Maryland Department of Natural Resources
Chesapeake Bay Water Quality
Monitoring Program

Nutrient/Bioassay
Component

Covering the Period
August 1990 - December 1996

May 1997 Report

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Executive Summary

In August, 1990 we initiated a research program on resource limitation of phytoplankton growth in Chesapeake Bay. The goal of this research is to provide information on the temporal and spatial variation of resource limitation of algal growth rates in order to create a scientific basis for evaluating regional strategies of nutrient management in Chesapeake Bay watersheds. We have employed monthly bioassays at 9-10 stations to measure light and nutrient limitation of phytoplankton growth in MD waters of Chesapeake Bay and its tributaries.

Responses of phytoplankton growth rates in the bioassays showed considerable variation. 69% of the 601 bioassays conducted between August 1990 and Dec. 1996 responded to either N or P, and Si responses were rare (<1%). Light limitation (no response to nutrient additions) was less common (16%), especially at the tidal fresh stations. There were large seasonal and spatial variations in resource limitation, and it was not possible to characterize phytoplankton growth at any station as limited predominantly by a single resource.

There was clear evidence for a seasonal progression in the dominance of light, P, and N in controlling algal growth rates during winter, spring, and summer/fall. During winter (Dec.-Feb.), light and phosphorus exerted dominant control over algal growth rates due to the combination of low temperatures, deep mixing, high freshwater discharge, high turbidity, and abundant

nutrients. Nutrient-replete or slightly P-limited algal populations were mixing within a surface layer which was too deep and turbid (optically shallow) for significant net growth in situ. During spring (Mar.-May), P was the dominant control over algal growth rates in mesohaline waters of Chesapeake Bay. DIN was usually abundant because of continuing high freshwater discharge, but the importance of P declined in late spring at the end of May or early June, coincident with the onset of bottom water anoxia and decline of DIN in the water column. During the summer and early fall (July-Oct.), N exerted dominant control over growth rates because DIN was usually depleted except near freshwater sources. Fall was a transition period, and from September into winter the importance of N declined, and P responses increased as DIN was replenished by increasing runoff. By November, P occasionally (1992, 1994, 1995) became the dominant factor controlling growth rates, usually after fall turnover in October. During the late fall, the importance of both P and N in controlling growth rates declined and light increased in importance.

In addition to seasonal variation, there was also significant interannual variability in resource limitation of algal growth. The interannual variability appears to be due to interannual changes in hydrology and nutrient delivery. In addition to years with unusual hydrology, there was a consistent decline in winter light limitation as well as a tendency for increasing P limitation over the period of record. This pattern

of decreasing light limitation and increasing P limitation may be due to the decline in inputs of P and suspended particulates to the Bay, which appear to be decreasing the severity of light limitation during winter and increasing the severity of P limitation during spring.

There was also significant spatial variability in these data. The mesohaline Patuxent, in particular, showed little response to P additions compared to other mesohaline stations, although large and consistent N responses were observed each summer. This suggests weak P limitation and an abundance of P, probably due to the large amounts of wastewater inflows to this tributary compared to other areas. In addition, algal growth at the tidal fresh stations was primarily controlled by light from fall through spring, and the summer was the period of greatest nutrient limitation.

We have made considerable progress in identifying simple diagnostic tools other than bioassays to measure resource limitation. P deficiency is readily identified by alkaline phosphatase activity >10 nmol PO_4 μg chla^{-1} h^{-1}. In addition, C:P and N:P ratios of particulate organic matter in excess of Redfield proportions and DIN/PO_4 >300:1 are also associated with P deficiency and P responses in the bioassays. N responses may be predicted by DIN concentrations <5 μM (0.070 mg NO_3-N ℓ^{-1}). Furthermore, C:P and N:P particulate ratios less than Redfield proportions and DIN/PO_4 <30:1 are also useful indicators of N deficiency and N response in the bioassays. We have also had

sucess with the use of an intracellular amino acid ratio (glutamine/glutamate) as an indicator of N limitation. Our goal with these indicators is to obtain simple field tests that will enable rapid and repeated mapping of resource limitation over large areas of the Bay. Such maps of resource limitation could then be used as monitoring tools to provide finer resolution of temporal and spatial variations in resource limitation and to examine in a cost-effective manner the effects of watershed management actions on adjacent waters of the Chesapeake Bay.

Introduction

There is considerable variability in the nutrient(s) limiting algal growth and accumulation in aquatic systems. Nitrogen (N), phosphorus (P), and silicon (Si) are all candidate limiting elements (Caraco et al. 1987, Caraco 1988, Conley and Malone 1992, Elser et al. 1990, Fisher et al. 1992, Hecky and Kilham 1988, Howarth 1988, Smith et al. 1989, Webb 1988). Temperate lakes appear to be primarily P-limited (e.g., Dillon and Rigler 1974, Schindler 1977) because of high N:P loading, N fixation, and sediment retention of P (Levine and Schindler 1992). However, there is greater recognition of the importance of N in temperate lakes (e.g., Elser et al. 1990), which appear to become N depleted under summer stratification (Dodds and Priscu 1990) and with increasing eutrophication (McCauley et al. 1989). Marine waters are often considered N-limited (Ryther and Dunstan 1971, Howarth 1988) due to enhanced sediment release of P relative to N (Nixon et al. 1980, Caraco et al 1990), slow N fixation (Howarth et al. 1988), and high denitrification (Seitzinger 1988). However, there are many reports of P limitation in estuaries and coastal areas influenced by large rivers (D'Elia et al. 1986, Harrison et al. 1990, Fisher et al. 1992, Pennock and Sharp 1994). Caraco et al. (1990) have hypothesized that the difference between marine and freshwater systems is primarily related to the lower phosphorus immobilization capacity of marine sediments and the higher

concentrations of sulphate. Si may also limit silicious phytoplankton such as diatoms in lakes (Tilman 1982), estuaries (Conley and Malone 1992), and coastal regions (Malone et al. 1980, Officer and Ryther 1980).

In estuaries and coastal ponds, which are seasonally varying mixtures of fresh and seawater, there is evidence for seasonal and spatial variations in the limiting nutrient (Caraco et al. 1987, Caraco 1988, D'Elia et al. 1986, Fisher et al. 1992a and b, Webb 1988). For example, in the Patuxent and York subestuaries of Chesapeake Bay, meso-scale bioassays indicated P limitation of biomass accumulation during winter and spring and N limitation during summer (D'Elia et al. 1986, Webb 1988). Fisher et al. (1992a, b) and Pennock and Sharp (1994) present evidence for similar seasonal alternations in light, P, and N limitation of algal growth rates in the Chesapeake and Delaware estuaries.

An understanding of the variability of resource limitation is important. In addition to contributing to our basic knowledge of the structure and function of aquatic systems, studies of resource limitation have direct application to water quality management. Large sums of money will be spent for future nutrient reduction strategies in watersheds of estuaries such as Chesapeake Bay. Wastewater treatment plants may be upgraded, land uses may be limited, and best management practices may be mandated for the agricultural community. The cost and type of nutrient reduction strategy varies considerably with the nutrient which is targeted (e.g., Clasen and Bernhardt 1987, Wetzel 1983),

and a sound scientific foundation is needed for management decisions concerning nutrient reductions.

This is a progress report primarily summarizing 4.5 years of data from July 1992 - December 1996. Although we present selected data covering the entire project period of August 1990 to December 1995, a previous report (Fisher et al. 1992b) summarized the details of the data from August 1990 to June 1992. In July 1992 we changed our protocols for nutrient addition bioassays, and we added two new indicators of P and N deficiency: alkaline phosphatase activity and the ammonium enhancement ratio. In July 1994 we also added intracellular ratios of amino acids as an indicator of N deficiency. This report gives cumulative statistics on bioassays from August 1990 to December 1996, and in the body of the report we emphasize the last 4.5 years of data on indicators of N and P deficiency and their potential use in future monitoring efforts.

Methods

Bioassays are sensitive measures of nutrient limitation of algal growth rates (Elser et al. 1988). Nutrient limitation is assessed by changes in growth rates over several days after additions of the limiting nutrient alone and in combination with other nutrients. In the bioassays reported here on water samples from MD waters of the Chesapeake, changes in phytoplankton growth rates were estimated as changes in algal biomass (chlorophyll a, $\mu g\ \ell^{-1}$) and in photosynthetic potential ($^{14}C\text{-}CO_2$ incorporation at saturating light, 1 hour at 200 $\mu E\ m^{-2}\ s^{-1}$, units = cpm). All responses to nutrient additions were normalized to that of a control with no added nutrients. Details of the conceptual basis for the interpretation of the bioassays are presented in Fisher and Gustafson (1994).

The responses in the bioassays appear to be those of the original algal populations in each sample. Subsamples of each treatment have been preserved with buffered Lugol's solution for enumeration of species, although only a subset of 10 bioassays have been taxonomically evaluated (reported in Fisher et al. 1992b). The data showed that no exotic species bloomed under the bioassay conditions, and that the bioassay responses were due to increases in the natural populations.

Water samples for the bioassays were subsamples of those obtained during the MDE sampling periods (Table 1). Samples were stored at reduced light and ambient temperature on the ship and

Table 1. Station descriptions and sampling schedule for bioassays of resource limitation of phytoplankton growth. The number of stations varies within sampling periods due to bad weather, boat mishaps, etc.

sampling area		description	MDE sta. ID	sampling day	our ID#
Main Bay stas.		Bay bridge	MCB 3.3C	tues.	4
		Point-no-point	MCB 5.2	mon.	1
		R64 buoy	MCB 4.3C	tues.	5
Potomac	(tidal fr.)	Indian Head	XEA6596	mon.	2
	(mesohaline)	Ragged Pt	MLE 2.2	mon.	3
Patux.	(tidal fr.)	Nottingham	PXT0402	a.mon.	9
	(mesohaline)	Jack Bay	XDE 5339	a.mon.	10
Choptank	(tidal fr.)	Ganey Wharf	MET 5.1	tue.	6
	(mesohaline)	Cambridge	MET 5.2	tue.	7

month	sampling periods	stations
August **(1990)**	1	7
September	1	10
October	1	10
November	1	9
December	1	8
January **(1991)**	1	8
February	1	10
March	1	10
April	1	10
May	2	18
June	2	19
July	2	15
August	1	10
September	1	10
October	1	10
November	1	10
December	1	10
January **(1992)**	1	8
February	1	10
March	1	8
April	1	10
May	2	20
June	2	20
July	2	12
August	1	6
September	1	9
October	1	6
November	1	6
December	1	6

Table 1. Station descriptions and sampling schedule for bioassays of resource limitation of phytoplankton growth (CONTINUED).

month	sampling periods	stations
January **(1993)**	0	0
February	0	0
March	1	6
April	1	6
May	2	12
June	2	5
July	2	12
August	1	6
September	1	9
October	1	5
November	1	6
December	1	6
January **(1994)**	0	0
February	0	0
March	1	6
April	1	6
May	2	12
June	2	9
July	2	12
August	1	6
September	1	9
October	1	6
November	1	6
December	1	6
January **(1995)**	0	0
February	0	0
March	1	6
April	1	6
May	2	11
June	2	10
July	1	9
August	1	6
September	1	9
October	1	5
November	1	6
December	1	6
January **(1996)**	0	0
February	0	0
March	1	6
April	1	6
May	2	11
June	2	10
July	1	9
August	1	6
September	1	9
October	1	5
November	1	6
December	1	6
TOTAL	72	530

transported on the day of collection to Horn Point Environmental Labs for overnight storage in a incubator regulated at ambient water temperature and adjusted to the timing of the natural light cycle with artificial light (200 μE m^{-2} s^{-1}). The next day subsamples were taken for initial analyses, and each large volume (~ 20 ℓ) water sample was then subdivided into 3 ℓ subsamples in plastic, transparent cubetainers. There were two controls with no additions, an N addition, a P addition, and an N+P addition. The amount of the nutrient additions were chosen to saturate uptake rates and provide temporary relief from nutrient limitation. A flow diagram for sample processing is shown in Fig. 1.

Changes in growth rates were measured following the incubation with added nutrients. After approximately 48-72 hours in an incubator on the HPEL dock at ambient temperature and 60 % natural light, each treatment was subsampled in duplicate for chlorophyll a and particulate phosphorus (chl a and PP) and photosynthetic potential (^{14}C-CO_2 incorporation). The incubations allowed sufficient time for replenishment of internal nutrient pools and alleviation of nutrient limitation. The 2-3 day incubation time also eliminated the possibility of short term (1-6 h) energy competition between carbon fixation and nutrient assimilation (Healey 1979, Lean and Pick 1981).

