

isoprenoid cyclic disulphides were also present in most of the Peruvian samples, although the linear 1,2-dithianes were virtually absent (Fig. 1c). However, the most important extractable organic sulphur compound (compound IV, which is sometimes the most abundant compound of the aromatic hydrocarbon fraction) gives a mass spectrum with a molecular ion at $m/z = 376$ ($C_{20}H_{40}S_3$; based on exact mass measurements), an ion at $m/z = 344$ ($M^+ - 32$), and a fragmentation pattern similar to that observed for the C_{20} isoprenoid 1,2-dithianes ($m/z = 101, 157, 255$ and 311). Loss of sulphur from a parent ion ($M^+ - 32$) has been reported for molecules with two or more adjacent sulphur atoms^{21,25-27}. The product of Raney nickel desulphurization of the aromatic hydrocarbon fraction is almost solely phytane. This compound was therefore identified as 5-methyl-4-(3,7,11-trimethyldodecyl)-1,2,3-trithiepane (compound IV). This cyclic trisulphide also occurs as a minor compound in the bituminous shale of the Vena del Gesso basin (Fig. 1). We note that the sporadic occurrence of compound IV in the Peruvian sediments excludes its formation after sample preparation.

The structures of these novel organic sulphur compounds cannot be related to known naturally occurring di- and trisulphides²⁸. By analogy with the hypothesis put forward to explain the origin of other organic sulphur compounds⁶⁻¹¹, the incorporation of abiotic sulphur into specific functionalized lipids can explain their occurrence. For example, phytadienes (derived from ubiquitous phytol) can act as suitable precursors for the newly identified C_{20} isoprenoid cyclic di- and trisulphides. In contrast to previously suggested incorporation models¹¹, addition of H_2S cannot be invoked to explain the occurrence of a C_{20} isoprenoid cyclic trisulphide. The cyclic disulphides may still originate from reactions of H_2S through intermediate dithiols which, after oxidation, may yield 1,2-dithianes. Chemically and/or microbially generated inorganic polysulphides^{29,30} are suitable sulphur species for the formation of cyclic trisulphides, although also microbially produced polysulphides occur the most prominent ones occurring in natural aqueous solutions²⁹ are HS_4^- , HS_5^- , S_4^{2-} and S_5^{2-} .

It is known^{28,31} that organic polysulphides are thermally unstable and therefore we suggest that if tetra- and pentasulphides are formed they will easily degrade to tri- and disulphides during prograde diagenesis. This also implies that the latter compounds may be seen as potential precursors for sulphides (thiolanes). We note that the younger and less deeply buried Peruvian sediment samples contain the trisulphide in high abundance in comparison to disulphides, a situation which is reversed in the older and once more deeply buried bituminous shale from the Vena del Gesso basin (Fig. 1).

Di- and trisulphides may prove to be useful tools for the reconstruction of palaeoenvironments because the occurrence of inorganic polysulphides is known to be sensitive to variations of the pH and redox potential Eh^{29} . □

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Phytoplankton production pulses and episodic settlement of a temperate marine fish

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THE settlement of post-larval marine invertebrates^{1,2} and fishes³⁻⁵ fluctuates massively both within and between years; this variability significantly affects the structure of adult populations^{5,6}. The causes of these fluctuations are not well known, but they are typically attributed to variation in some element of the planktonic environment that determines the distribution and rates of survival of the larvae^{3,7-9}. Here we report that over a three-year period, pulses of settlement of a species of temperate reef fish were invariably preceded by brief, irregularly occurring peaks of phytoplankton production. The lag time was consistent with a 'critical period' hypothesis¹⁰, in which settlement rates are determined by irregular variation in the availability of food for newborn larvae. Although they are difficult to detect, transient but intense pulses of production may be common in the oceanic water column¹¹ and could underlie the extreme temporal variability of settlement characteristic of many marine organisms.

The viviparous rocky reef fish *Heteroclinus* sp. ("Scott's Weedy Fish" in ref. 12), occurs in large numbers in tide pools and shallow reef areas along the coast of southern Australia. During a parturition season that lasts from October to late December, females produce clutches of up to 2,700 larvae asynchronously about every 17 days (J.S.G. and R.E.T., unpublished manuscript). At birth, the larvae vary from 7.1-9.4 mm Standard Length, are active swimmers and are well developed, with functional jaws and eyes, no evident yolk sac and an open gut. The larvae of this and other clinid species are found predominantly inshore, in coastal bays and inlets. The duration of the planktonic larval stage varies seasonally from 3 to 6 weeks, after which the fish settle as lightly pigmented juveniles, 14-16 mm Standard Length, in tide pools and shallow rocky habitats.

