. 6. Surface distribution of F_M (maximized fluorescence) ('Sprightly'). The units are TU (Turner Units).

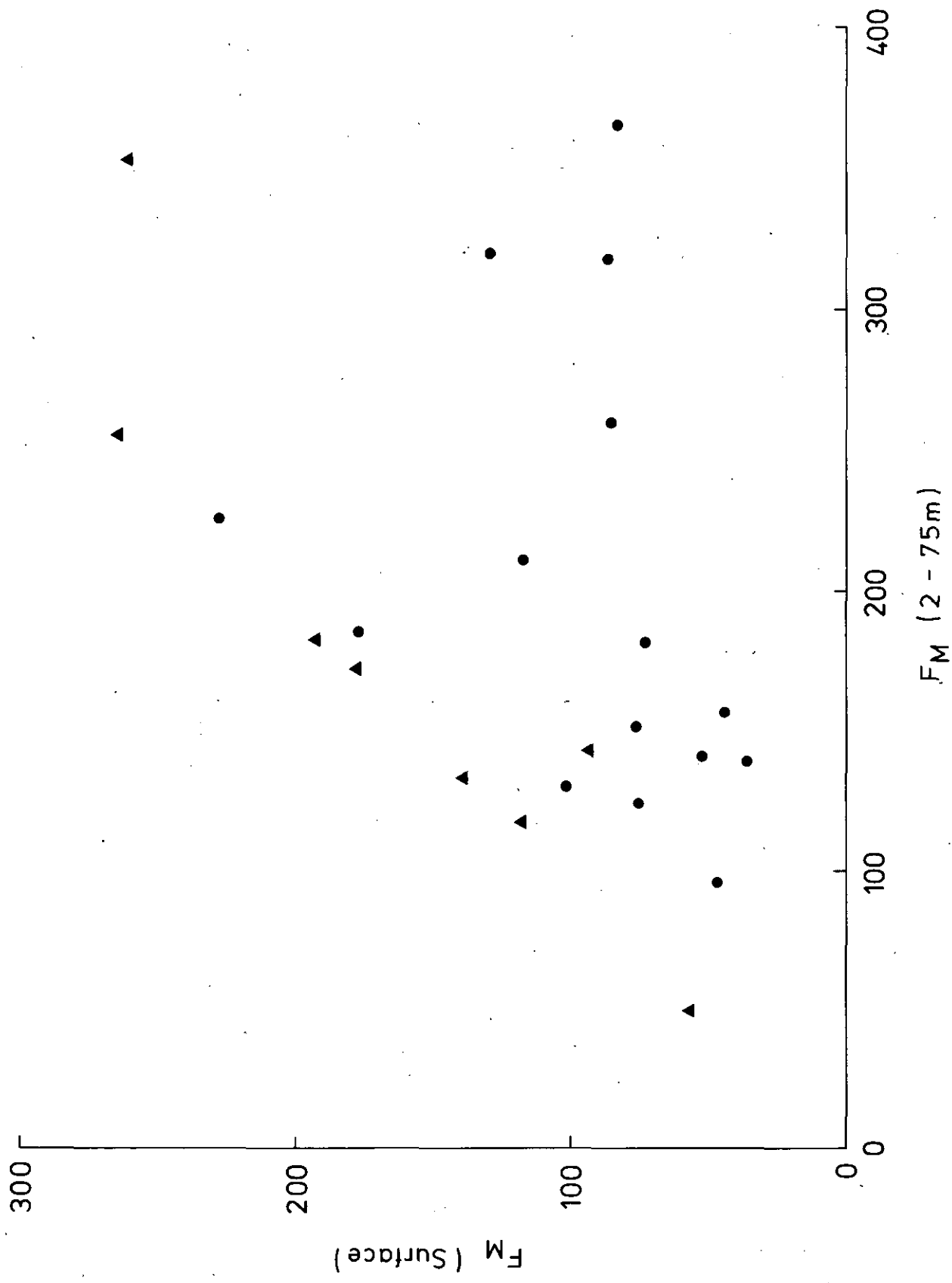
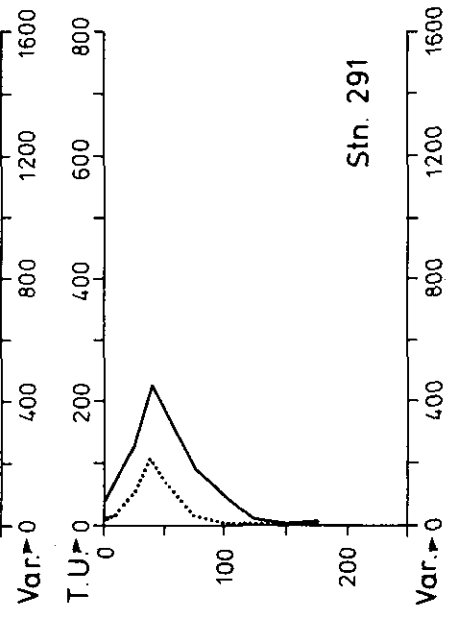
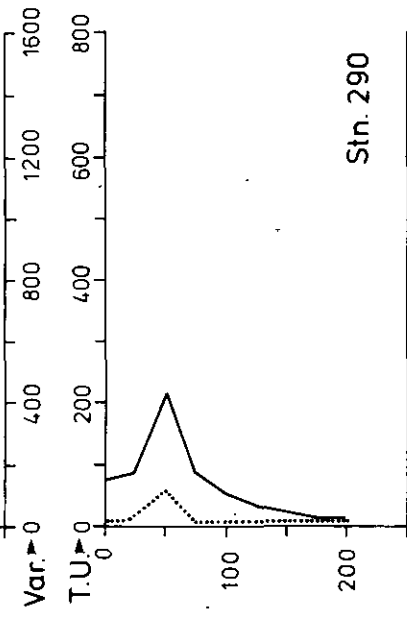
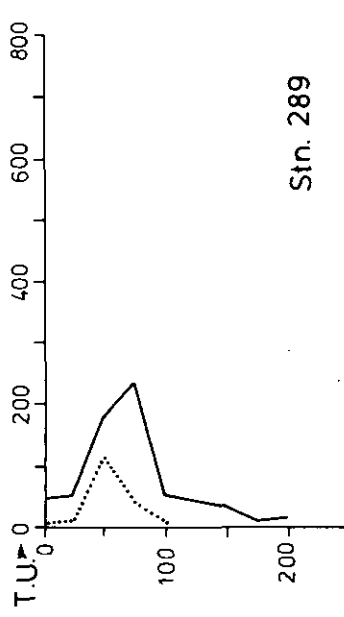
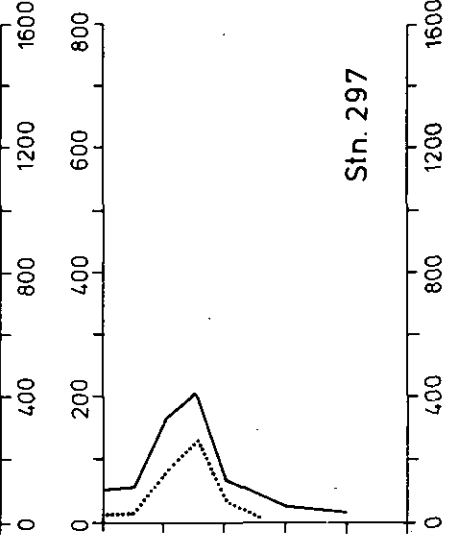
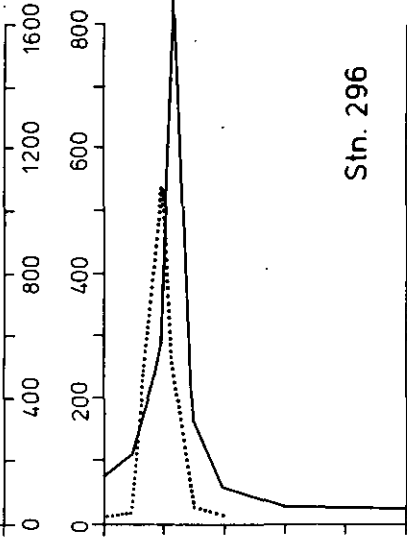
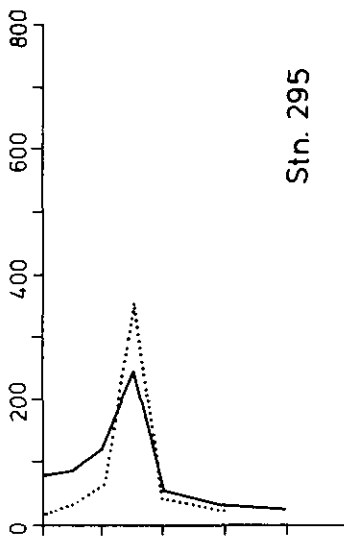