Responses to nutrient additions in treatments were normalized to those of the control without nutrient additions. Responses equivalent to those of the control therefore equal 100 %. Increases in chlorophyll a and carbon fixation rate in a

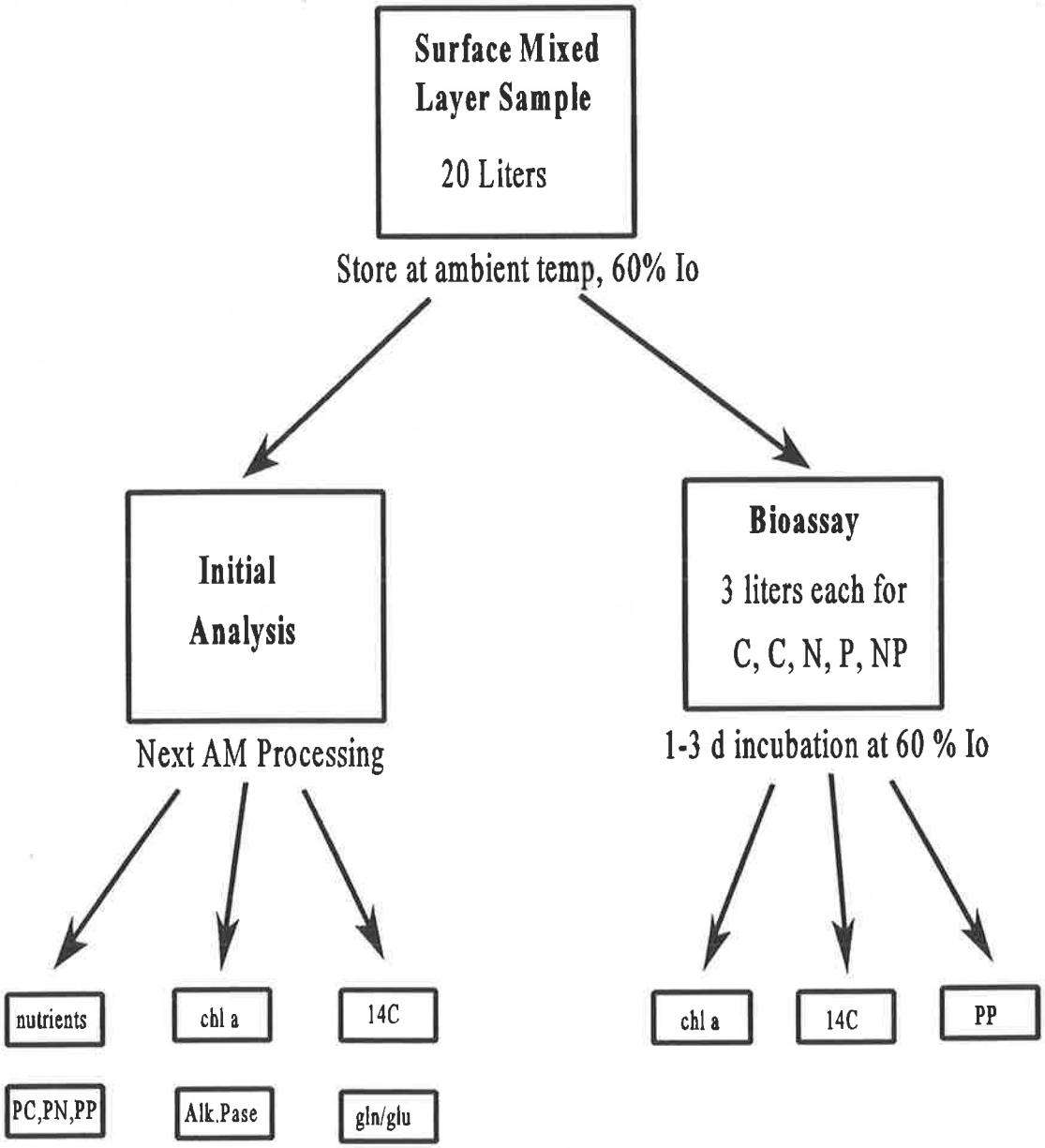

Fig 1. Flow diagram for processing of samples for analysis of nutrient limitation.

treatment (relative to the control) were usually proportional to each other and were interpreted as indicative of a growth rate increase in response to the addition.

The significance of a response greater than the control was based on decision rules (Table 2). The rules were formulated from a statistical study of the frequency distribution of the maximum response of each bioassay conducted during the period Aug. 1990 - Dec. 1991 (Vaas and Magnien 1992). The threshholds for a significant response were set at approximately the 90^{th} percentile of the upper tail of the frequency distribution during winter months (Dec. - Mar., 120 % of control), somewhat below the 90^{th} percentile during April and November (130 %), and considerably below the 90^{th} percentile in warm months (May - Oct., 140 %). This approach automatically creates a small bias towards no response in winter months, because small but significant responses may be excluded. However, it was necessary because cumulative experimental errors in bioassays approach 20%. If the November through April threshholds are set at levels lower than 120-140 %, spurious results frequently occurred (e.g., apparent N or P limitation with responses of 105-110 % of control under conditions of low algal biomass in the presence of substantial concentrations of DIN and/or PO_4). The decision rules (Table 2) avoid this problem and provide a more consistent set of bioassay results. The decision rules do not exclude large, significant responses in winter (incubations provide conditions for responses up to 400 %), although these are rarely found.

Table 2. Decision rules used for the classification of responses obtained in nutrient addition bioassays in Chesapeake Bay.

1- Bioassays are classified as "inconsistent" (INC) if two or more observations of chlorophyll a (CHAA) or C fixation (CFIX) in any treatment are < 75% of the control.

2- A treatment is considered significantly greater than the control:

months	if both CHAA and CFIX are >	or if one is >
Dec.-Mar.	120%	140%
Nov., Apr.	130%	160%
May-Oct.	140%	180%

3- Using the treatments significantly greater than the control, bioassays are classified according to the conceptual model in Fig. 2. Classifications with significant responses are "exclusive N" (EXN), "primary N" (PRN), "balanced NP" (BNP), "primary P" (PRP), and "exclusive P" (EXP).

4- Bioassays with no significant responses are classified as "no response" (NOR).

5- Bioassays not conforming to the conceptual model in Fig. 2 are classified as "inconsistent" (INC).

6- Bioassays which are classified as EXN, PRN, or BNP by the above rules, but which also have nitrate concentrations exceeding 10 μM (0.14 mg NO_3-N L^{-1}), are reclassified as "XN1", "XN2", and "XN3", respectively. This is necessary because of the preference of phytoplankton for the experimentally added ammonium over the ambient nitrate already present in the sample. Light-limited samples sometimes respond to the ammonium additions when adequate nitrate is present, giving a false N classification. Since adequate N and P are already present in the sample (NO_3 > 10 μM or 0.14 mg NO_3-N L^{-1} and no response to added PO_4), these reclassified bioassays will be grouped with NOR for statistical summaries. However, they will retain the XN1-XN3 classification in the data files.

However, application of the decision rules results in a somewhat larger number of bioassays being classified as 'inconsistent' and 'balanced N&P' in comparison with the t tests for significance employed in previous reports by Fisher et al. (1991, 1992).

The results of the bioassays were interpreted using the conceptual model summarized in Fig. 2. Exclusive N or P limitation (EXN or EXP) was considered to occur when additions of the other nutrient had no influence on the chlorophyll a and C fixation responses in the +N+P treatment; i.e., +N or +P was the same as +N+P. Primary N or P limitation (PRN or PRP) occurred when the other nutrient had no significant effect by itself, but significantly elevated the responses of the +N+P over and above that of the primary element alone. Balanced N&P limitation (BNP) occurred when positive responses relative to the control were present only when both were added. No significant responses to any nutrient additions (NOR) were interpreted as nutrient saturation and light limitation. Bioassay results not matching any of the above were classified as 'inconsistent' (INC).

We added three additional classifications to our complete data set this year (see decision rule 6 in Table 2). One of the problems which we have encountered is an apparent response to ammonium additions (+N treatment), when substantial amounts of DIN are present as nitrate. This occasionally occurs at tidal fresh stations with relatively low algal biomass and high DIN. We have decided to interpret these as algal responses to the added ammonium, which is universally used by phytoplankton (McCarthy

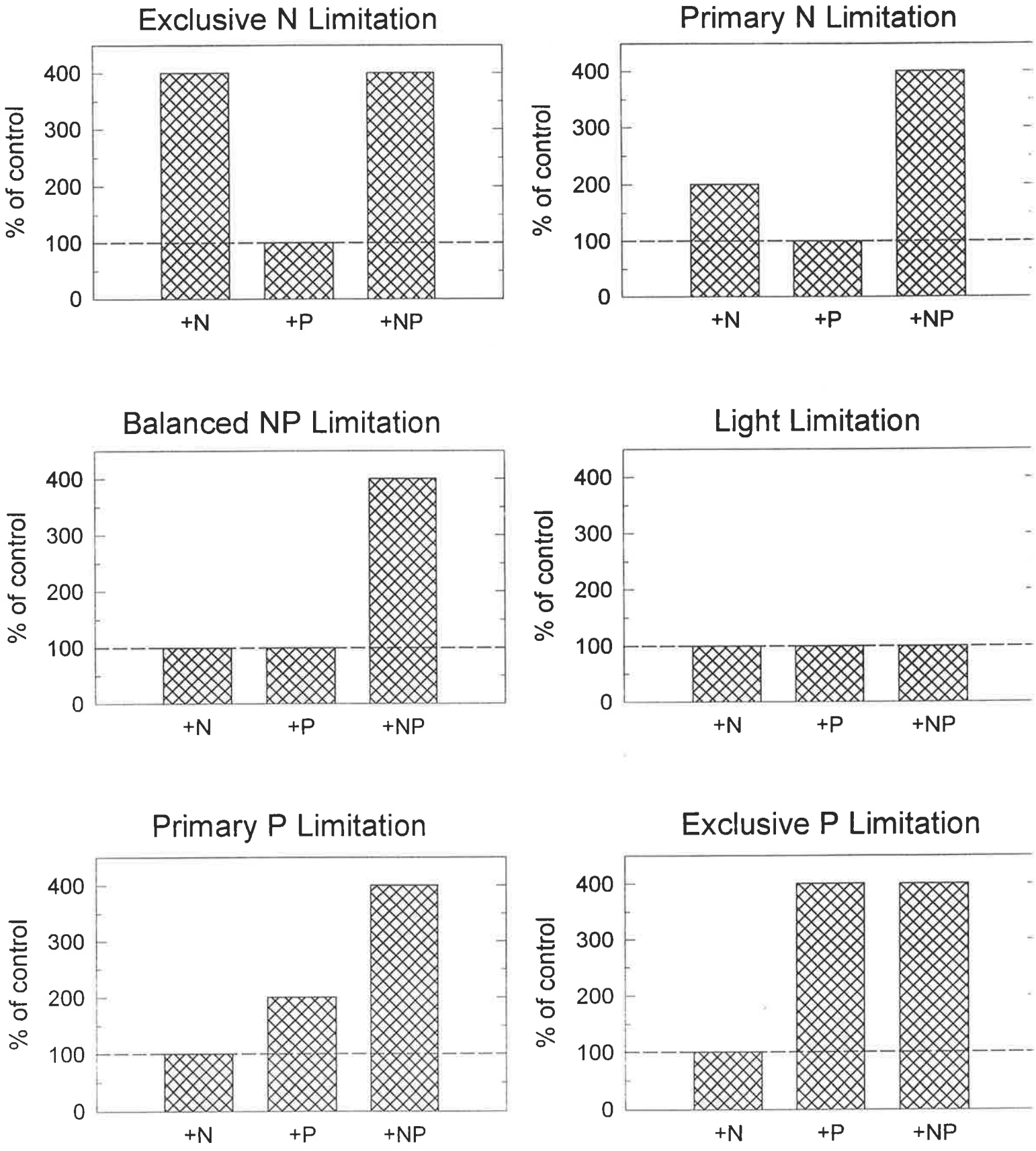

Fig. 2. Conceptual model for the classification of nutrient addition bioassays performed after 1 July 92.

1981), in preference to the ambient nitrate under low-growth, light-limited conditions. Therefore, any classifications of EXN, PRN, or BNP with [NO_3] > 10 μM (0.14 mg NO_3-N L^{-1}) were reclassified as XN1, XN2, or XN3, respectively. The 10 μM cutoff was chosen as a level twice the normal range of half-saturation constants for uptake of nitrate, an amount adequate to saturate uptake rates (McCarthy 1981). These new classifications were then grouped with NOR responses in statistical summaries, since it was likely that the populations were really light-limited, with sufficient ambient N and P.

Indices of nutrient and light limitation were computed using the classified bioassays. After excluding the INC bioassays, an index was calculated by weighting each bioassay as shown in Table 3 and dividing by the total number of bioassays. This procedure yields a number ranging from 0, indicating no limitation, to 1, which indicates complete N, P, or light limitation.

In addition to bioassays, we are using physiological indicators of nutrient limitation. P deficiency is indicated by alkaline phosphatase activity and particulate C:P and N:P; N deficiency is indicated by intracellular amino acid ratios, [DIN], and particulate N:P. Details of the alkaline phosphatase and intracellular amino acid methods are described below.

Alkaline phosphatase is a cell surface enzyme, the activity of which is enhanced under P stress (Healey and Hendzel 1979). Duplicate 15 ml subsamples from each station were incubated at in situ temperature with 10 μM methy-umbelliferyl phosphate (MUF-

Table 3. Weighting factors used to compute indices of N, P, and light limitation of algal growth in Chesapeake Bay using nutrient addition bioassays. Each classified bioassay (see Table 2 and Fig. 2) contributed the amounts shown below to the index, which was then divided by the total number of bioassays. Each index = $(\sum w)/n$, where w is the weighting factor assigned to each of the n bioassays. This results in an index ranging from 0 (no limitation) to 1 (completely limited). Abbreviations: EXN = exclusive N; PRN = primary N; BNP = balanced NP; PRP = primary P; EXP = exclusive P; NOR = no response to added nutrients.

	weighting factors					
Type of Index	EXN	PRN	BNP	PRP	EXP	NOR
N limitation	1.00	0.75	0.50	0.25	0.00	0.00
P limitation	0.00	0.25	0.50	0.75	1.00	0.00
Light limitation	0.00	0.00	0.00	0.00	0.00	1.00

PO_4) for 20-60 minutes, depending on season (shorter incubations in spring, longer at other times of year). Hydrolysis of the non-fluorescent MUF-PO_4 by alkaline phosphatase activity in the live planktonic community was indicated by fluorescence of MUF at pH 10. Rates of hydrolysis were normalized to chlorophyll a.

The intracellular concentrations of amino acids are used as an indicator of N limitation. The intracellular ratio of glutamine to glutamate has been shown to be related to N status of cultured and natural phytoplankton populations (Flynn et al. 1989, 1993, 1994). Both amino acids are essential to the assimilation of ammonium in the cyclic GS/GOGAT enzyme system. Glutamate with 1 amino group reacts with ammonium to form glutamine with 2 amino groups, and the glutamine reacts with α-oxoglutarate with no amino groups to regenerate two glutamates (Syrette 1981). The relative abundance of glutamate (glu) and glutamine (gln) reflects both the extracellular DIN supplying the amination of glu to gln as well as the supply of fixed C (α-oxoglutaric acid) from photosynthesis.