We measured seasonal variability in settlement by *Heteroclinus* sp. for three years (1985/86 to 1987/88) by sampling every two weeks at sites around Storm Bay, a large semi-autonomous¹³ embayment in southeastern Tasmania (43° 20'S, 147° 30'E). The date on which each juvenile settled was determined by examination of otolith microstructure¹⁴. Over the same period we measured phytoplankton abundance weekly at a station near

the centre of Storm Bay. Phytoplankton abundance was quantified by chlorophyll levels, using the hot-methanol extraction method¹³.

The number of newly settled *Heteroclinus* sp. collected per sample varied widely and irregularly each spawning season. The patterns of temporal variation in settlement differed markedly between years. One large prolonged peak dominated settlement in 1985/86; two small peaks, separated by several weeks of almost no settlement, were evident in 1986/87; in 1987/88, there was little settlement early in the year, but thereafter settlement was continuous, with two peak periods separated by about 5 weeks (Fig. 1, top).

The temporal pattern of settlement each year matched that of chlorophyll levels in Storm Bay several weeks earlier (Fig. 1, bottom). Over the three-year period, all the main peaks in settlement could be matched to a corresponding peak in chlorophyll levels 7–9 weeks earlier (modally 7 weeks); conversely, there were no peaks in chlorophyll levels that were not followed by a pulse of settlement. A Spearman rank correlation between numbers of settling fishes and preceding chlorophyll levels is significant ($P < 0.05$) in each of the three years, at identical lag times (the correlations are significant at lags of 6, 7 and 8 weeks in 1985/86, 7 and 8 weeks in 1986/87, and 7 and 8 weeks in 1987/88). The correlation between chlorophyll levels and settlement, pooled by calendar week, accounts for 56%, 37% and 23% of the variance in settlement for the 1985/86, 1986/87 and 1987/88 years, respectively.

By contrast, chlorophyll levels do not correlate significantly with subsequent settlement when years are pooled (maximum Spearman rank correlation coefficient $r_s = 0.23$, $n = 40$, lag of 8 weeks), reflecting a poor relationship between year-class strength (total number of newly settled fishes per annum) and mean annual chlorophyll levels. Nor is there any apparent relationship among years between year-class strength and the minimum, maximum, variability (coefficient of variation) or sum of chlorophyll levels each year. Across years, settlement peaks coincide (after lagging) with chlorophyll levels greater than $\sim 2 \mu\text{g l}^{-1}$, but the magnitude of settlement often shows no relation to the magnitude of the corresponding peak in chlorophyll.

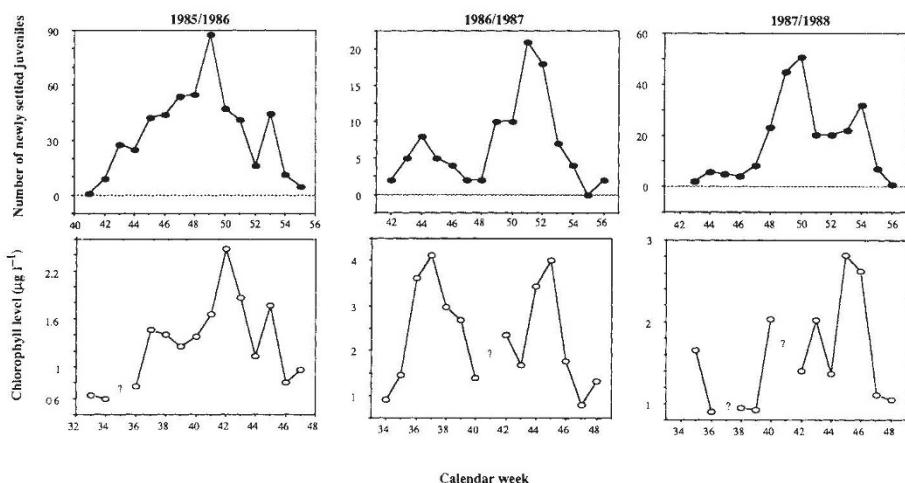
The lag between chlorophyll level and settlement is consistent with the hypothesis that variations in food availability for newborn larvae determine settlement rates. Gut contents of *Heteroclinus* larvae less than 5-days-old consist almost entirely of small copepods and similar sized microzooplankton. The abundance of these microzooplankton in the weekly samples