Fig. 7. Relationship between surface and subsurface standing crop (FM). The units are TU. "Subsurface" fluorescence is the mean of FM values at 25 m, 50 m and 75 m. September values (▲) are shown for comparison.



Depth (m)

T.U.

Var.

Var.

Var.

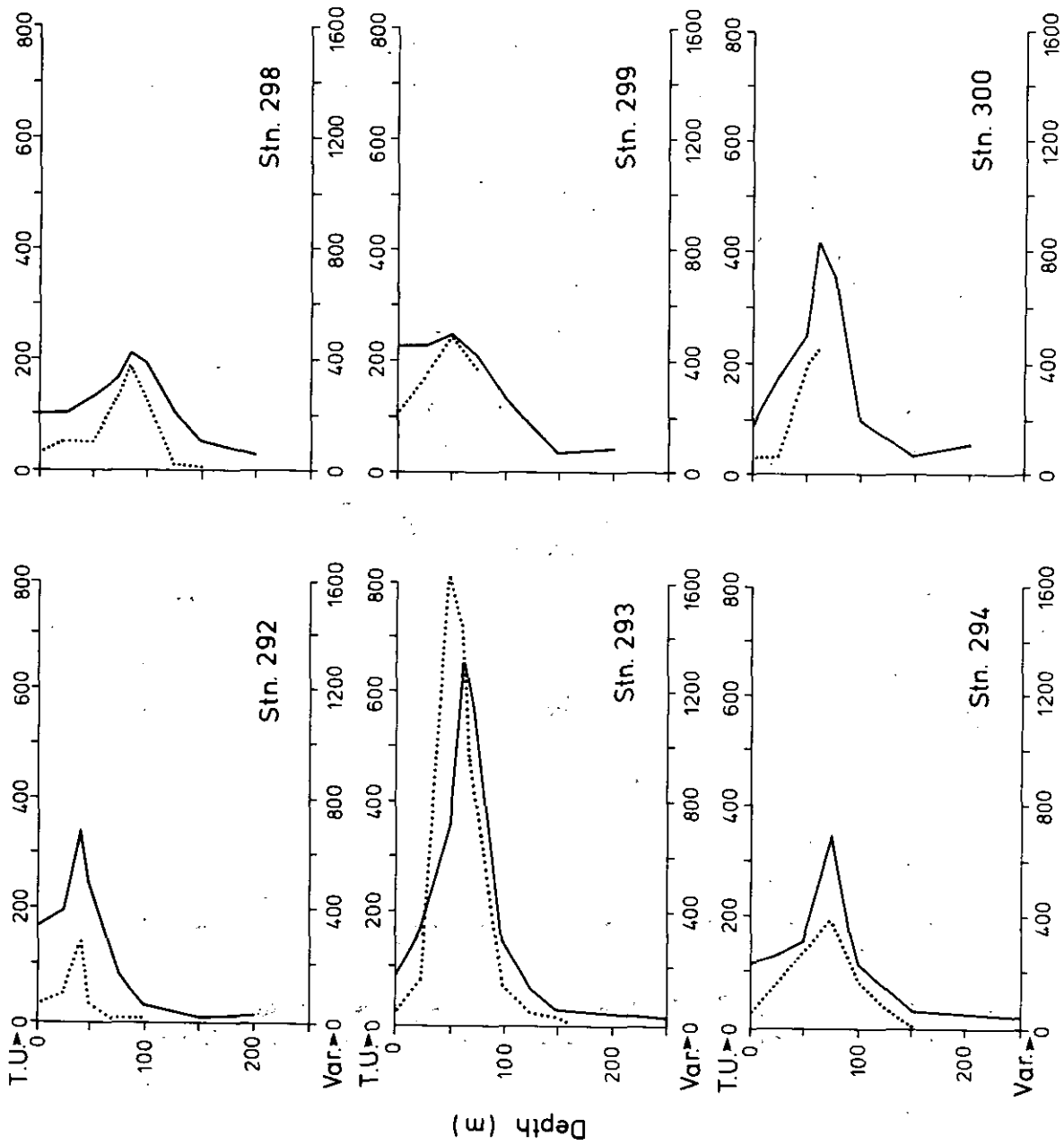


Fig. 8. Vertical profiles of phytoplankton measured (a) by the Variosens *in situ* fluorometer (·-·-·-·); (b) by the Turner Design laboratory fluorometer (FM) using batch samples from Niskin bottles (—·—·—·).