We used a standard HPLC procedure for intracellular amino acids. Concentrations were measured by lysing particulate samples on GFF filters at 80°C in deionized water, followed by HPLC analysis of the filtered extracts with a Hewlett Packard model 1090 series II HPLC using the HP AminoQuant Series II protocol. Dissolved, free amino acids were tagged using OPA and separated using reversed-phase gradient HPLC (L. Van Heukelem, HPEL analytical services lab, pers. com.).

Results

spatial and temporal variability

Planktonic populations at all stations showed a variety of responses to added nutrients over the period of study (Table 4). Of the 601 bioassays conducted between August 1990 and December 1996, 415 (69 %) exhibited significant responses to either N or P. Light limitation (NOR, no response to nutrient additions) was less common (16 %), although NOR was the dominant response at the tidal fresh stations. Inconsistent bioassays, those not meeting the criteria of Table 2, were a small percentage of the total (13 %), and bioassays classified as XN1, XN2, and XN3 (high ambient nitrate with a response to experimentally added ammonium) were collectively the smallest group (3 %).

Examples of bioassays showing light, primary N, and primary P limitation are shown in Fig. 3. In the example of light limitation, there were responses in all treatments relative to the initial conditions, including the control. Chlorophyll a (horizontal barring) showed the strongest increase. However, there were no significant increases in any treatments relative to the control. We interpret this as a response from an energy-starved algal population deeply mixing in an optically shallow water column (light limitation). The other two examples of primary N and primary P limitation showed nearly equal increases in both chlorophyll a and ^{14}C fixation in the N or P treatments, but the greatest responses occurred in the N+P treatments. Hence

Table 4. Summary of bioassay results at the ten stations over the period August, 1990 through December, 1996. The number of bioassays classified in each type of responses at each station are given. Abbreviations: EXN = exclusive N limitation, PRN = primary N limitation, BNP = balanced NP limitation, PRP = primary P limitation, EXP = exclusive P limitation, NOR = no response (nutrient saturation, light limitation), INC = inconsistent, and XN = N responding bioassays with NO_3 > 10 μM (0.14 mg NO_3-N L^{-1}, see Table 2). Within each group, stations are arranged from most fresh to most saline, with the main bay stations first and tributary stations arranged from north to south and from tidal fresh to mesohaline. The last three lines are indices of N, P, and light limitation computed from bioassay responses.

	main bay stations			Balt.H.	Choptank River		Patuxent River		Potomac River		
type	MCB3.3C	MCB4.3C	MCB5.2	MWT5.1	MET5.1	MET5.2	PXT0402	XDE5339	XEA6596	MLE2.2	Σ
EXN	3	3	2	0	10	11	12	16	0	4	61
PRN	11	20	21	0	1	21	3	24	0	20	116
BNP	10	13	17	0	0	4	1	10	1	10	95
PRP	21	23	16	8	0	13	0	6	6	17	107
EXP	4	8	5	4	0	0	1	3	8	5	36
NOR	14	6	9	6	13	7	15	8	17	9	95
INC	11	5	11	6	14	8	5	6	8	6	80
XN	5	3	1	2	0	3	3	0	2	2	21
Σ	79	81	82	26	38	67	40	73	42	73	601
N index =	0.34	0.42	0.43	0.11	0.45	0.57	0.46	0.60	0.06	0.43	0.44
P index =	0.44	0.50	0.44	0.56	0.01	0.30	0.07	0.28	0.41	0.43	0.38
Light in.=	0.22	0.08	0.13	0.33	0.54	0.13	0.47	0.12	0.53	0.14	0.18

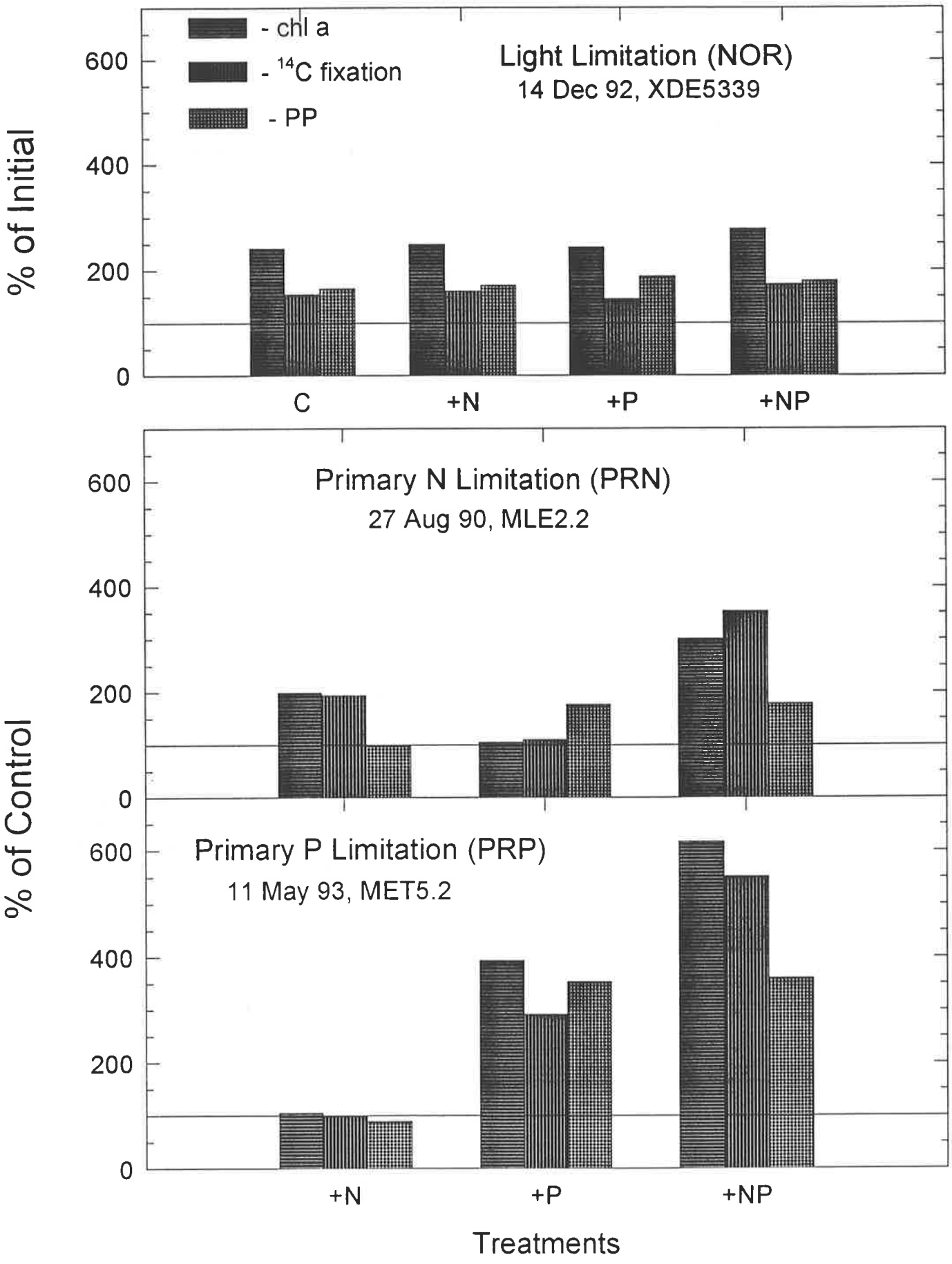

Fig. 3. Examples of bioassays showing light (NOR), primary N (PRN), and primary P (PRP) limitation. C = control, +N = NH_4 addition, +P = PO_4 addition, +NP = NH_4 and PO_4 addition. Horizontal line (100%) = no response relative to control or initial.

one nutrient supplied the primary limiting element, but the small surplus of the other was depleted when an excess of the primary limiting element became available.

PP responses occurred only when P was added (+P, +NP) and were largest under primary P limitation. However, increases in PP were also significant in the primary N bioassay, indicating that internal P pools were not completely filled. The frequency of each bioassay classification at all stations is shown in Fig. 4.

There was considerable spatial variability in the bioassay results. Indices of algal growth rate limitation at each station over the period of study typically varied between 0.1-0.6 (Table 4), and no station could be categorized as limited by only one resource (light, N, or P). Based on their responses to nutrient additions, the stations fell into three groups: (1) the three main bay stations (MCB3.3C, MCB4.3C, and MCB5.2) plus the Choptank and Potomac mesohaline stations (MET5.2 and MLE2.2), (2) the Patuxent mesohaline station (XDE5339), and (3) the three tidal fresh stations (MET5.1, PXT0402, and XEA6596). Bioassay results from a station within each group are given in Figs. 5-7.

Five mesohaline stations (group 1) showed regular seasonal changes in bioassay responses (see Fig. 5 for an example). During winter (December - February), there were usually weak or no significant responses to N or P additions relative to the control (light limitation - see Fig. 3). During spring (March - May), there were usually no significant responses to N additions, but algal growth rates responded to P and N+P (primary P limitation -

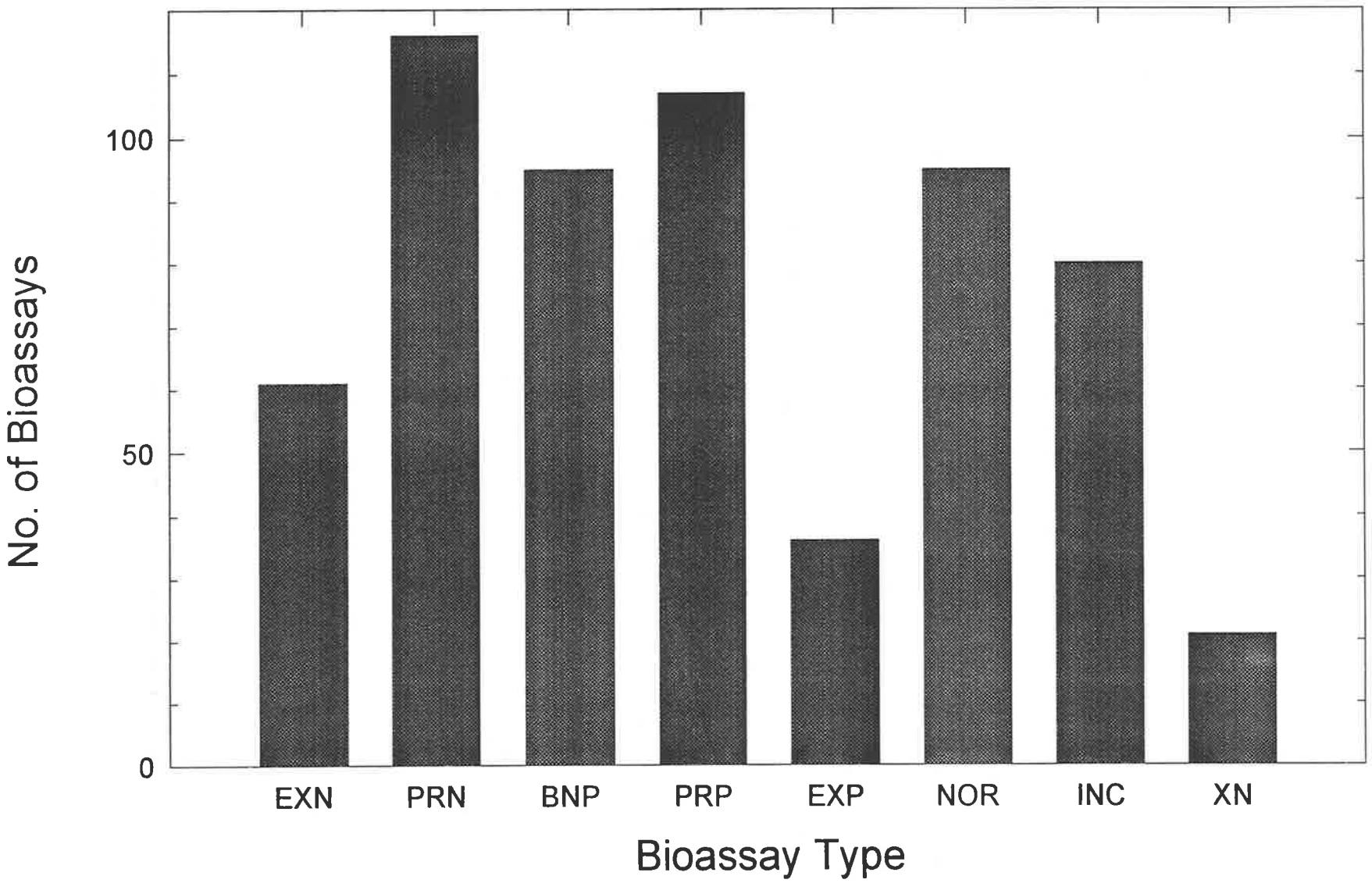

Fig. 4. Frequency distribution of bioassay response types for all stations over the period Aug. 1990 - December 1996. Total bioassay number = 601. Bioassay classification types are defined in Table 2 and Fig. 2.