correlates strongly with that of phytoplankton, peaking 1–4 weeks (highest cross-correlation at a lag of 2 weeks) after each phytoplankton peak (G.P.H., L.A.C. and F. B. Griffiths, manuscript in preparation). These larvae spend, on average, 4 weeks in the plankton ($\bar{x} = 28.8$ days, $n = 511$, years pooled), varying seasonally from a mean of ~6 weeks early in the spawning season to 3.5 weeks in mid-summer. The sum of the chlorophyll-microzooplankton lag and the duration of the fish's larval stage, therefore, ranges from ~4.5–9 weeks, and averages 6–7 weeks. This compares with a correlation between chlorophyll level and settlement at lags that range from 6–8 weeks and average 7 weeks.

It is not possible to falsify the hypothesis that the temporal patterns of production and settlement are independent responses to a third, forcing function. Nonetheless, we consider this possibility unlikely. The timing of chlorophyll peaks in Storm Bay is determined by episodic bouts of strong winds, which turn over the water column and result in nutrient enrichment and, about three weeks later, a phytoplankton bloom (G.P.H., L.A.C. and F. B. Griffiths, manuscript in preparation). Hence the physical event responsible for chlorophyll peaks occurs, on average, 10 weeks before the settlement peaks and 5 weeks before the birth of the larvae that constitute those peaks. If wind events directly determine settlement variation, then they would have to operate by affecting pregnant females, producing short-term variability in brood size or larval competence. Brood sizes, however, are set before the onset of the parturition season, and neonate size, at least, varies only slightly seasonally and does not correlate with settlement variability (J.S.G. and R.E.T., unpublished manuscript). Alternative hypotheses based on, for example, the effects of wind on patterns of larval advection are possible, but difficult to reconcile with the lag times observed. Moreover, water-mass characteristics indicate that exchange in and out of Storm Bay is relatively slow¹³ and that the large scale episodic flushing that would be required to cause marked variability in settlement is unlikely.

Observations of the larvae in aquaria also support the hypothesis that short-term variations in food availability directly mediate the link between water-column production and settlement rate. As yet, we have been unable to get newborn *Heteroclinus* larvae to feed; all but a few of the several thousand larvae that we have produced in the laboratory died, apparently of starvation, within 12 h after birth. The short period to starvation is consistent with the lack of yolk sacs of these larvae at birth¹⁵. Older larvae, however, collected in the field and held under the same conditions, fed readily and metamorphosed as expected.

FIG. 1 Total numbers of newly settled *Heteroclinus* sp. recruiting to three sampling sites in Storm Bay, pooled by calendar week, in the 1985/86, 1986/87 and 1987/88 reproductive seasons. Note the different scales on the ordinates. Bottom, temporal variation in chlorophyll levels 8 weeks before the beginning of the reproductive season each year of *Heteroclinus* sp. measured at a weekly sampling station near the centre of Storm Bay. Question marks represent missing data. Note that the first main peak in settlement in 1987/88 occurred 8 weeks after a missing datum for chlorophyll levels. Although we cannot be certain of a production peak that week, chlorophyll levels rose abruptly the week before the missing sample (as did settlement 8 weeks later), and the missing sample was preceded by a short duration nutrient pulse (see ref. 13), both of which are consistent with a peak in chlorophyll during the missing period.



If *Heteroclinus* larvae must eat very soon after birth, as our experience and the absence of yolk reserves indicates, then it is plausible that short-term variations in microzooplankton abundance could markedly affect the numbers of larvae that survive the first 24 h after birth, along the lines of the critical period hypothesis previously suggested to account for interannual variations in recruitment success¹⁰.

Short-term transients of nutrient enrichment and subsequent phytoplankton production, on time scales of hours to days, can result from a range of oceanographic features, including meso-

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Cortical magnification factor and the ganglion cell density of the primate retina

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IT has long been contentious whether the large representation of the fovea in the primate visual cortex (V1)^{1–8} indicates a selective magnification of this part of the retina^{7,9–11}, or whether it merely reflects the density of retinal ganglion cells^{12–14}. The measurement of the retinal ganglion-cell density is complicated by lateral displacements of cells around the fovea and the presence of displaced amacrine cells in the ganglion cell layer. We have now identified displaced amacrine cells by GABA immunohistochemistry and by retrograde degeneration of ganglion cells. By reconstructing the fovea from serial sections, we were able to compare the densities of cones, cone pedicles and ganglion cells; in this way we found that there are more than three ganglion cells per foveal cone. Between the central and the peripheral retina, the ganglion cell density changes by a factor of 1,000–2,000, which is within the range of estimates of the cortical magnification factor^{1–8}. There is therefore no need to postulate a selective magnification of the fovea in the geniculate and/or the visual cortex.