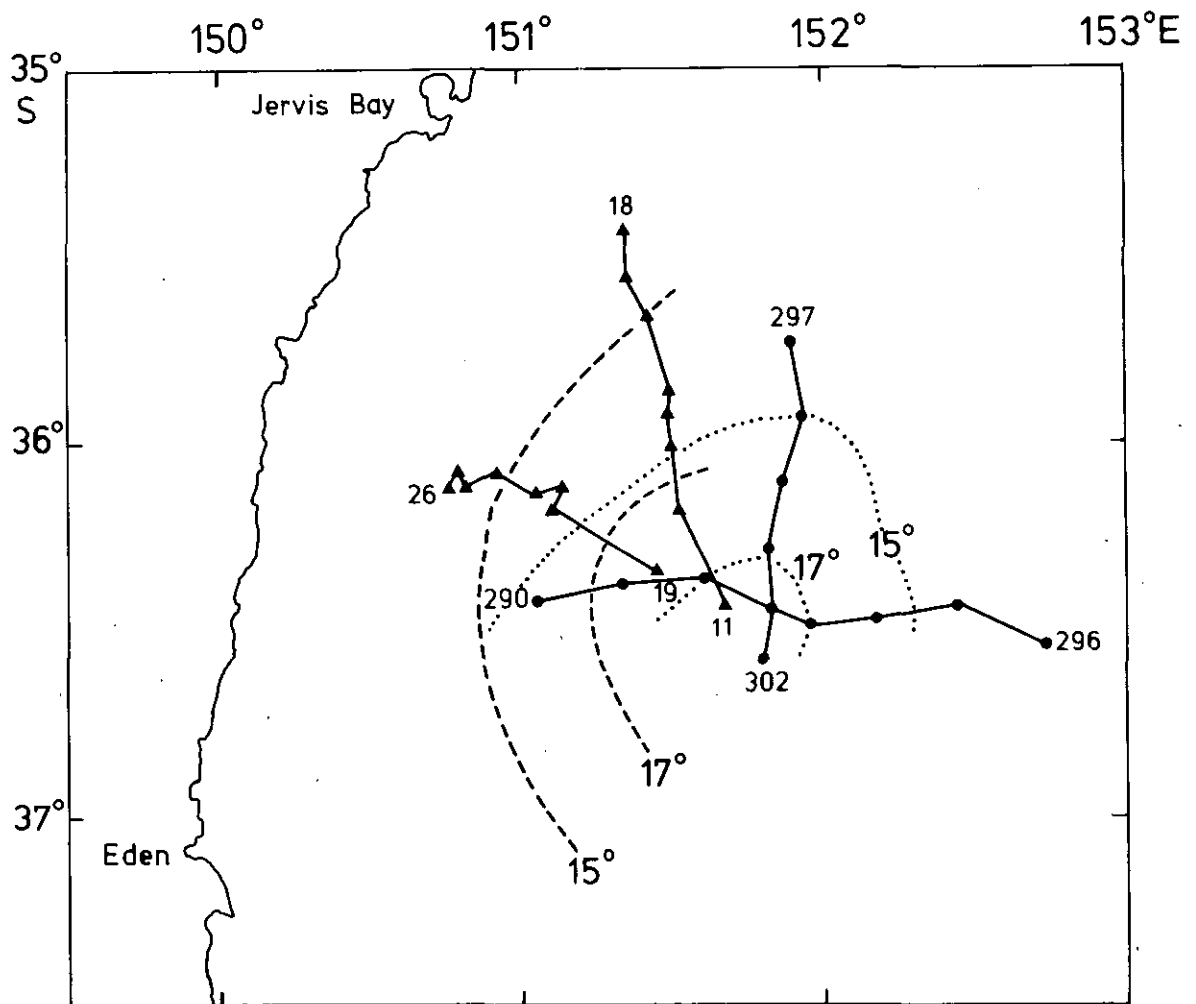


Fig. 9. Location of selected "Sprightly" and "Courageous" transects where the vertical distribution of temperature, standing crop and nutrients were measured.

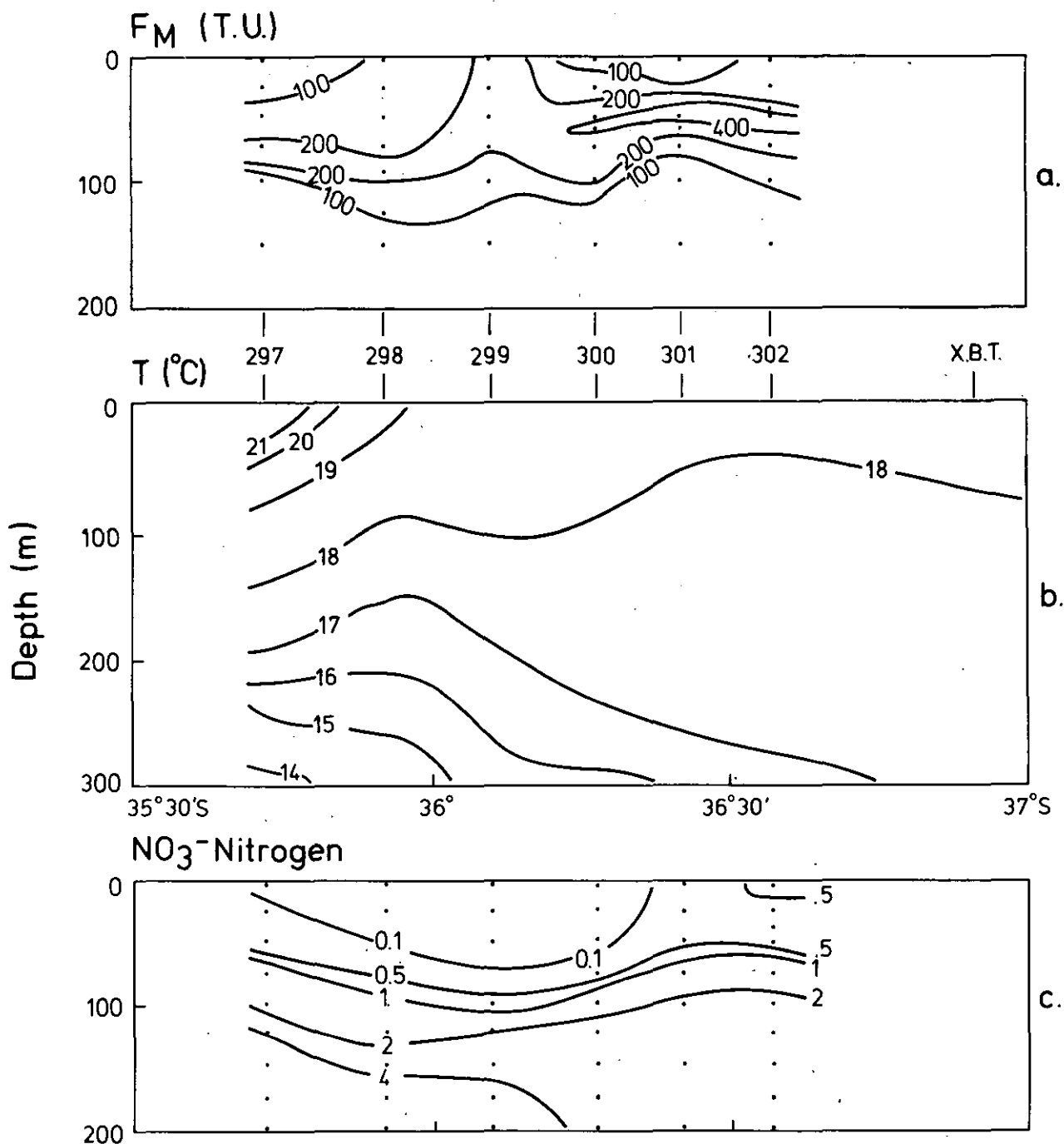


Fig. 10. "Sprightly" transect 297/302 from beyond the northern edge of eddy "F" to near the eddy centre. (a) F_M (TU); (b) temperature ($^{\circ}\text{C}$); (c) nitrate ($\mu\text{g-at N l}^{-1}$).