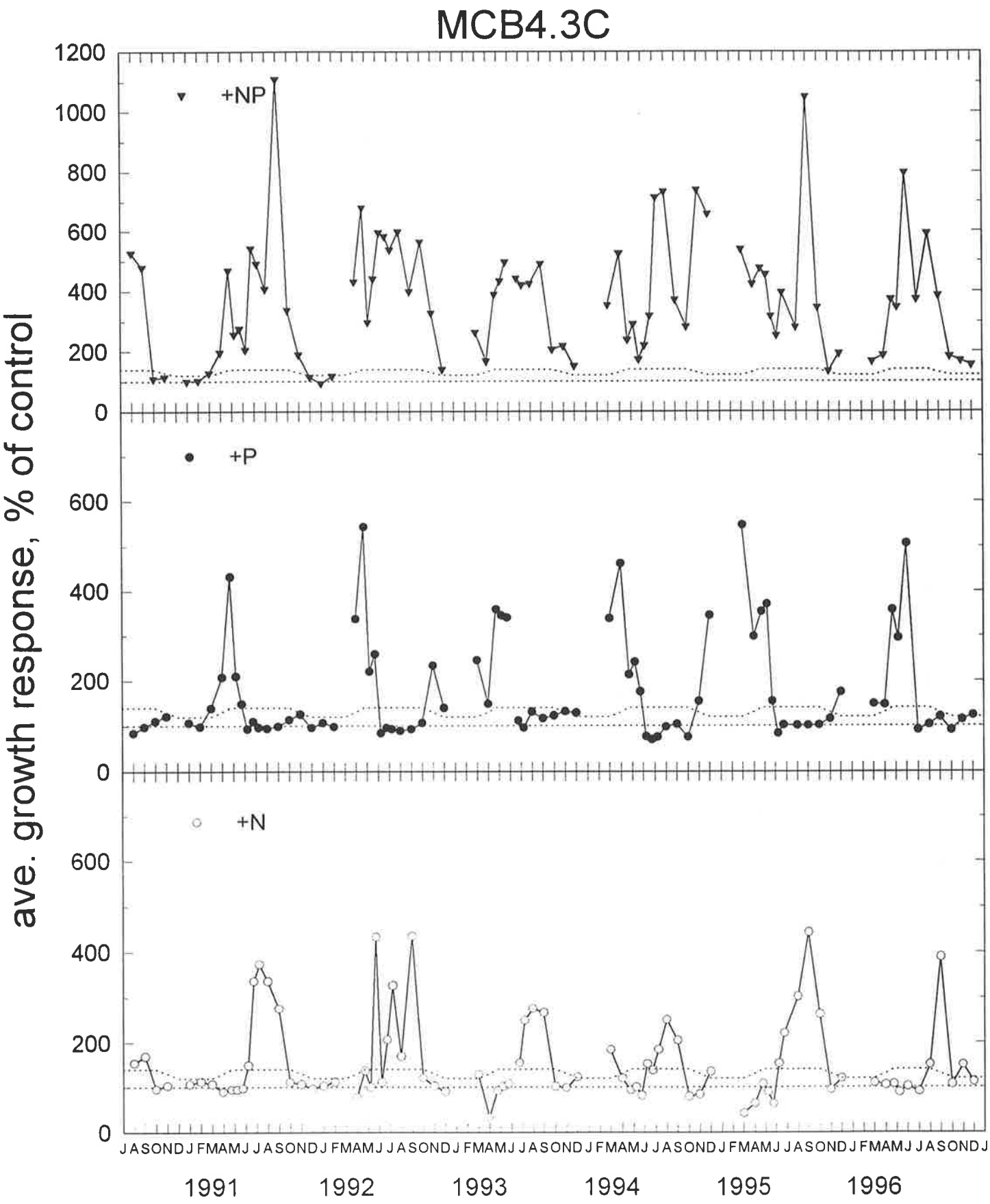

Fig. 5. Bioassay results at the mesohaline main bay station MCB 4.3C. Straight dotted lines represent 100% of control (no response), and fluctuating dotted lines represent seasonally varying thresholds for significant responses.

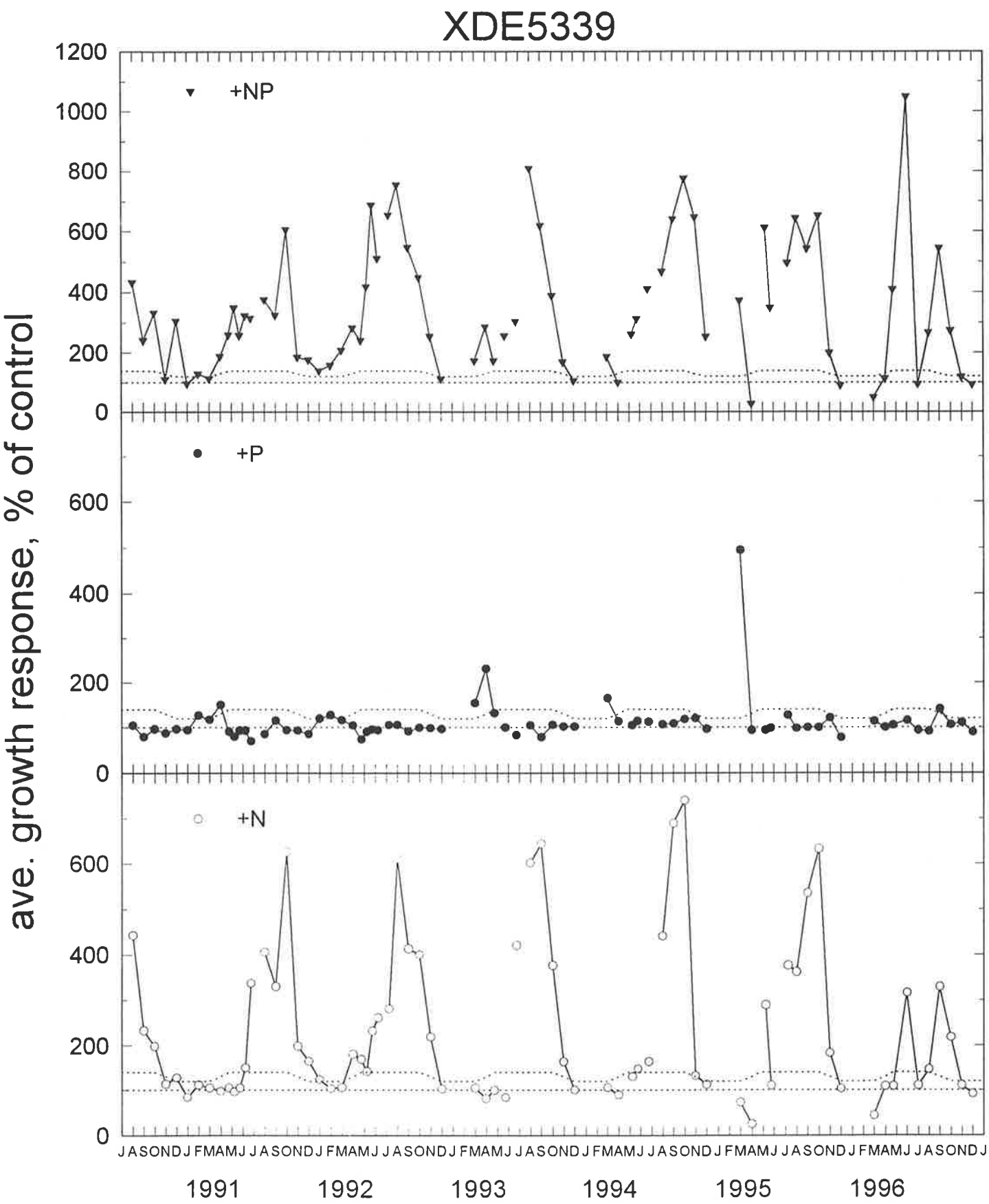

Fig. 6. Bioassay results at the mesohaline Patuxent station XDE5339. Straight dotted lines represent 100% of control (no response), and fluctuating dotted lines represent seasonally varying thresholds for significant responses.

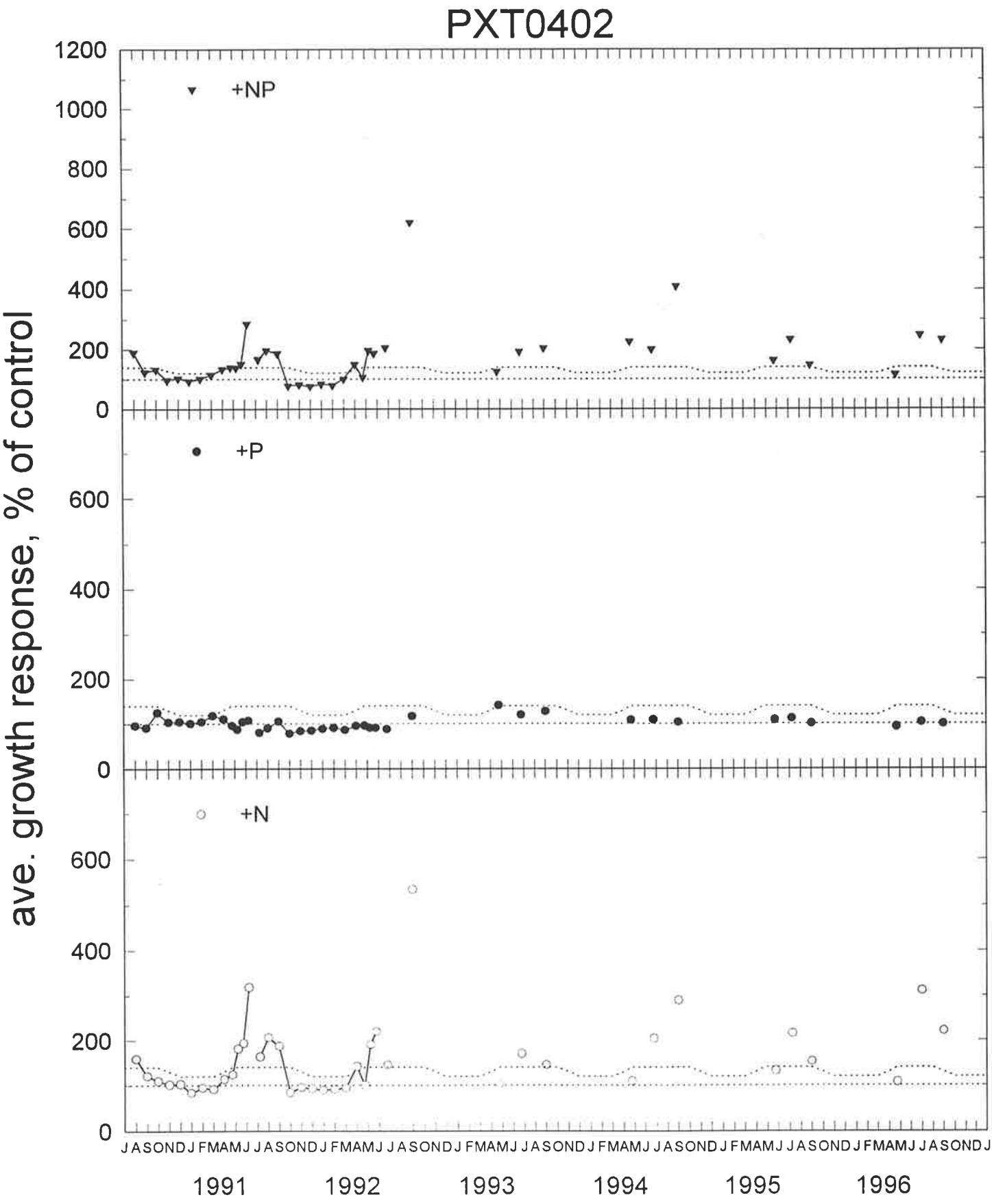

Fig. 7. Bioassay results at the Patuxent tidal fresh station PXT0402. Straight dotted lines represent 100% of control (no response), and fluctuating dotted lines represent seasonally varying thresholds for significant responses.

see Fig. 3). June was a transition month during which P responses declined and N responses increased. During summer (July - September), there were usually no responses to P alone, but growth rates responded to additions of N and N+P, which we interpreted as primary N limitation. During fall (October-November), P responses were also sometimes observed before a return to winter light limitation, most notably in 1992, 1994, and 1995 (middle panel of Fig. 5).

The mesohaline Patuxent (XDE5339) was considerably different from the other five mesohaline stations (Fig. 6). XDE5339 exhibited only a few significant responses to P in spring, and the N responses were larger, extended into the fall, and were nearly equivalent to the N+P additions. This station clearly is more N and less P limited throughout the year than the other mesohaline stations (contrast Figs. 5 and 6).

The three tidal fresh stations were much more light-limited than the other two groups (see Fig. 7 for an example). These stations showed only a few significant P or N responses, mainly in summer when DIN or PO_4 were occasionally depleted. In general, these stations are turbid and nutrient-rich, and phytoplankton populations are primarily light-limited.