There are three main problems in quantifying the ganglion cell density gradient of a primate retina. First, the population of displaced amacrine cells has to be estimated. In all mammalian retinae it is difficult to distinguish displaced amacrine cells from ganglion cells^{15,16}. Second, in the fovea, the spatial offset between cone inner segments and ganglion cells due to the cone fibres (Henle fibres, Fig. 2e) makes it difficult to estimate the highest sampling density of ganglion cells^{17–19}. Finally, the density of cells in the foveal region changes so rapidly with eccentricity that pooling data from experiments involving different animals, as well as different methods and shrinkage factors, produces inaccuracies. In the study reported here we have attempted to overcome these difficulties.

scale eddy formation¹¹, storm surges¹⁶, current meanders¹⁷ and tidally induced internal density waves (solitons)¹⁸. Although difficult to detect because of the temporal and spatial limitations imposed by ship-based sampling^{11,19}, these transients have recently been suggested to have important consequences for biogeochemical cycling and productivity in the ocean^{19,20}. Our data indicate that these transients also underlie the extreme temporal patchiness of settlement by marine organisms and may have profound effects on the population ecology of such organisms. □

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To differentiate ganglion cells from displaced amacrine cells, ganglion cells were retrogradely degenerated by interrupting their axons, and the surviving neurons were counted (Fig. 1a, b). The density of these neurons decreased from 3,500 cells mm^{-2} close to the fovea to ~ 500 cells mm^{-2} in the peripheral retina (Fig. 3). Selected fields of this retina were processed for GABA (γ -aminobutyric acid)-like immunoreactivity. Between 80 and 90% of the surviving neurons were stained. The number of neurons in the ganglion cell layer (GCL), which expressed GABA-like immunoreactivity, was also counted in a normal monkey retina (Fig. 1d). Close to the fovea a peak of 3,000 cells mm^{-2} was found, and the number decreased to ~ 500 cells mm^{-2} in the peripheral retina. These data show that most (80–100%) of the neurons that survive retrograde degeneration are GABA-ergic displaced amacrine cells.

Foveal topography was studied from the distribution of cone inner segments, cone pedicles and ganglion cells within the central 3 mm of one monkey retina. Cone density (Fig. 2a) decreased from a peak of 250,000 mm^{-2} in the fovea to $\sim 11,500 \text{ mm}^{-2}$ at 3 mm eccentricity. There are very few cone pedicles in the centre of the fovea (Fig. 2b). By 200 μm eccentricity, their density increases steeply, flattens out at 500 μm eccentricity and peaks in a plateau at 800 μm eccentricity, corresponding to a density of 32,000 mm^{-2} . Close to the fovea the pedicles tend to be elongated circumferentially and are densely packed in a regular way (Fig. 1c). The ganglion cell density curve (Fig. 2c) is comparable to the density curve for the cone pedicles; up to 2.5 mm eccentricity, however, there are substantially more ganglion cells than cone pedicles (see Fig. 2d). There is a plateau at 800 μm eccentricity corresponding to a maximum ganglion cell density of 60,000 mm^{-2} . These data are not corrected for shrinkage; the linear shrinkage factor was 0.9 and the areal was 0.8.

Figure 2e represents the geometry of the fovea. The foveal cone pedicles are displaced from their inner segments by Henle fibres as long as 350 μm ^{17–19}. Between cone pedicles and ganglion cells there is a further displacement of $\sim 50 \mu\text{m}$ owing to obliquely running bipolar processes and ganglion cell dendrites¹⁹. These displacements must be allowed for to determine which ganglion cells are connected to which cones. As illustrated in Fig. 2e, it is possible to get the ratio of ganglion cells to cones of the fovea from a cumulative count. The most central 10,000 cones must be connected to the most central 10,000 cone pedicles, because the Henle fibres have an orderly mapping^{19–21}. The radius of the circle that includes these 10,000 cone pedicles