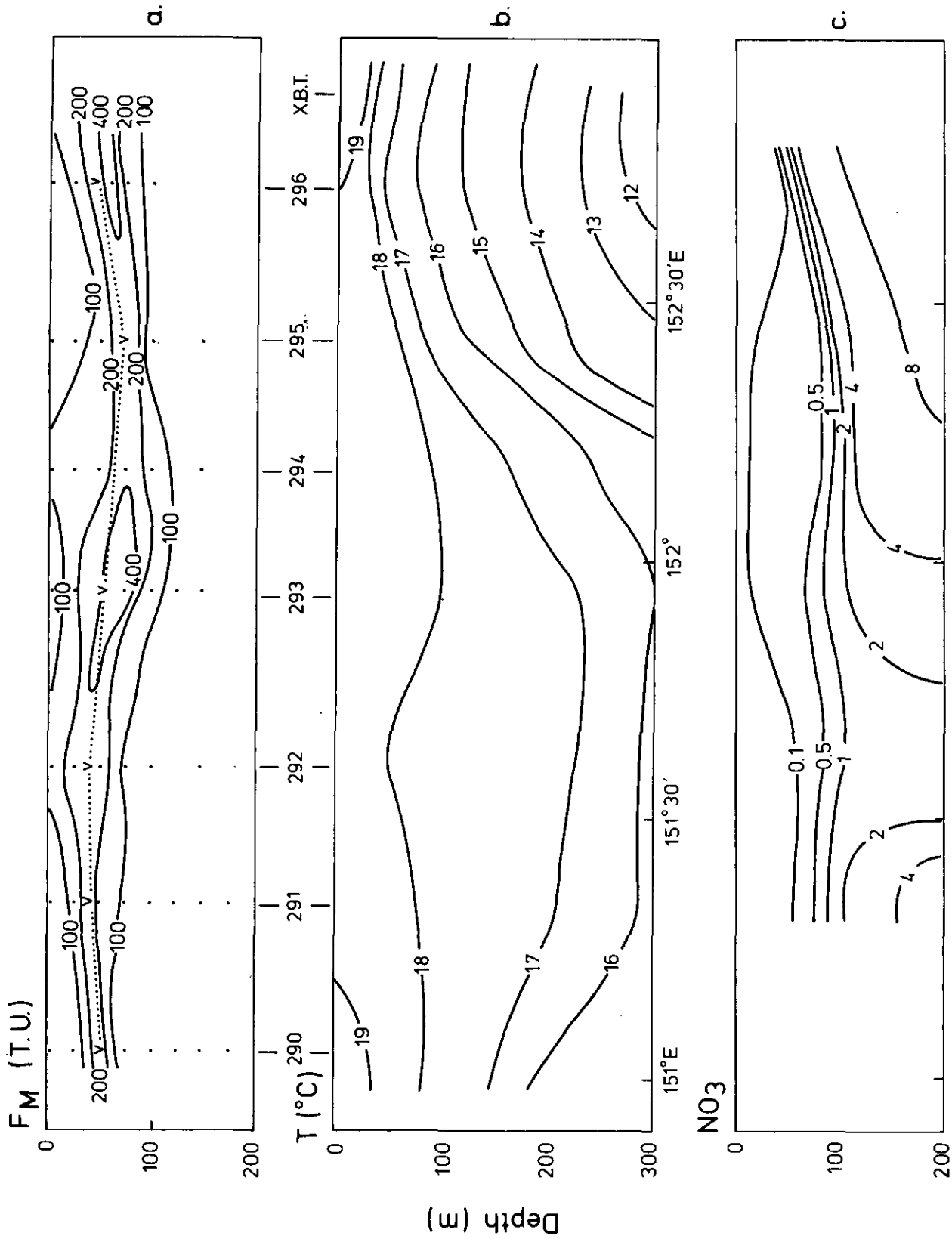


Fig. 11. "Sprightly" transect 290/296 from the western boundary of the eddy to beyond the eastern boundary just north of centre. (a) FM (TU); (b) temperature ($^{\circ}\text{C}$); (c) nitrate ($\mu\text{g-at N l}^{-1}$).

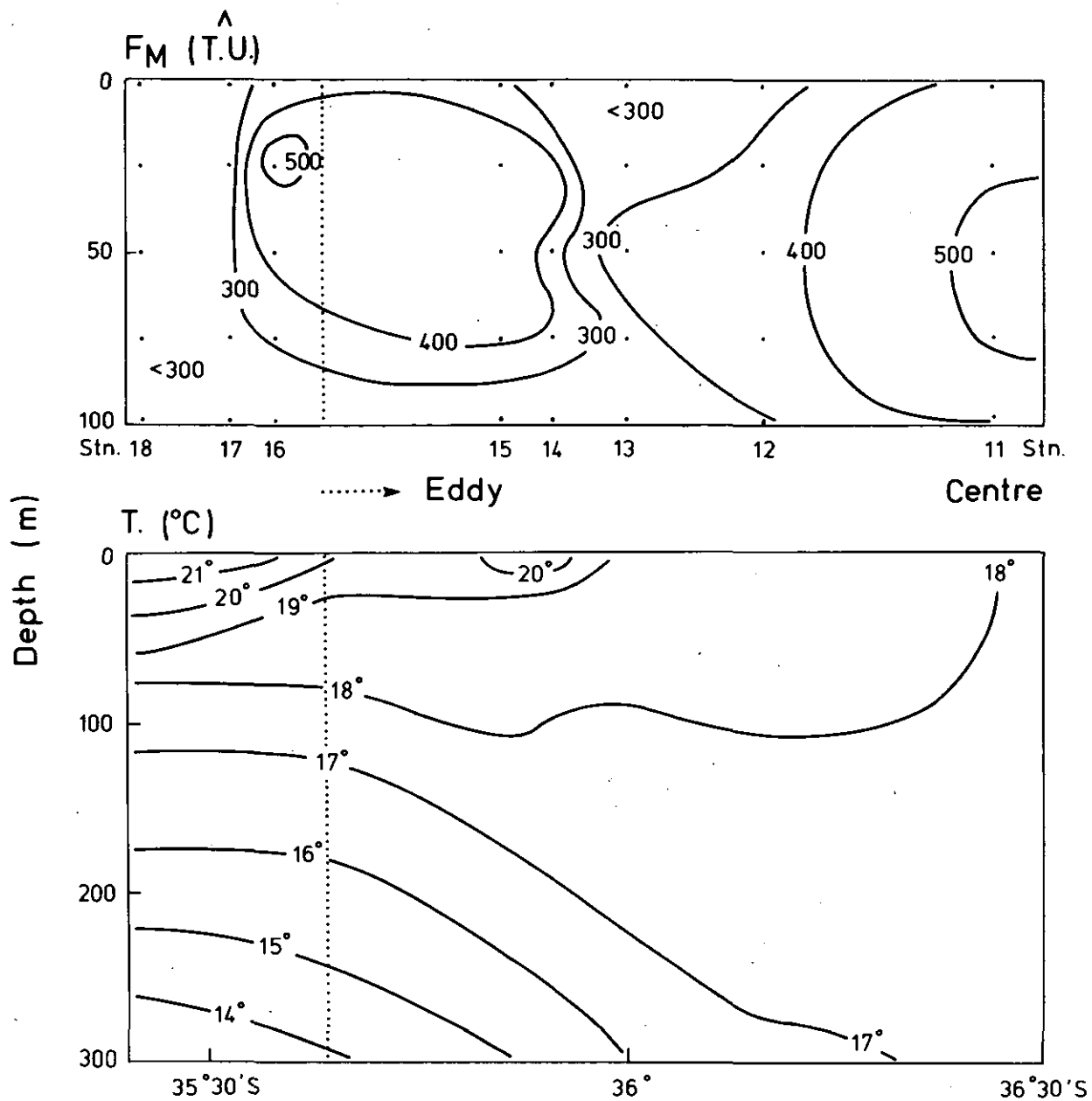


Fig. 12. "Courageous" transect 11/18 from near the eddy centre to beyond the northern boundary. (a) \hat{F}_M (TU); (b) temperature ($^{\circ}C$). The station spacing was based on equal T_{250} intervals.