The seasonal progression in the limiting resource for the five similar mesohaline stations can be visualized more readily in Fig. 8 (MCB4.3C). This figure illustrates the monthly mean flow of the Susquehanna River (top panel) and average monthly indices of resource limitation over the period of record (bottom

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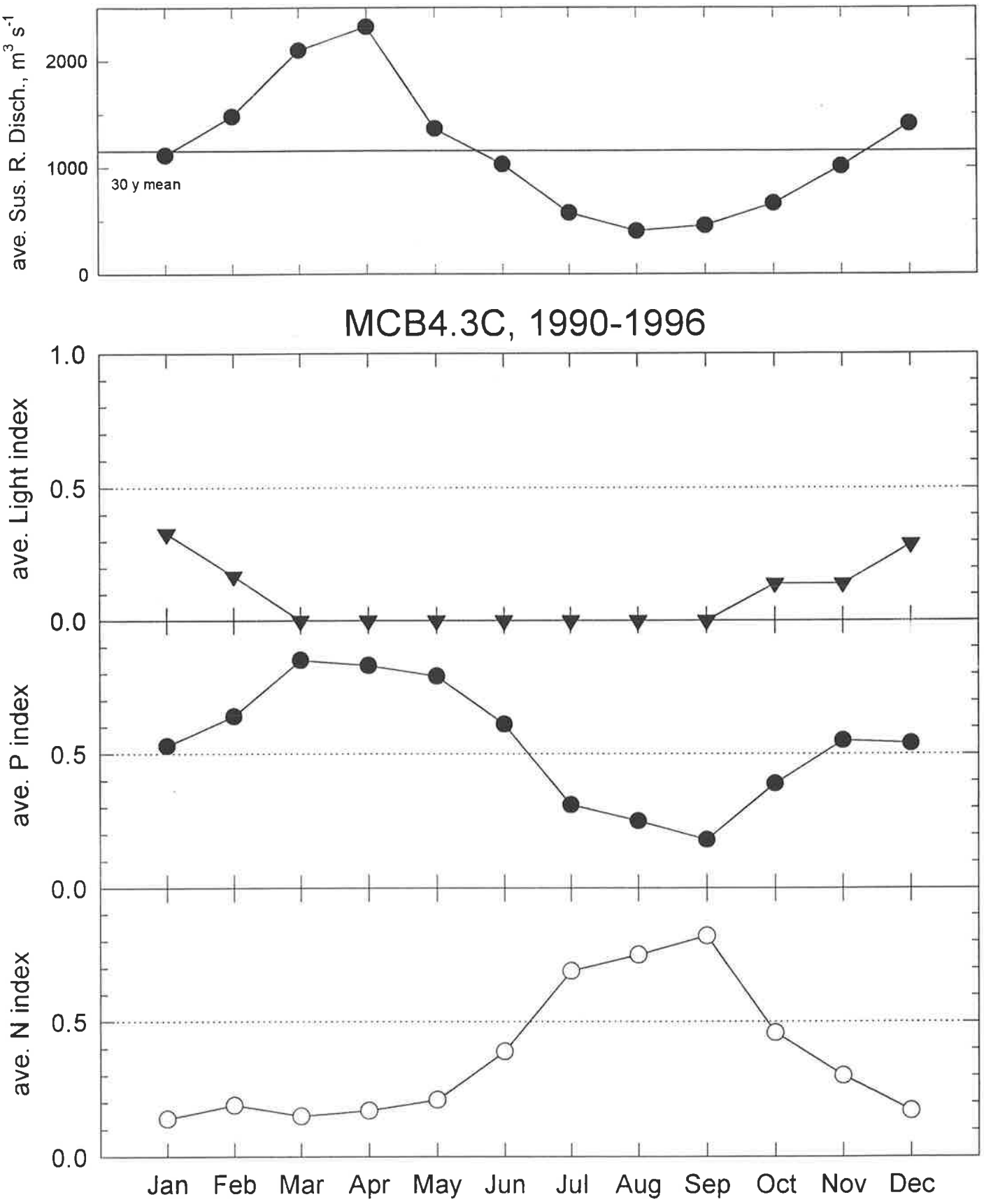

Fig. 8. Monthly summary of Light, P, and N indices for mesohaline station MCB4.3C during 1990-1996. Values of the index > 0.5 indicate dominance by that resource.

three panels). Light and P are the primary limiting resources in winter (Dec.-Feb.); P is limiting during spring (Mar.-May); and, N is the primary limiting resource in summer and early fall (June-Sept.), with a brief return to P limitation in late fall. These seasonal changes appear to be the result of low light and temperature in winter, large inputs of fresh water with high DIN/PO_4 in spring, large fluxes of PO_4 from sediments following the development of anoxia in bottom waters in late spring, and turnover (reaeration) of the water column in October.

The monthly summary of indices for the mesohaline Patuxent (XDE5339, Fig. 9) shows a much reduced role for P at this station. Since the computation of the indices does not include the magnitude of the response, the indices in Fig. 9 magnify the effect of the small responses to P in spring in Fig. 6. However, the brief dominance of P and longer dominance of N is clearly shown. The lesser importance of P at this station is probably due to sewage inflows with low N/P and lower seasonal variation of flow in the Patuxent (spring:summer = 3:1 compared to 6:1 in the Susquehanna; compare top panels of Fig. 8 and 9).

The monthly summary of indices for the example of a tidal fresh station (PXT0402, Fig. 10) shows a dominant role for light limitation. Responses to added nutrients were observed only in summer (high temperatures and low flow) when N (Patuxent, Choptank) or P (Potomac) was depleted. These stations represent small volumes and areas of Chesapeake Bay and are turbid, nutrient-rich transition zones with short water residence times.

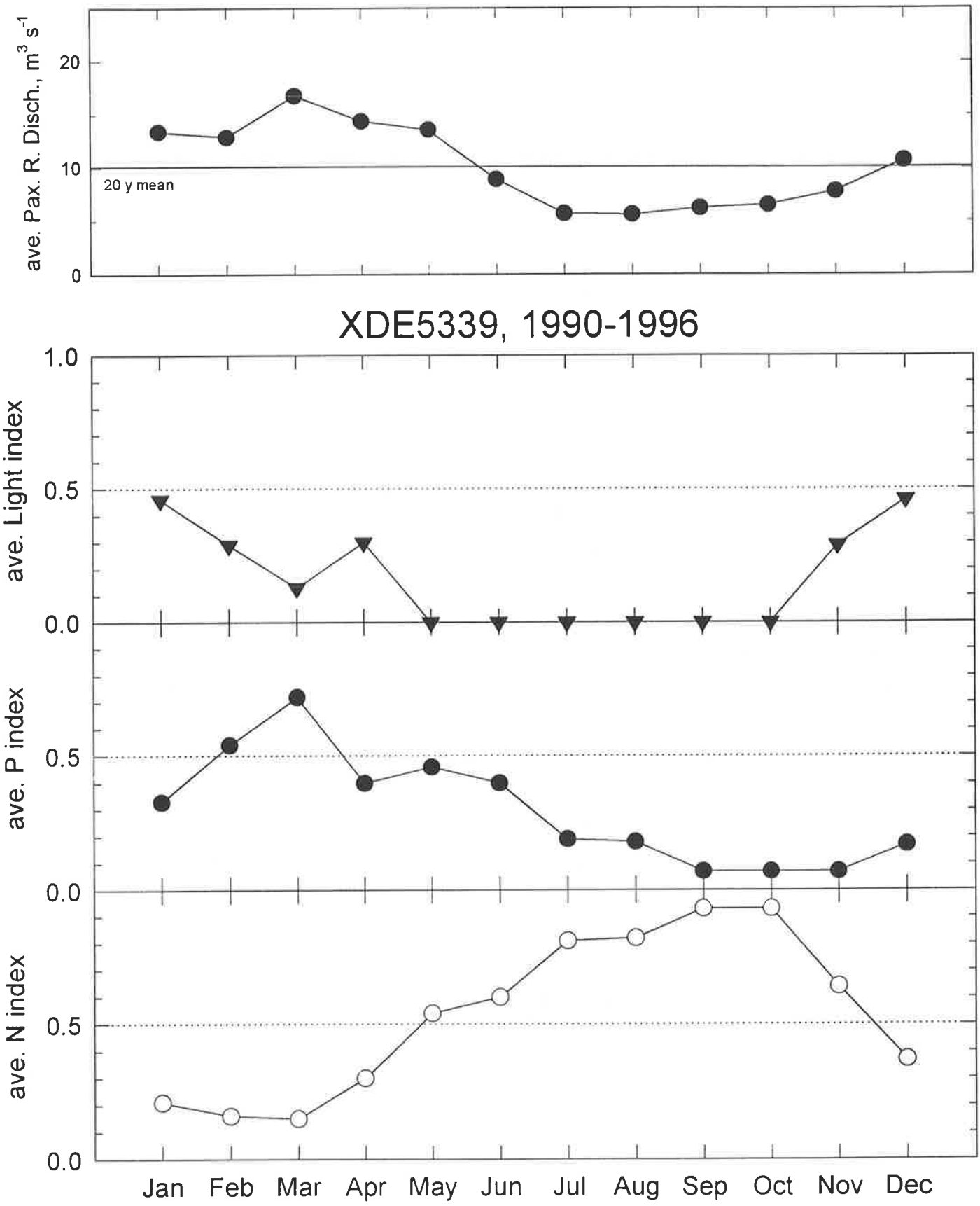

Fig. 9. Monthly summary of Light, P, and N indices for mesohaline station XDE5339 during 1990-1996. Values of the index > 0.5 indicate dominance by that resource.

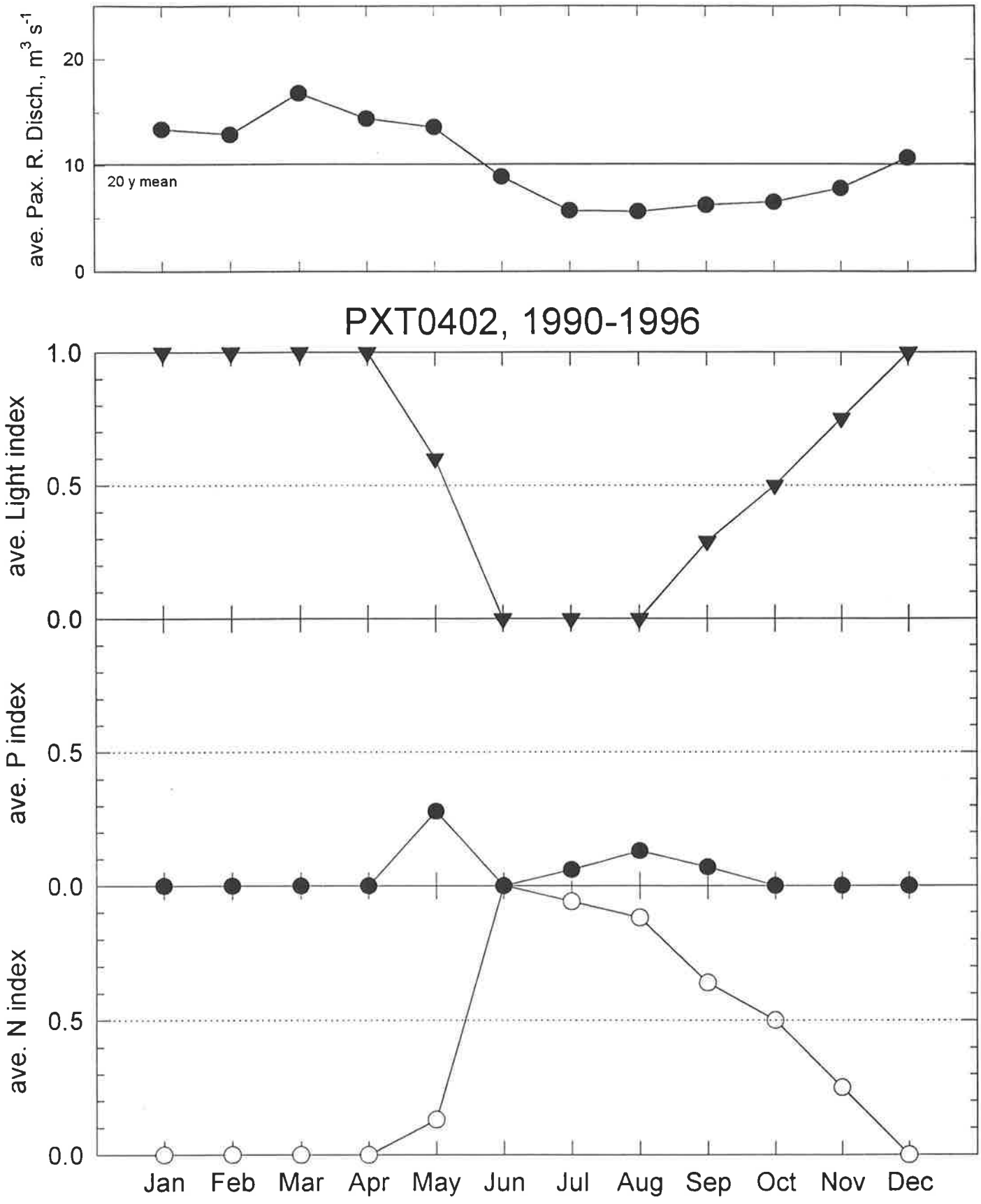

Fig. 10. Monthly summary of Light, P, and N indices for tidal fresh station PXT0402 during 1990-1996. Values of the index > 0.5 indicate dominance by that resource.

The dominance of light limitation for much of the year is expected in these regions.

Interannual trends at the three stations are shown in Figs. 11-13. At main Bay station MCB4.3C, representative of the five similar mesohaline stations, there was a clear reduction in light limitation and increases in N and P limitation, particularly from 1990 to 1993. Wet years in 1994-1996 may have obscured the earlier trends in water quality improvement. At the Patuxent mesohaline station (XDE5339, Fig. 12), the only trend was a reduction in the annual N index unrelated to variations in river discharge. Light and P indices varied little over the seven year period. At the tidal fresh statons, there were no consistent interannual trends in indices, although there is a suggestion of a lagged effect of wet years (see Fig. 13).