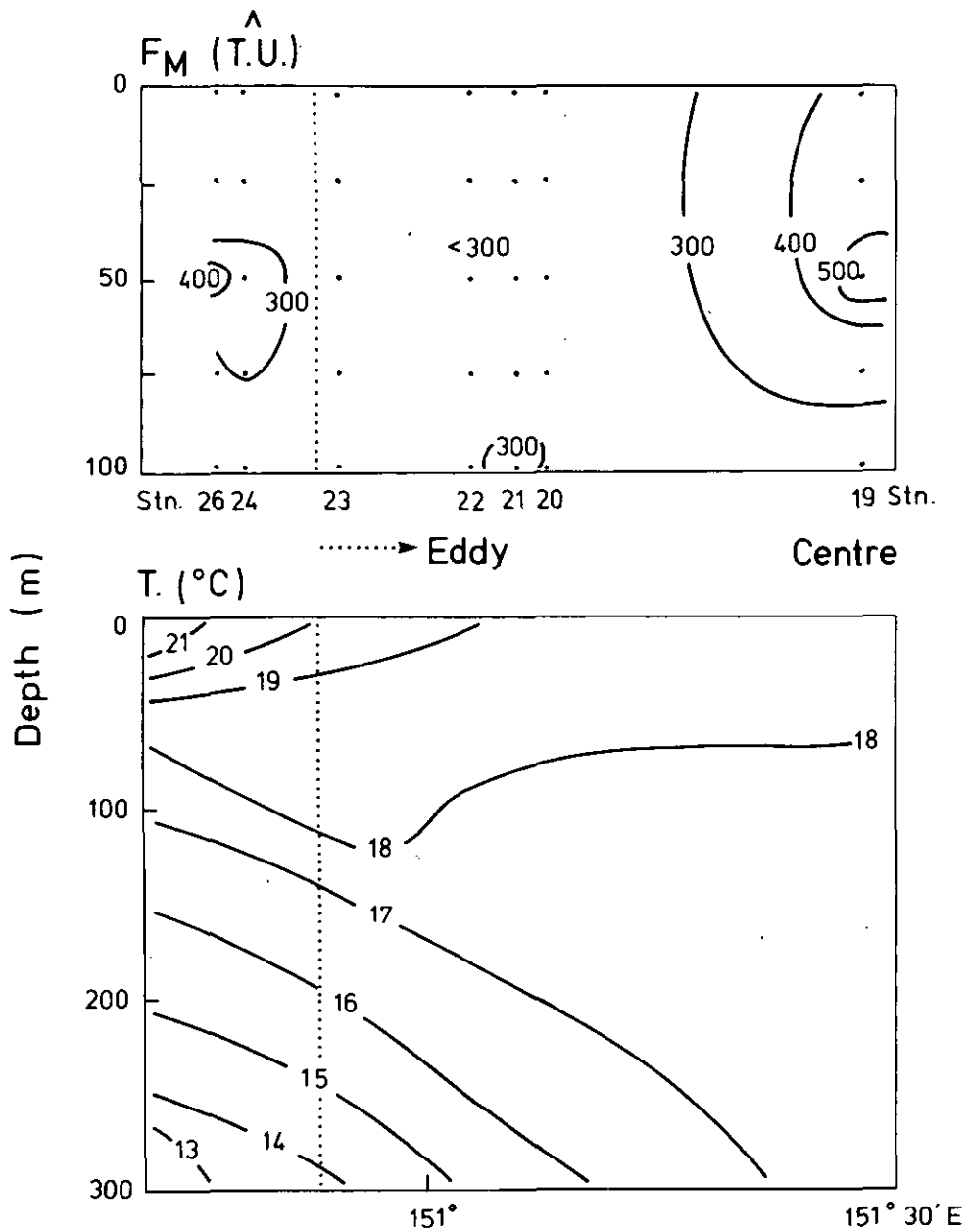


Fig. 13. "Courageous" transect 19/26 from near the eddy centre to beyond the western boundary. (a) F_M (TU); (b) temperature ($^{\circ}\text{C}$).

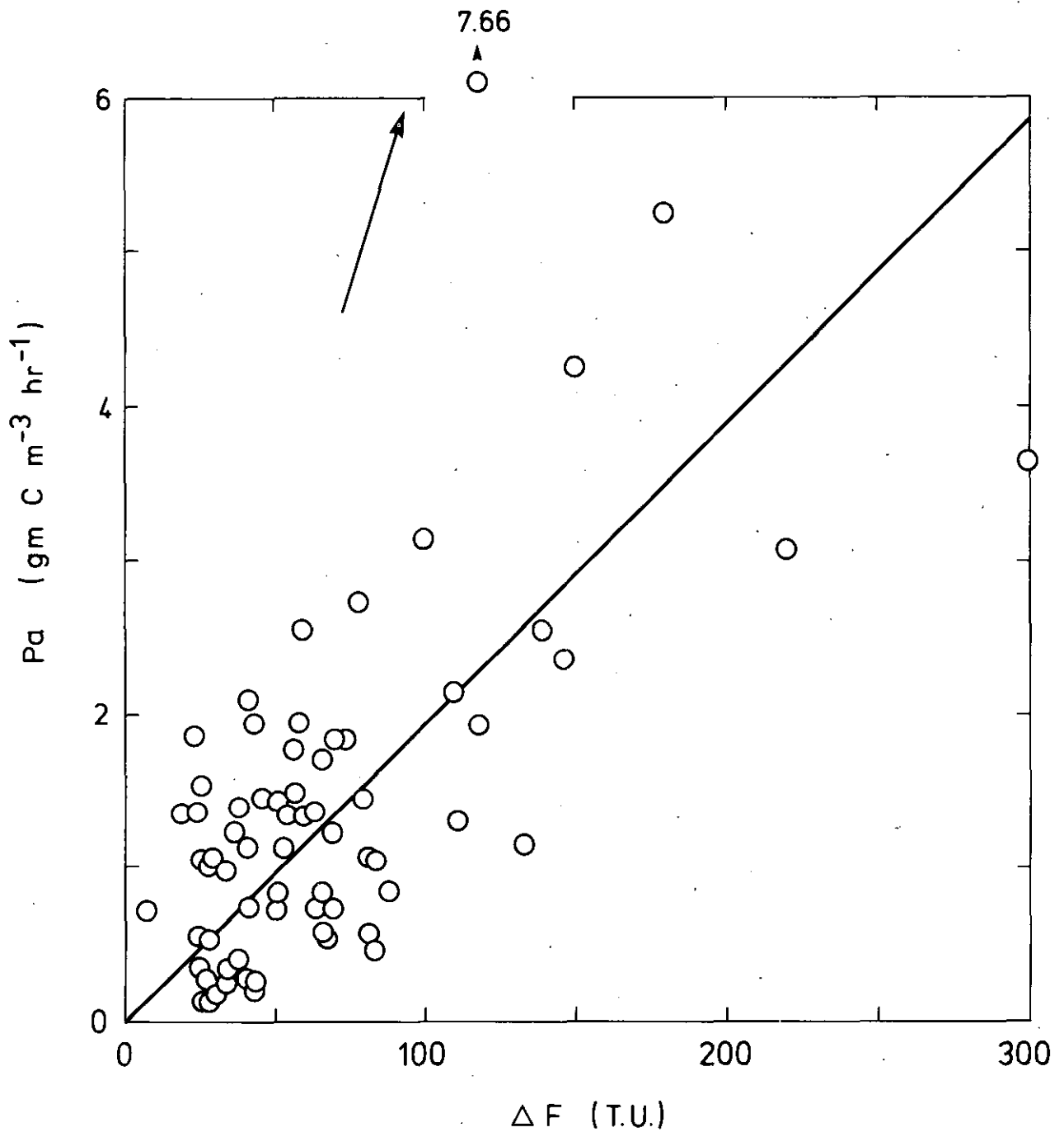
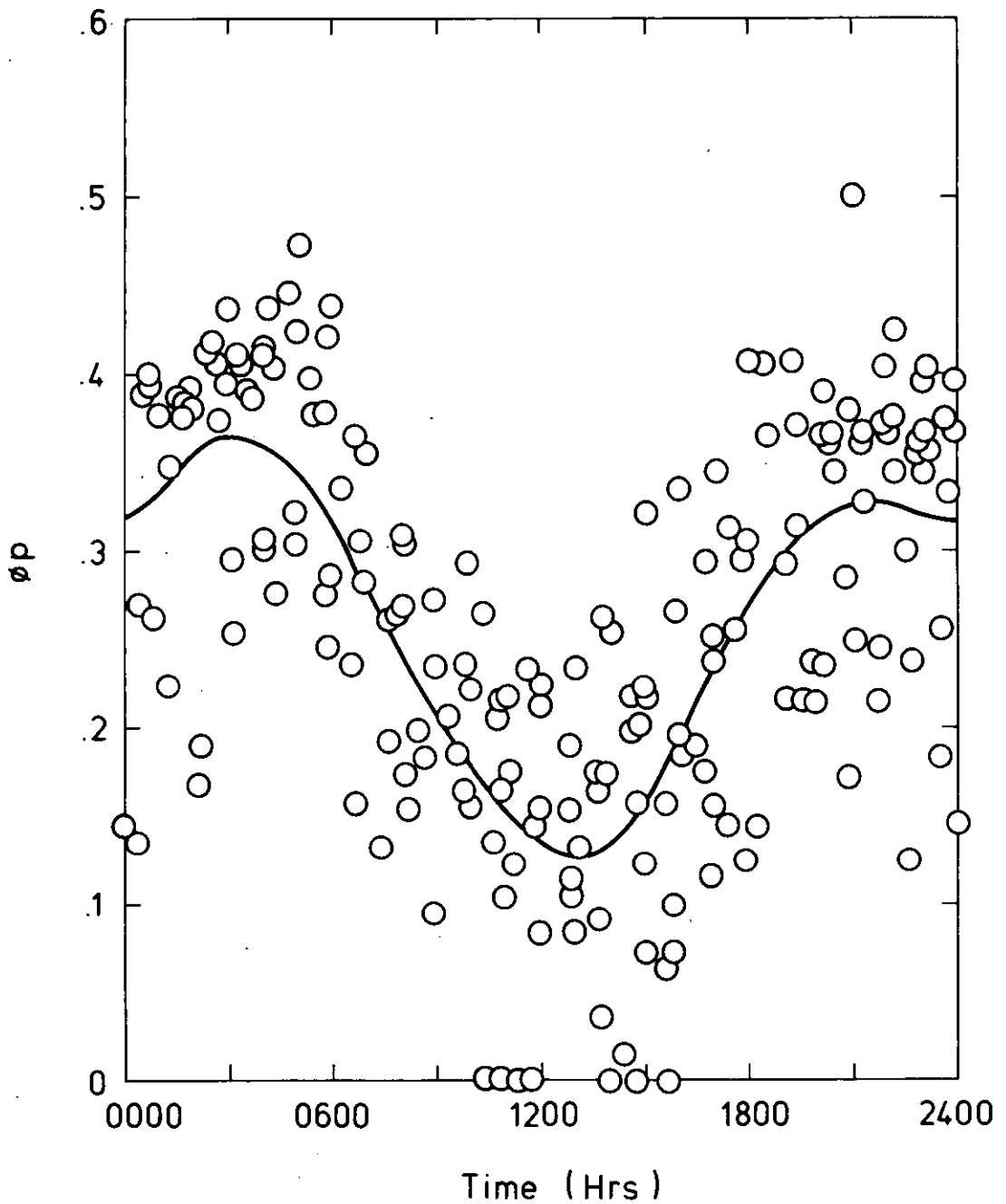


Fig. 14. Regression between (ΔF) (enhanced fluorescence resulting from inhibition of photosynthesis) and P_A (^{14}C uptake at saturation light, $\text{mg C m}^{-3} \text{ hr}^{-1}$) for the same aliquots of Niskin bottle samples taken from various depths at "Sprightly" stations. The linear equation for predicting P_A from $F_M - F_A$, regression through 0,0, is:

$$P_A = 1.96 \times 10^{-2} (F_M - F_A),$$

$$(R_1^2 = 0.37, n = 68)$$



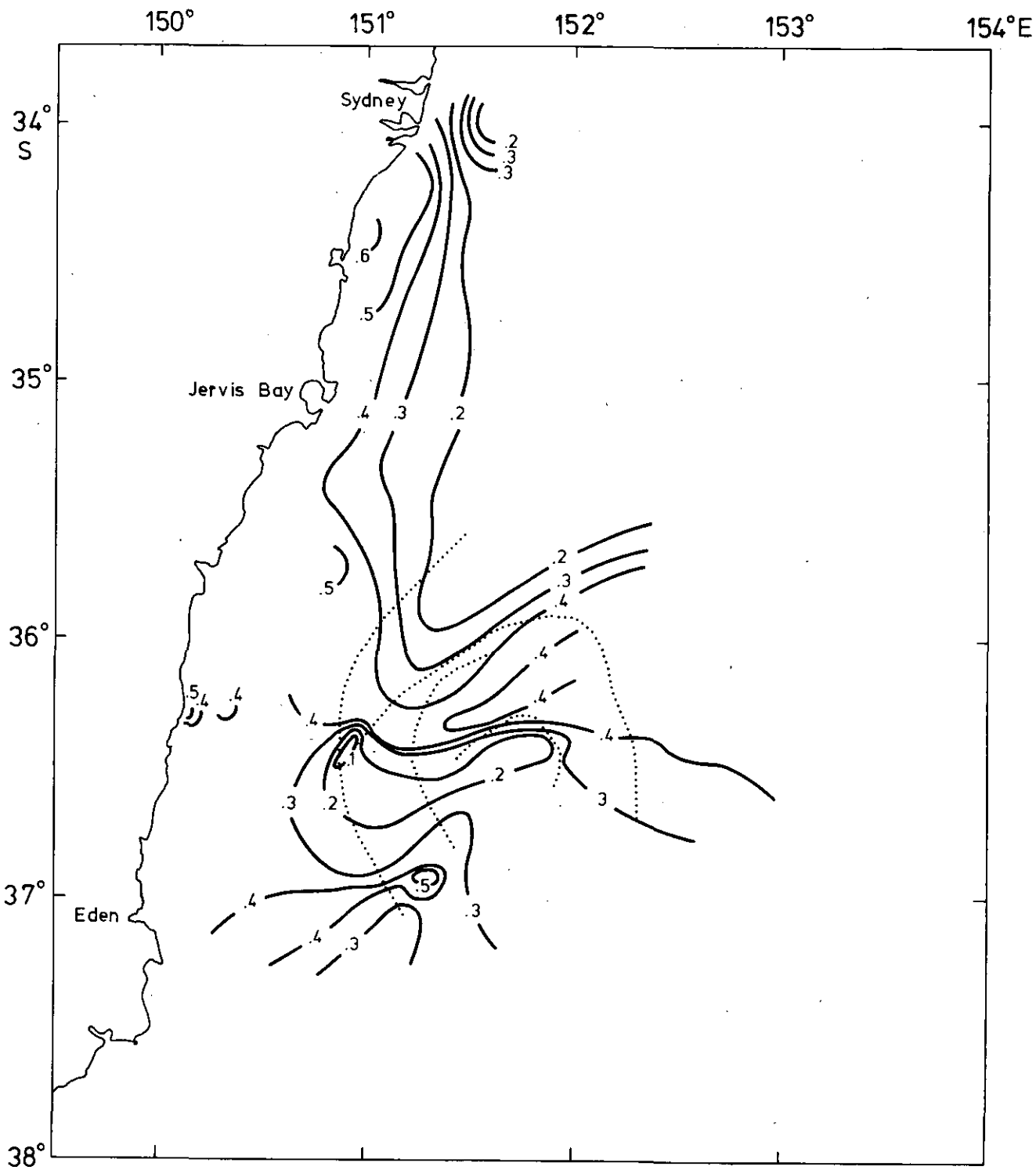


Fig. 16. Surface distribution of $\hat{\phi}_p$ ($\hat{\phi}_p$ is the photosynthetic efficiency ϕ_p corrected for diel variation).