Diagnostic Indicators of Resource Limitation

We have identified several diagnostic indicators which are correlated with bioassay results. Extracellular dissolved inorganic N (DIN) and intracellular amino acid ratios (glutamine/glutamate, gln/glu) are indicators of N limitation, and extracellular phosphate (PO_4) and alkaline phosphatase activity (Alk. Pase) are indicators of P limitation. We have also explored the use of three molar ratios as indicators of both N and P limitation: particulate organic C/particulate P (POC/PP), particulate N/particulate P (PN/PP), and DIN/PO_4. Summary statistics are shown in Table 5. In the coming year, we plan to

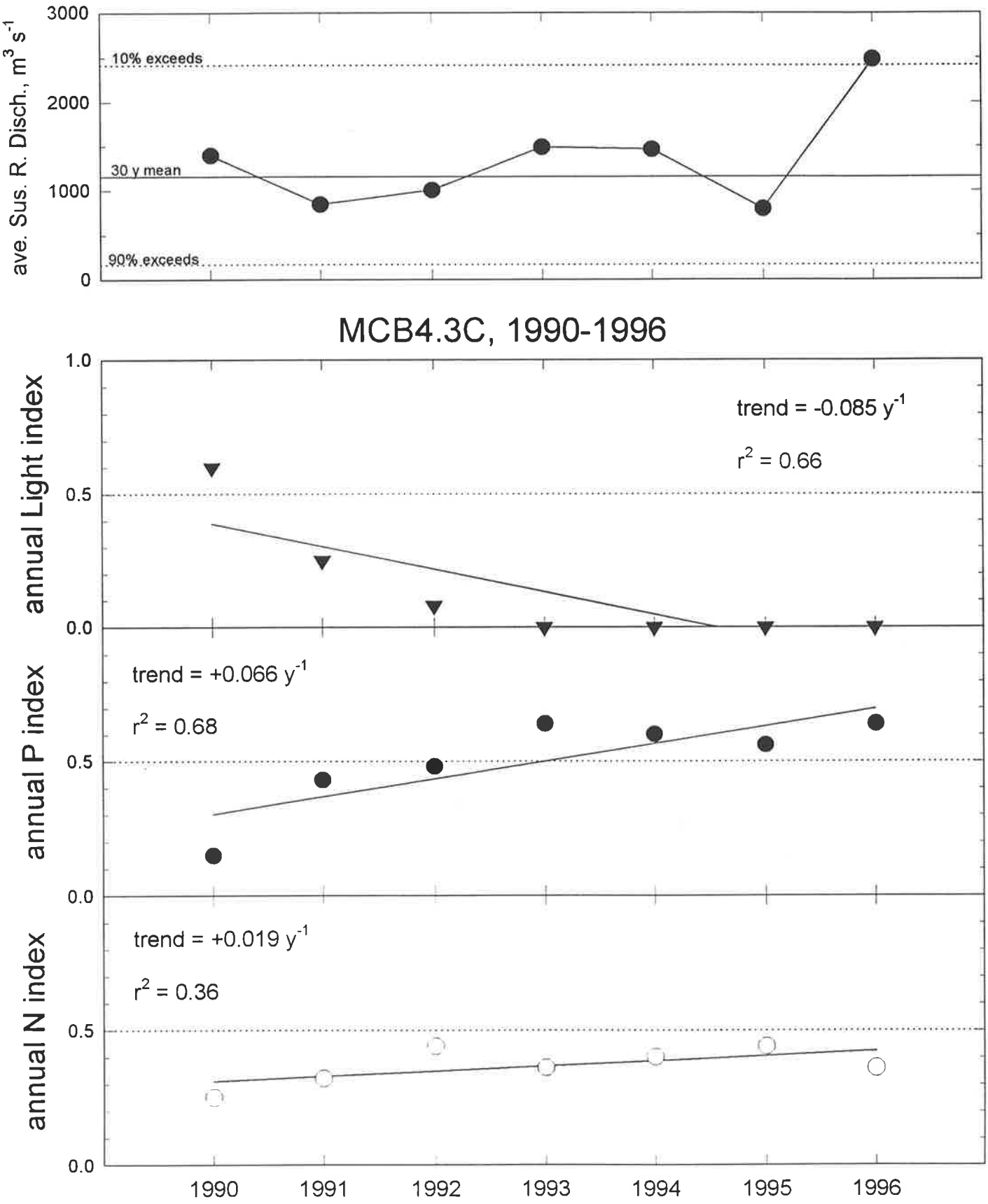

Fig. 11. N, P, and Light indices at mesohaline station MCB4.3C during calendar years 1990-1996. Indices > 0.5 indicate the dominant resource limiting phytoplankton growth in each year. Discharge data in top panel from USGS.

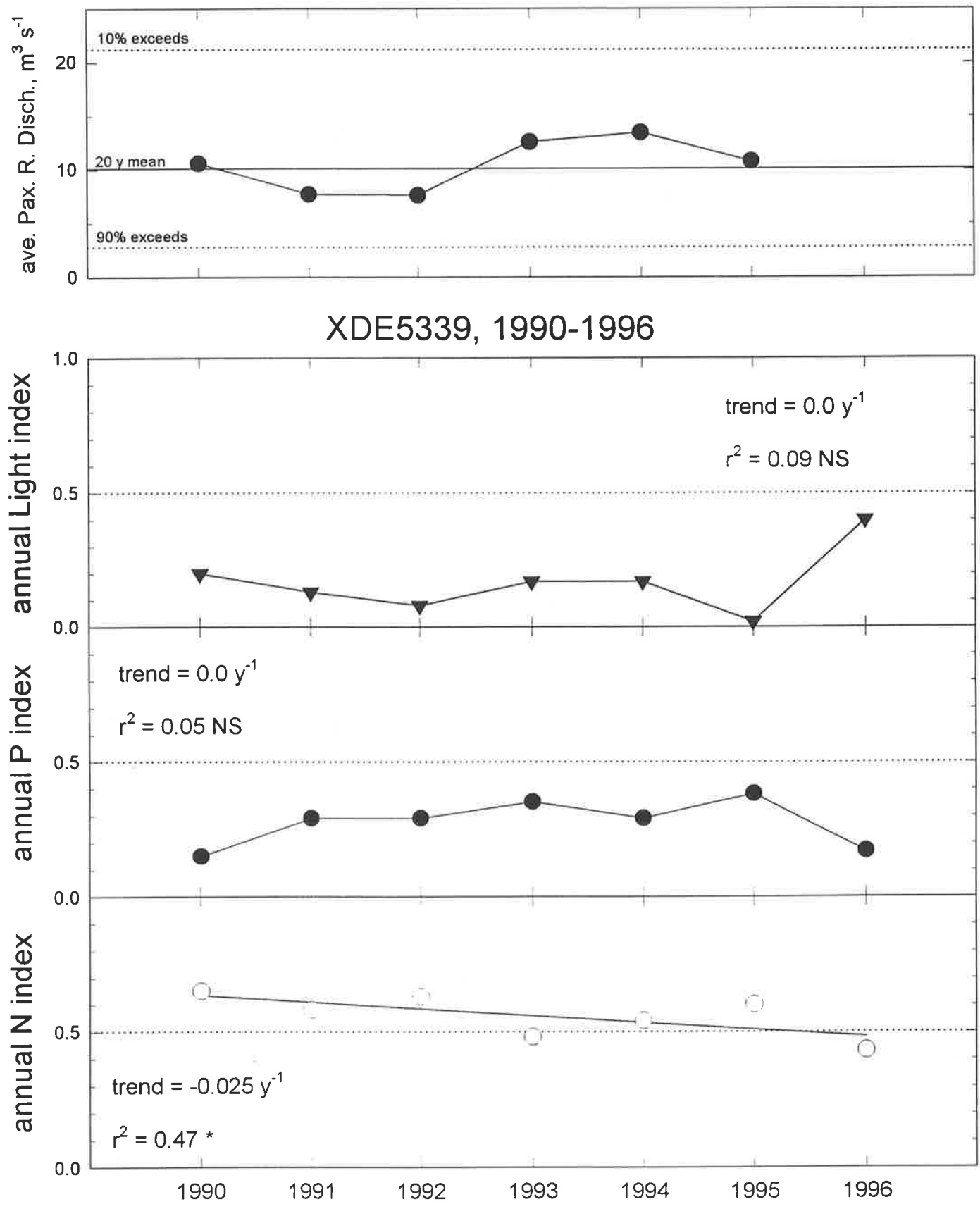

Fig. 12. N, P, and Light indices at mesohaline station XDE5339 during calendar years 1990-1996. Indices > 0.5 indicate the dominant resource limiting phytoplankton growth in each year.

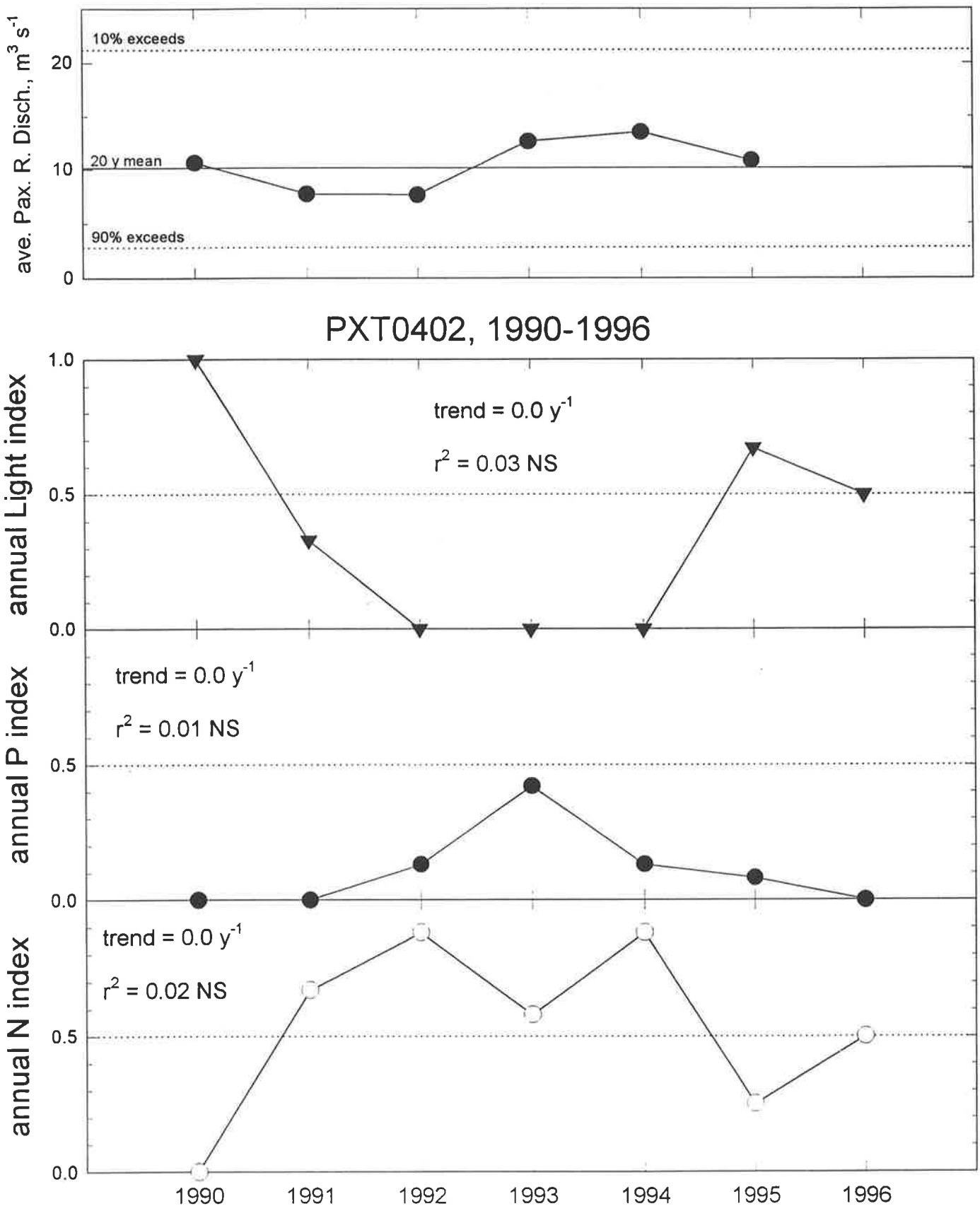

Fig. 13. N, P, and Light indices at tidal fresh station PXT0402 during calendar years 1990-1996. Indices > 0.5 indicate the dominant resource limiting phytoplankton growth in each year.

Table 5. Statistics on indicators of resource limitation in Chesapeake Bay for the seven bioassay classifications and for all (summary) observations. The mean and standard errors were computed for untransformed data.

indicator	statistic	EXN	PRN	BNP	PRP	EXP	INC	NOR	ALL
DIN	n	37	86	43	70	22	26	36	341
	minimum	0.0	0.0	0.0	1.6	12.3	0.0	0.5	0.0
	maximum	6.3	7.6	12.6	171.5	144.7	89.6	283.3	283.3
	mean	0.9	1.3	5.4	35.7	46.8	21.7	46.1	20.4
	std. error	0.2	0.2	0.6	3.3	6.8	4.8	8.8	1.7
gln/glu	n	10	18	13	18	9	1	16	91
	minimum	0.05	0.07	0.00	0.04	0.06	0.13	0.00	0.00
	maximum	0.69	0.48	0.41	0.91	10.58	0.13	2.97	10.58
	mean	0.18	0.20	0.21	0.49	2.29	0.13	0.52	0.53
	std. error	0.06	0.03	0.03	0.08	1.11	-	0.17	0.13
POC/PP	n	37	85	43	65	22	26	35	331
	minimum	40.2	42.9	45.7	67.9	48.4	34.8	45.7	34.8
	maximum	133.1	514.9	993.0	721.7	499.8	1064.4	482.2	1064.4
	mean	82.4	117.2	172.8	175.2	179.9	196.7	135.7	147.8
	std. error	3.4	9.5	24.7	16.3	24.5	52.2	17.2	7.3
PN/PP	n	37	85	43	65	22	26	35	331
	minimum	5.7	5.7	8.1	8.9	7.2	5.5	5.6	5.5
	maximum	21.3	66.3	97.6	71.5	66.5	123.5	62.8	123.5
	mean	11.3	16.7	25.1	25.0	23.4	24.3	18.5	20.0
	std. error	0.5	1.3	2.9	1.7	2.9	5.2	2.3	0.9
DIN/PO_4	n	37	86	43	70	22	26	36	341
	minimum	0.0	0.0	0.4	13.6	27.7	0.0	1.1	0.0
	maximum	58.0	237.0	1003.0	>9999	4073.0	1142.2	3147.3	> 9999
	mean	6.9	22.3	114.4	1151.9	752.4	282.8	375.4	411.4
	std. error	2.1	4.3	25.7	268.3	185.8	58.1	98.3	63.8
AP/chla	n	35	80	43	70	21	25	36	331
	minimum	0.3	0.6	0.8	0.7	0.8	1.2	0.1	0.1
	maximum	17.8	65.2	173.4	170.2	244.1	237.9	75.0	244.1
	mean	4.2	11.5	28.1	29.8	26.8	28.1	11.9	19.2
	std. error	0.7	1.4	5.3	4.1	11.8	10.0	2.7	1.7
PO_4	n	37	86	43	70	22	26	36	341
	minimum	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
	maximum	1.41	1.34	0.30	1.04	1.23	0.61	1.30	1.30
	mean	0.36	0.14	0.08	0.10	0.23	0.10	0.30	0.18
	std. error	0.05	0.02	0.01	0.02	0.07	0.02	0.06	0.01

explore the number of optical depths in the surface mixed layer an indicator of light limitation.