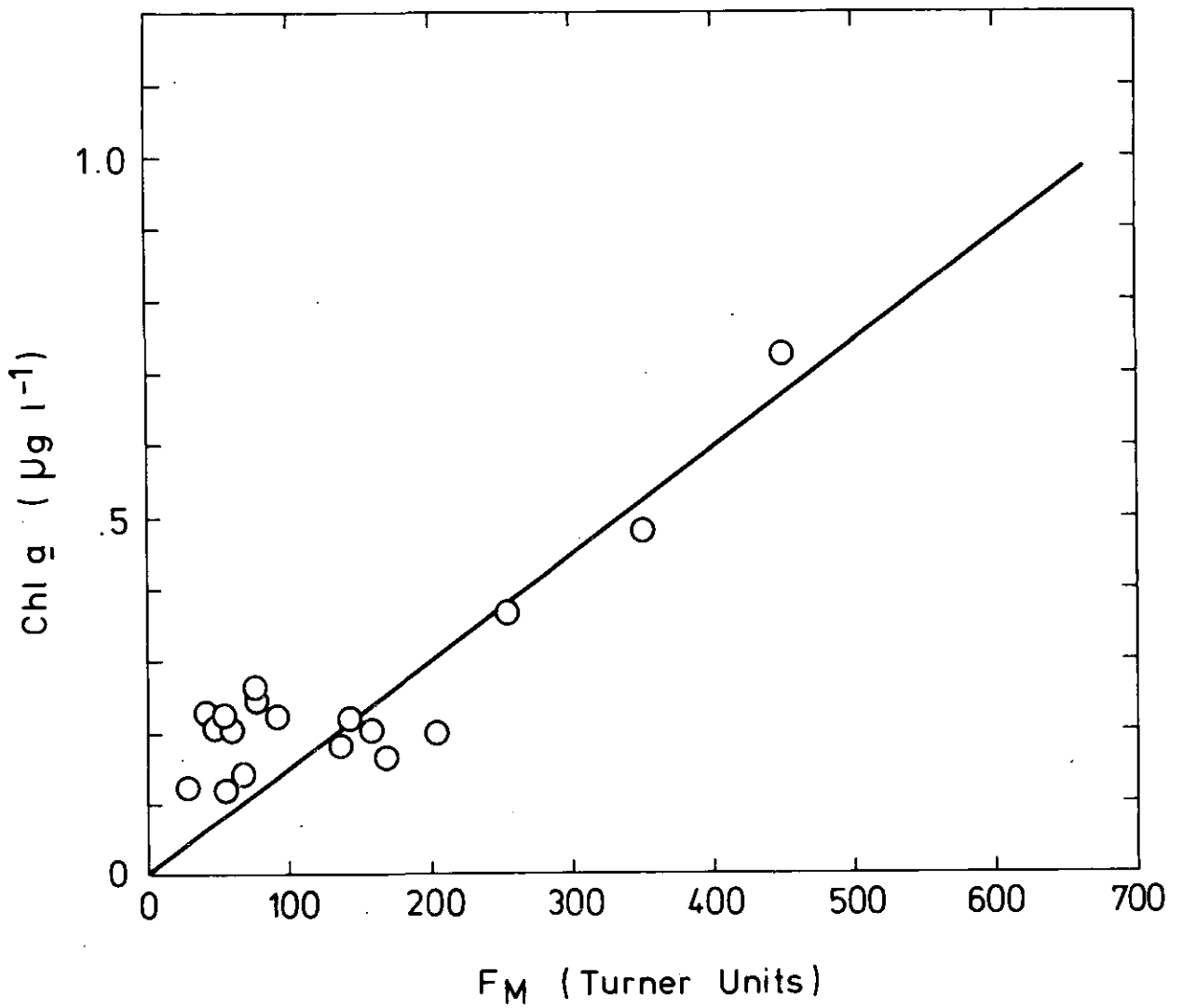


Fig. 17. Regression of chlorophyll a on F_M for on-stream surface samples. The regression equation, fitted through 0,0, is:

$$\text{Chl } a = 1.52 \times 10^{-3} F_M, R_1^2 = 0.59, n = 18.$$

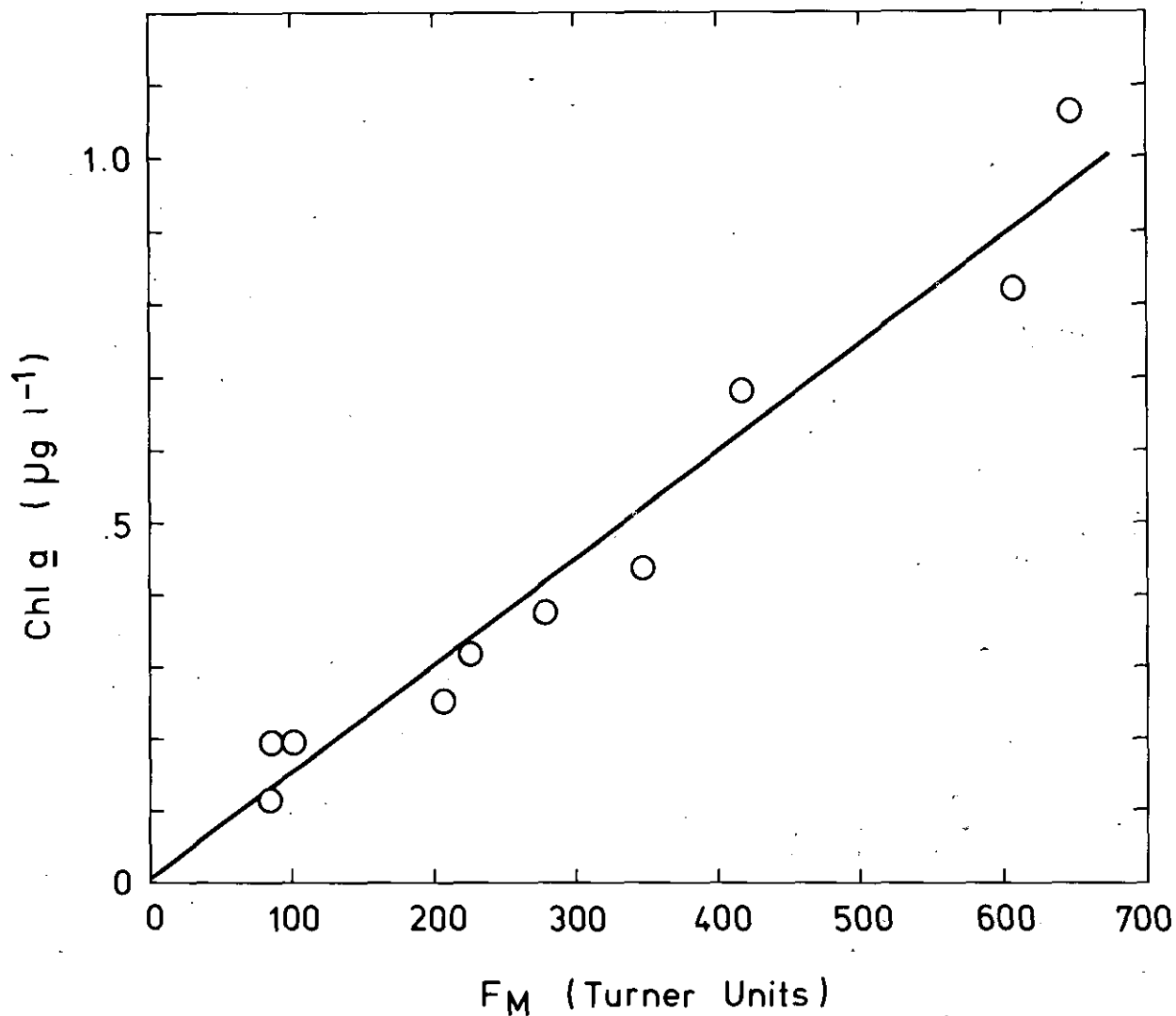


Fig. 18. Regression of chlorophyll a on F_M for Niskin bottle samples taken from depths to 75 m on 'Sprightly' 1-5 December 1978. The regression equation (through 0,0) is:

$$\text{Chl } a = 1.49 \times 10^{-3} F_M, R_1^2 = 0.96, n = 10.$$

This regression is indistinguishable from that for on-stream, surface samples (Fig. 15).