Indicators of N limitation are shown in Fig. 14. Dissolved inorganic N (DIN = NH_4 + NO_2 + NO_3) is an excellent predictor of responses in the bioassays. EXN and PRN bioassay responses occurred primarily at low DIN, and concentrations of DIN <5 μM (0.07 mg DIN ℓ^{-1}) are a good predictor of N responses. At higher DIN, P and light limitation were observed. The intracellular amino acid ratio is also a good predictor of N limitation (top panel, Fig.14). Molar values of intracellular glutamine/glutamate are clearly related to the bioassay results and N stress, and values <0.5 (the Flynn index, Flynn et al. 1989, 1993, 1994) can be used to predict N responses.

The particulate and nutrient ratios can be used to identify both N and P limitation (Fig. 15). Low ratios of all three were associated with N responses in bioassays, and high ratios occurred under P limitation. Note that the two particulate ratios corresponded closely to Redfield elemental proportions, and the mean values within each bioassay classification deviated only by approximately a factor of 2 from 106:1 and 16:1. However, DIN/PO_4 associated with P limitation greatly exceeded the Redfield stoichiometry of 16:1. EXP and PRP responses in the bioassays only occurred at very high molar ratios of DIN/PO4 > 300:1 (excess DIN and depleted PO_4 - see Table 5), probably because of the use of intracellular poly-PO_4 reserves as a source of P. In fact, the general pattern of response in Fig. 15 is probably the

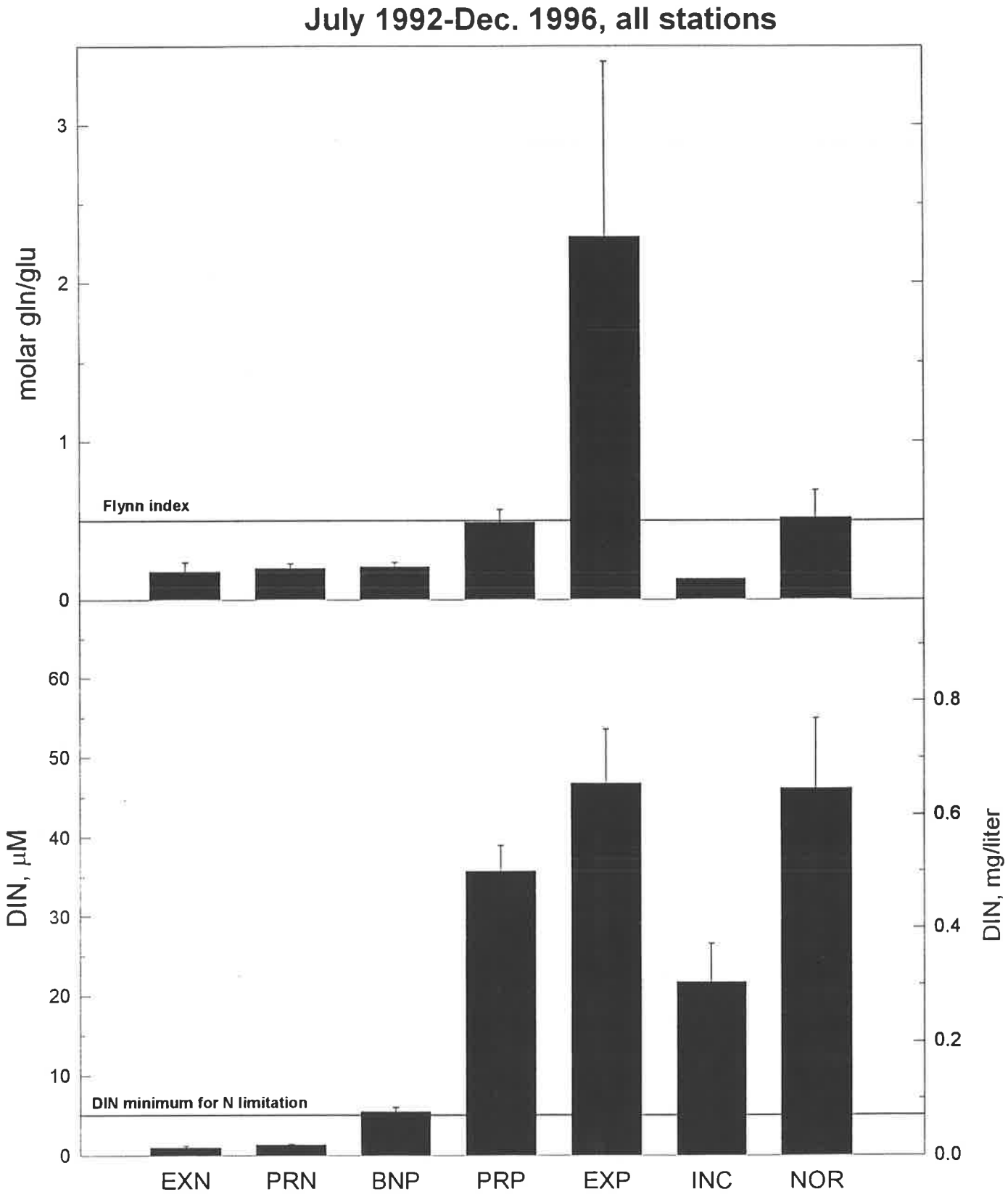

Fig. 14. Indicators of N limitation. Mean and standard error of dissolved inorganic N (DIN) and intracellular amino acid ratios (glutamine/glutamate) in Chesapeake Bay as a function of bioassay response type.

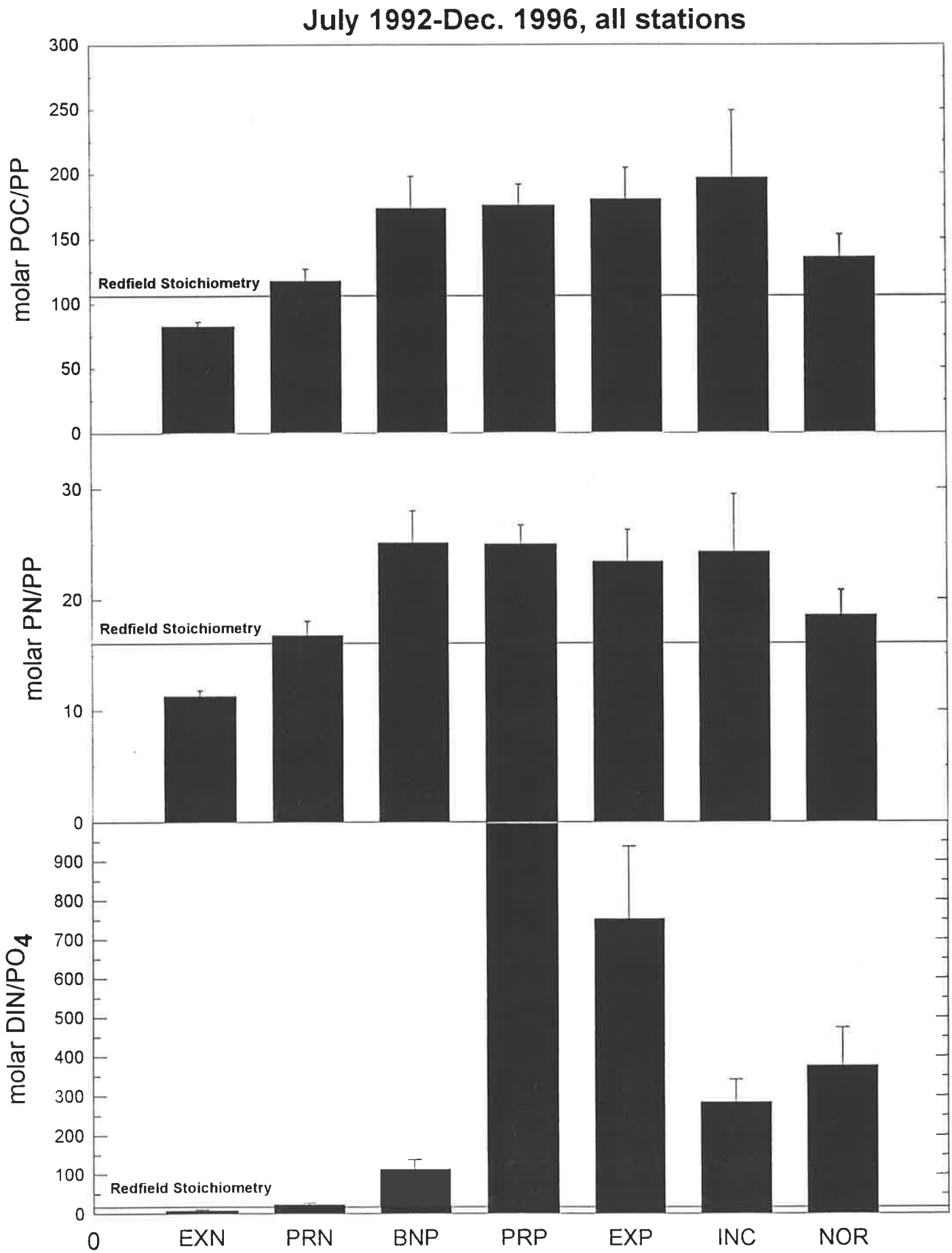

Fig. 15. Mean and standard error of molar ratios of POC/PP, PN/PP, and DIN/PO_4 in the plankton of Chesapeake Bay as a function of bioassay response type. Horizontal lines show Redfield stoichiometry.

result of relatively inflexible C and N content but varying P storage (Cembella et al. 1984). There is normally intracellular storage of poly-phosphates in P-sufficient plankton, and depletion of poly-phosphate stores in P-deficient plankton. Intracellular poly-PO4, perhaps normalized to PP, is another potential indicator of P limitation, but we have not investigated this parameter.

P limitation was readily identified by alkaline phosphatase activity (Fig. 16). Rates of activity in excess of 10 nmol PO_4 μg $chla^{-1}$ h^{-1} were associated with P responses; a similar level of activity (5 nmol PO_4 μg $chla^{-1}$ h^{-1}) was first suggested in culture studies of freshwater algae by Healey and Hendzel (1979), but our data suggest somewhat higher values for Chesapeake Bay. Our light limited bioassays (NOR) and N bioassays (EXN, PRN) exhibited mean activity levels of ~5-10 nmol PO_4 μg $chla^{-1}$ h^{-1}, while bioassays showing P responses had means >25 nmol PO_4 μg $chla^{-1}$ h^{-1}. Furthermore, the inconclusive bioassays (INC) also had very high activities, suggesting severe P deficiency and possible collapse of the control as a reason for the INC classification. Note that INC bioassays also had high particulate and nutrient ratios as well (Fig. 15).

Extracellular phosphate concentration was not a useful indicator of P limitation (Fig. 16). The highest average concentrations of PO_4 were associated with EXN, EXP, and NOR bioassays, indicating little predictability from PO_4 concentration alone. Note that the averages of all concentrations

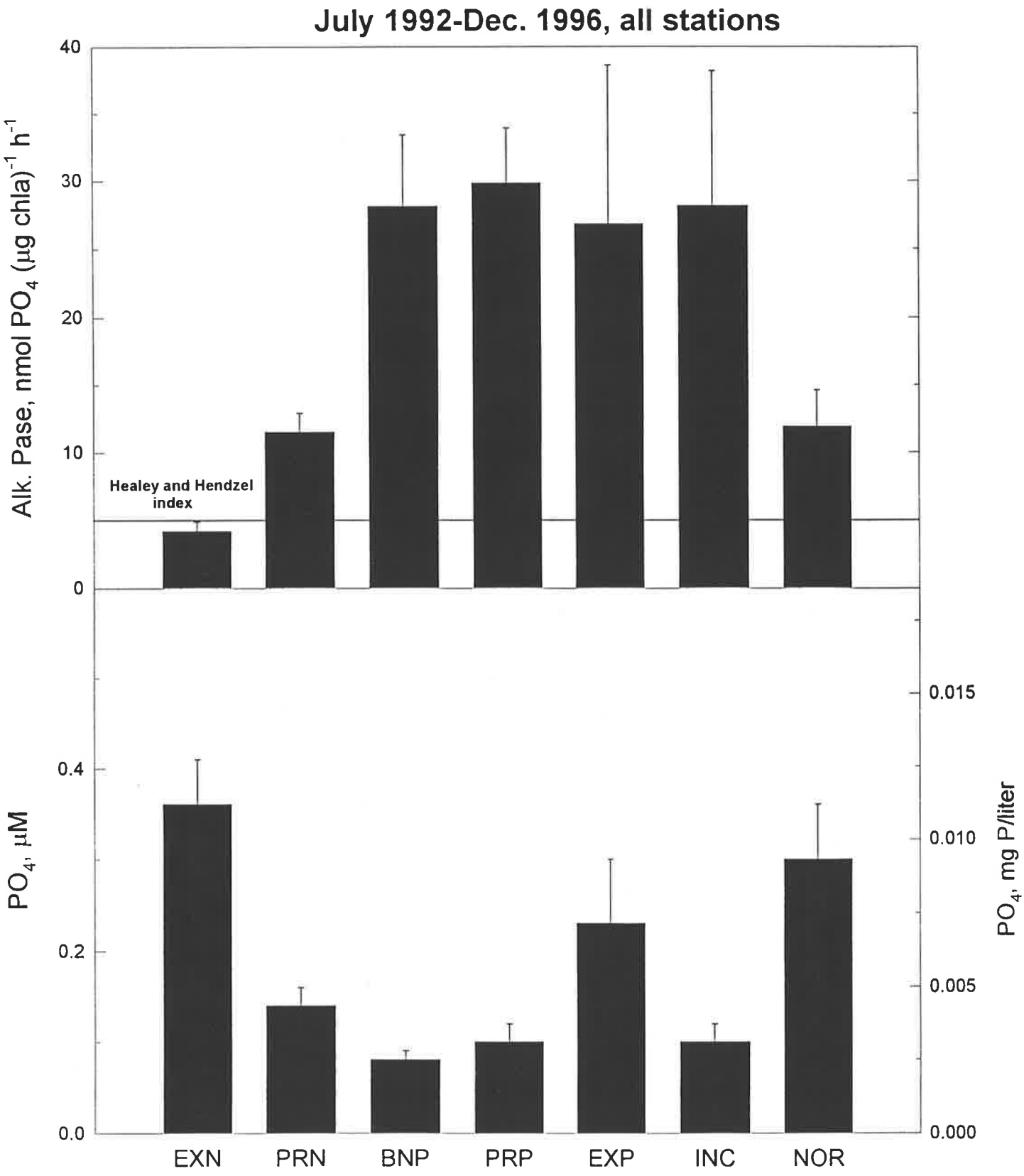

Fig. 16 Mean and standard error of dissolved reactive P (PO_4) and alkaline phosphatase activity per unit chlorophyll in Chesapeake Bay as a function of bioassay response type.

were quite low (0.1-0.4 μM or 0.002-0.012 mg PO_4-P ℓ^{-1}, see Table 5) and close to the colorimetric detection limit of ~0.02 μM (0.001 mg PO_4-P ℓ^{-1}), regardless of bioassay response. This suggests little excess P in Chesapeake Bay, even under N or light limitation, but also little predictive power for PO_4 concentration as an indicator of P limitation.