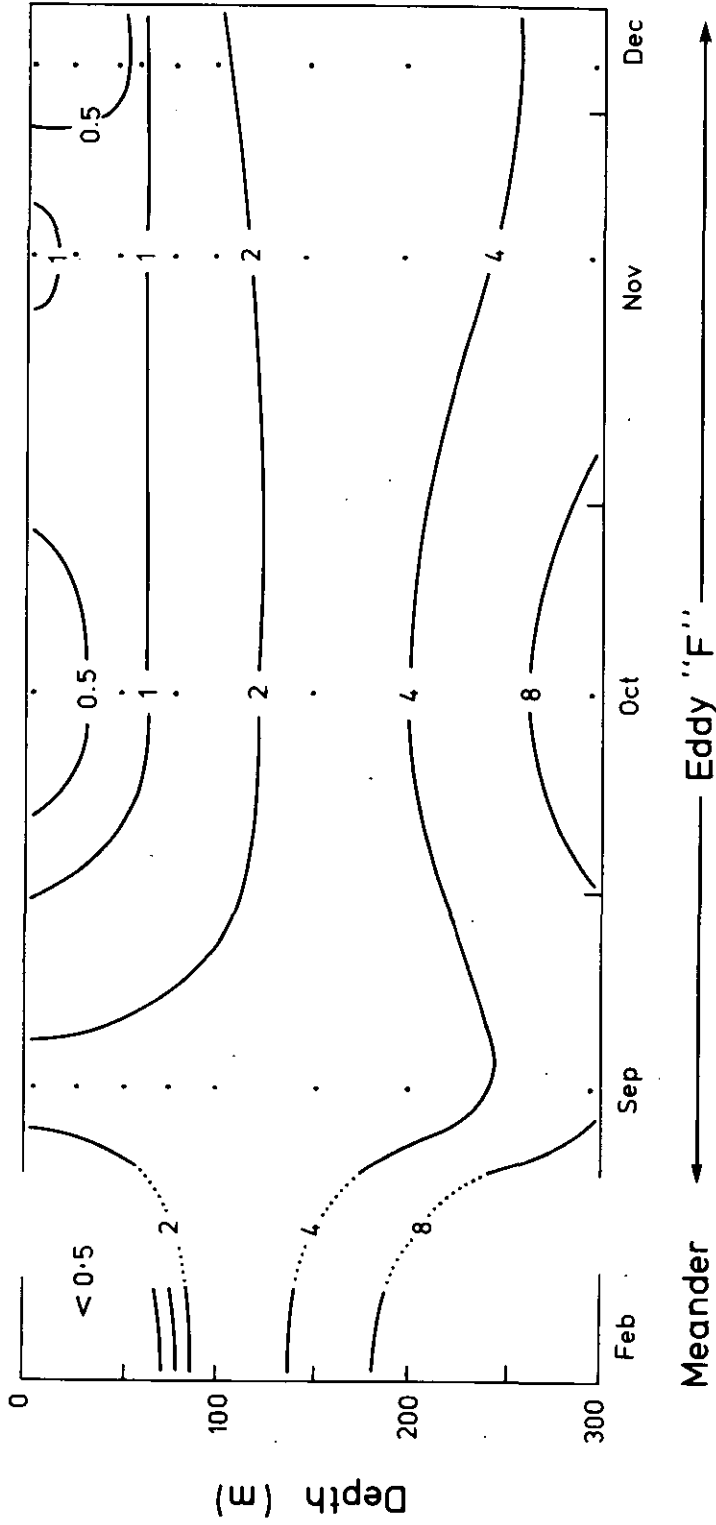


Fig. 20. Nitrate-N ($\mu\text{g-at l}^{-1}$) of the 0-300 m water column near the centre of eddy "F", between September and December 1978. Shown also is the February meander station.

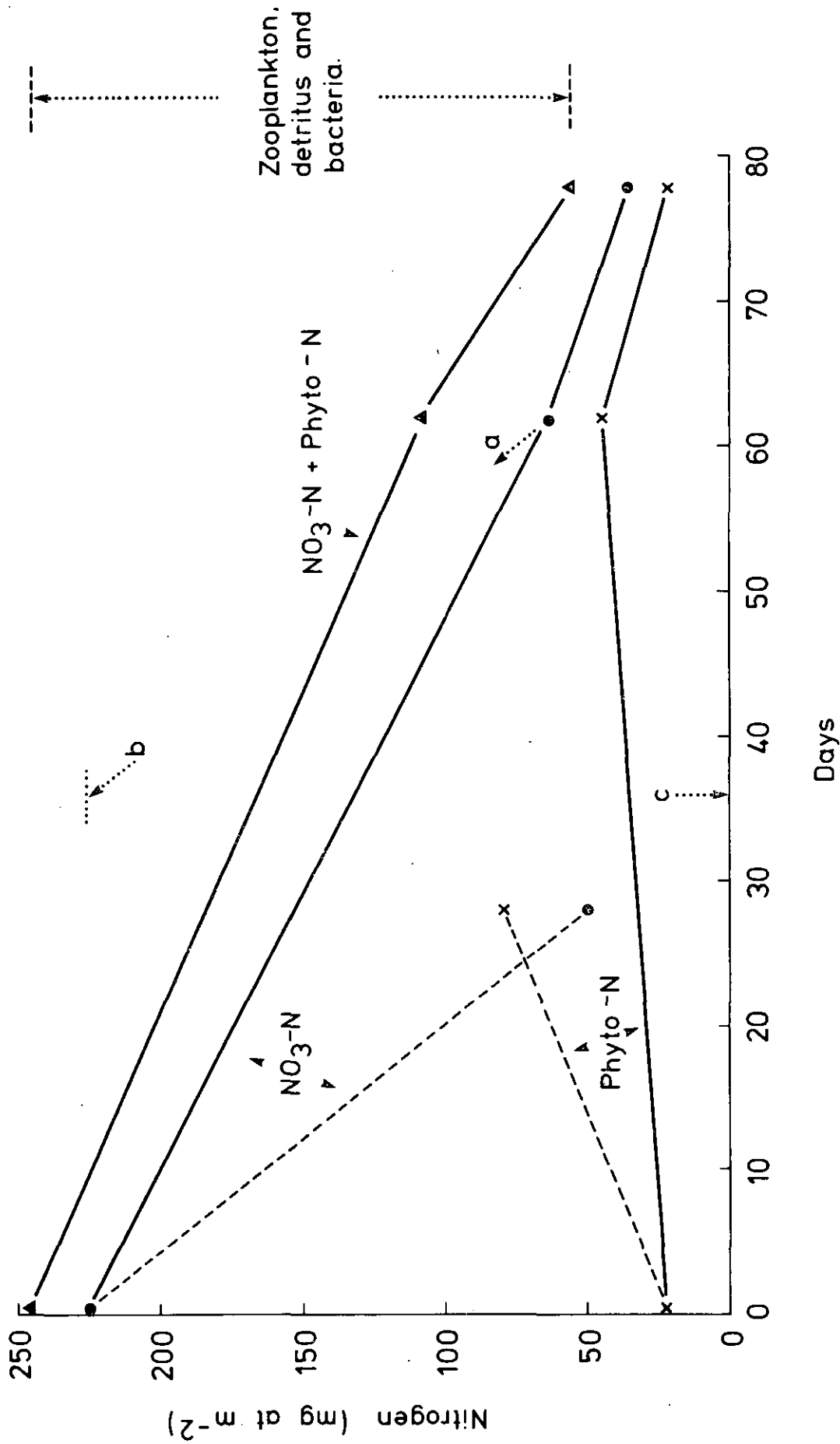


Fig. 21. Rates of nitrogen turnover in the euphotic water column (0-75 m) of eddy "F" during the spring phytoplankton bloom. The September-October trend is plotted separately because the October station was off-centre. (X phytoplankton N, • NO₃-N, Δ phyto-N + NO₃-N).



Fig. 22. The salp, *Thetys vagina*, which occurred in large concentrations near the phytoplankton peak (close to the thermocline).

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