Discussion

spatial and seasonal variability

We have demonstrated considerable spatial variability in resource limitation in Chesapeake Bay. Tidal fresh stations were turbid and nutrient-rich, and we obtained primarily light-limited (NOR) bioassays, except in summer when nutrients were occasionally depleted (Figs. 7, 10). The mesohaline Patuxent showed brief P limitation only in early spring due to large sewage inputs (Figs.6, 9); however, the remaining mesohaline stations in the main bay, lower Choptank, and lower Potomac uniformly exhibited a consistent seasonal progression of light, P, and N limitation throughout the year (Figs. 5, 8).

We have related this spatial variation in the bioassay responses to the N/P of inputs reported by Boynton et al. (1995). High N/P of total N and P inputs indicates high availability of N relative to P, and low N/P indicates high availability of P relative to N. Long-term mean indices of resource limitation in

mesohaline regions of the MD waters of Chesapeake Bay were significantly related to the N/P ratio of total N and P inputs reported by Boynton et al. (1995), as shown in Fig. 17. As the input N/P increased (increasing N availability), the long-term mean N indices decreased and the long-term mean P indices increased. The index of light limitation also increased significantly with increasing input N/P, probably because the highest nutrient loadings near rivers are associated with high N/P ratios. Note that the Patuxent, with its large sewage inputs, had the lowest N/P, the lowest P index, and the highest N index of all regions. Likewise, the Patapsco (data available only for 1990-1992, see Fisher et al. 1992b) had the highest N/P of inputs, the lowest N index, and the highest P index. In spite of the fact that the input data are from an earlier period (mid 1980's) than the bioassay data (1990's), it is clear that the input ratios are largely responsible for the spatial variability in resource limitation described above and that manipulations of the inputs is likely to be detected by the indices of resource limitation computed from the bioassay results.

There were also large temporal changes in resource limitation. These appear to be associated with annual events such as the spring freshet, the onset of anoxia, and the fall overturn of the water column. Interannual trends were also associated with wet and dry years as well as changing nutrient inputs from the bay's watershed (e.g., Fig. 16).

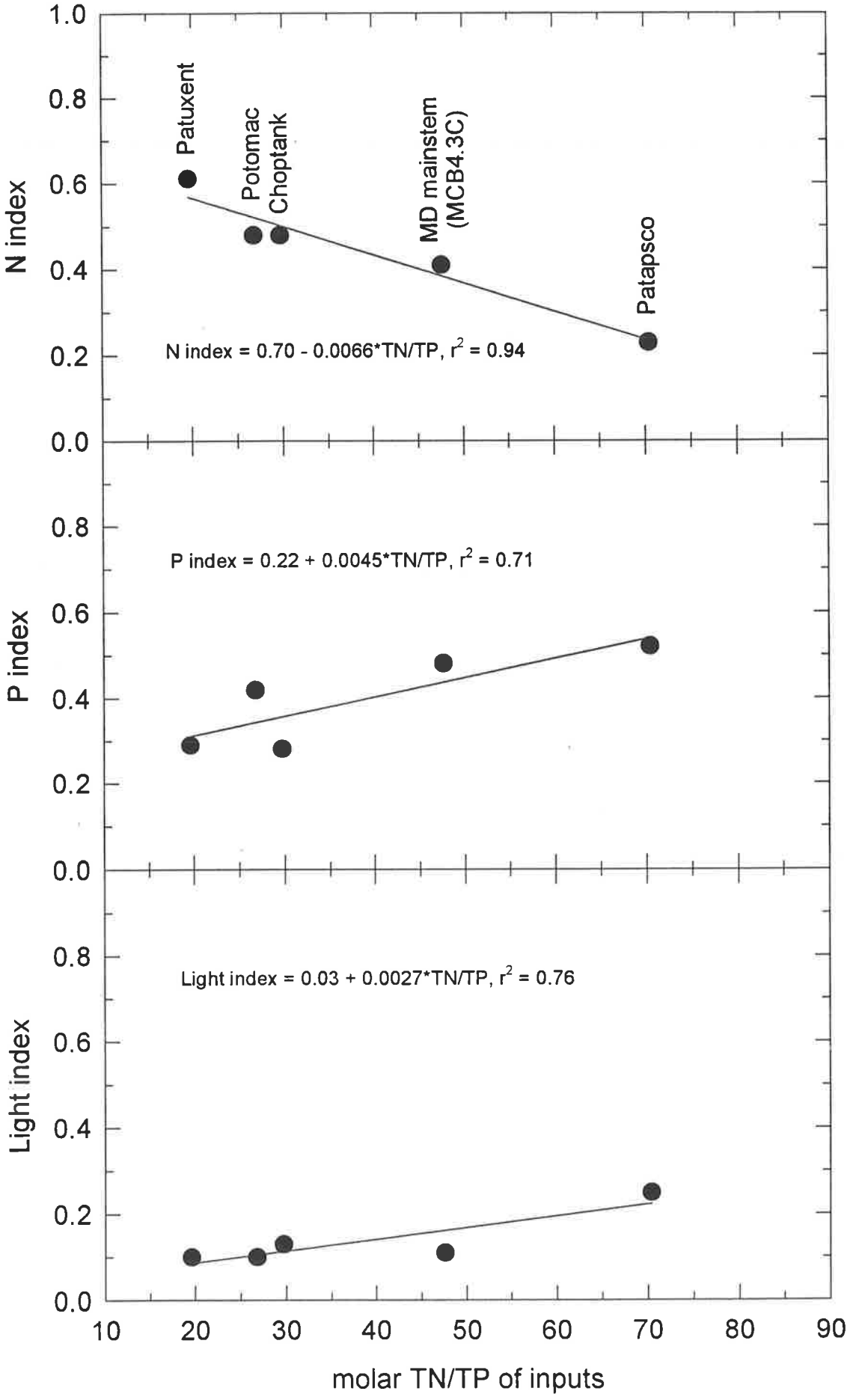

Fig. 17. Long-term mean indices of resource limitation at mesohaline stations (1990-1995) related to the molar ratio of nutrient inputs for the mid 1980's reported by Boynton et al. (1995).

status and trends

These data have been used to indicate the status of nutrients, chlorophyll a, and productivity at the nine stations. We have compiled DIN and PO4 data from our water samples used for bioassays and chla and productivity data obtained by R. Lacouture from split samples (R. Lacouture, pers. com.). The initial status of these parameters was computed over the first two years of the project (August, 1990 to July, 1992), and the current status was computed over the last three years of the project (January, 1994 to December, 1996). Data from months in which double sampling occurred (May, June, July) were averaged to produce monthly averages; due to large seasonal variations, missing data were interpolated between months to avoid biasing an annual average; and, at tidal fresh stations, data were compiled only over the months of May, July, and September to correspond with our current sampling periods.

These data suggest that water quality conditions have degraded in Chesapeake Bay during the period 1990-1996. Comparing the initial status (1990-1992) with the current status (1994-1996), dissolved inorganic nitrogen (DIN) increased at the three main Bay stations and two of the three tributary mesohaline stations (Fig. 18, upper left panel). DIN decreased in the Choptank, and the tidal fresh stations in the Patuxent and Potomac. Since DIN < 5 μM (0.07 mg DIN L^{-1}) is associated with N-limited growth (Fig. 14), DIN in the 0-10 range is considered "good water quality"; however, the average DIN at most stations

exceeded (or greatly exceeded) this range. Chlorophyll a (chla) increased at all stations, particularly at the three tidal fresh stations (Fig. 18, upper right), and phosphate (PO_4) decreased at most stations in response (Fig. 18, lower left). Water quality assessment for each of these parameters was considered good for chla < 5 $\mu g\ L^{-1}$ and PO_4 < 0.1 μM. Although phytoplankton biomass increased over the period of record, productivity did not have a consistent response (Fig. 18, lower right). Overall, Fig. 18 suggests that additional nutrient inputs are resulting in higher algal biomass, an accumulation of excess DIN, and depletion of limited phosphate stocks. The additional inputs may be due to the incidence of wet years in the period 1994-1996 (see Fig. 11).

The status of nutrient limitation showed a pattern similar to that described above for water quality parameters. Consistent with the decreasing mean PO_4 concentrations, the P index at most stations increased, indicating greater P limitation of growth rates (Fig. 19, lower panel). The only exceptions were small decreases in the P indices at the mesohaline Patuxent (XDE5339) and the tidal fresh Choptank (MET5.1), both of which showed small decreases in P status. In spite of increasing concentrations of DIN at many stations, the N indices increased at many of these stations (Fig. 19, upper panel), probably due to higher algal biomass and nutrient demand. For both indices, the minimum goal for each index has been set at 0.5. Since the indices sum to 1.0, each station can only achieve a total of 1.0 between the two indices, assuming control of growth rates by either N or P and no

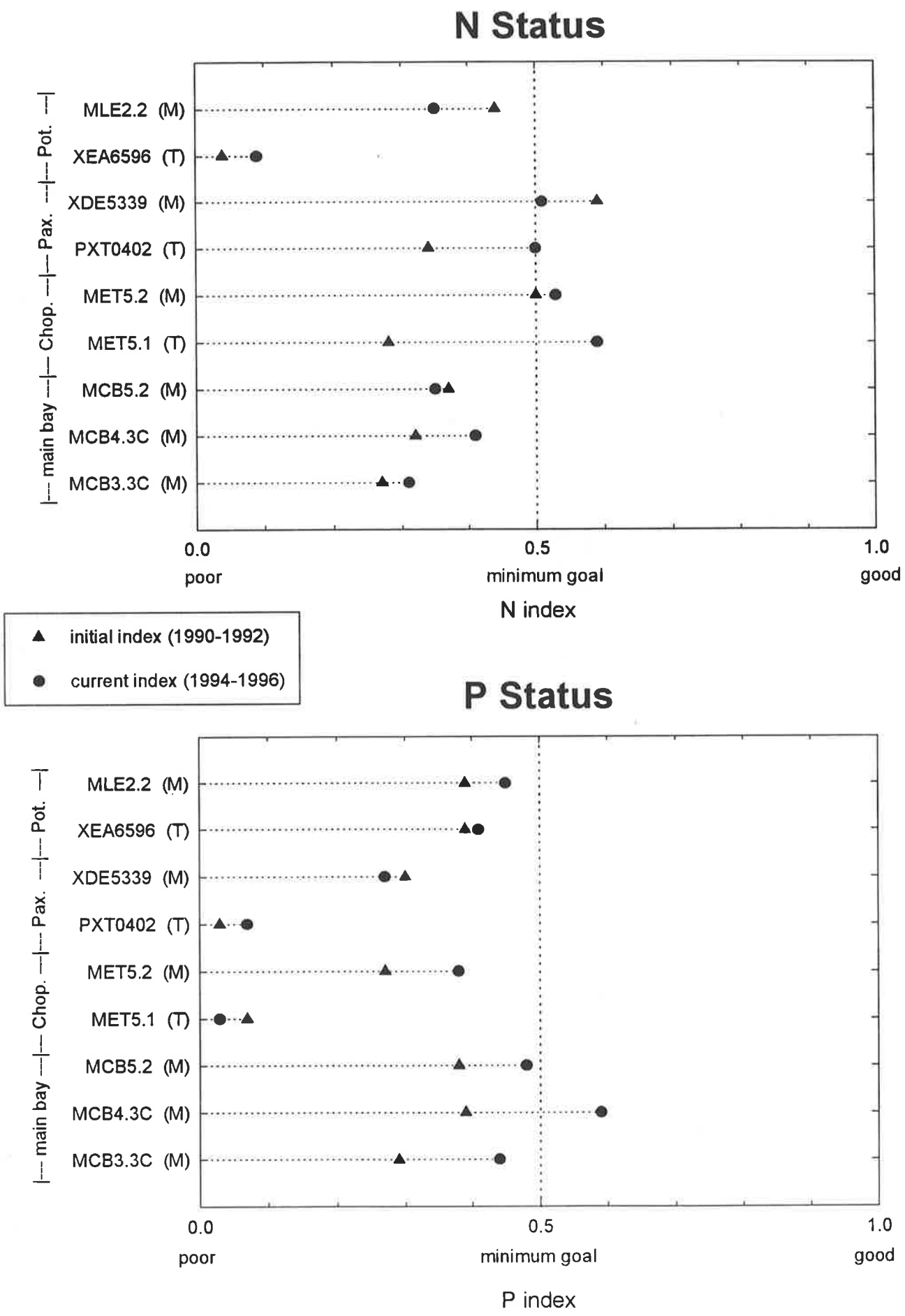

Fig. 19. Status of N and P indices of nutrient limitation of phytoplankton at 9 stations in MD waters of Chesapeake Bay. Station types (M=mesohaline, T=tidal fresh) are indicated in parentheses.

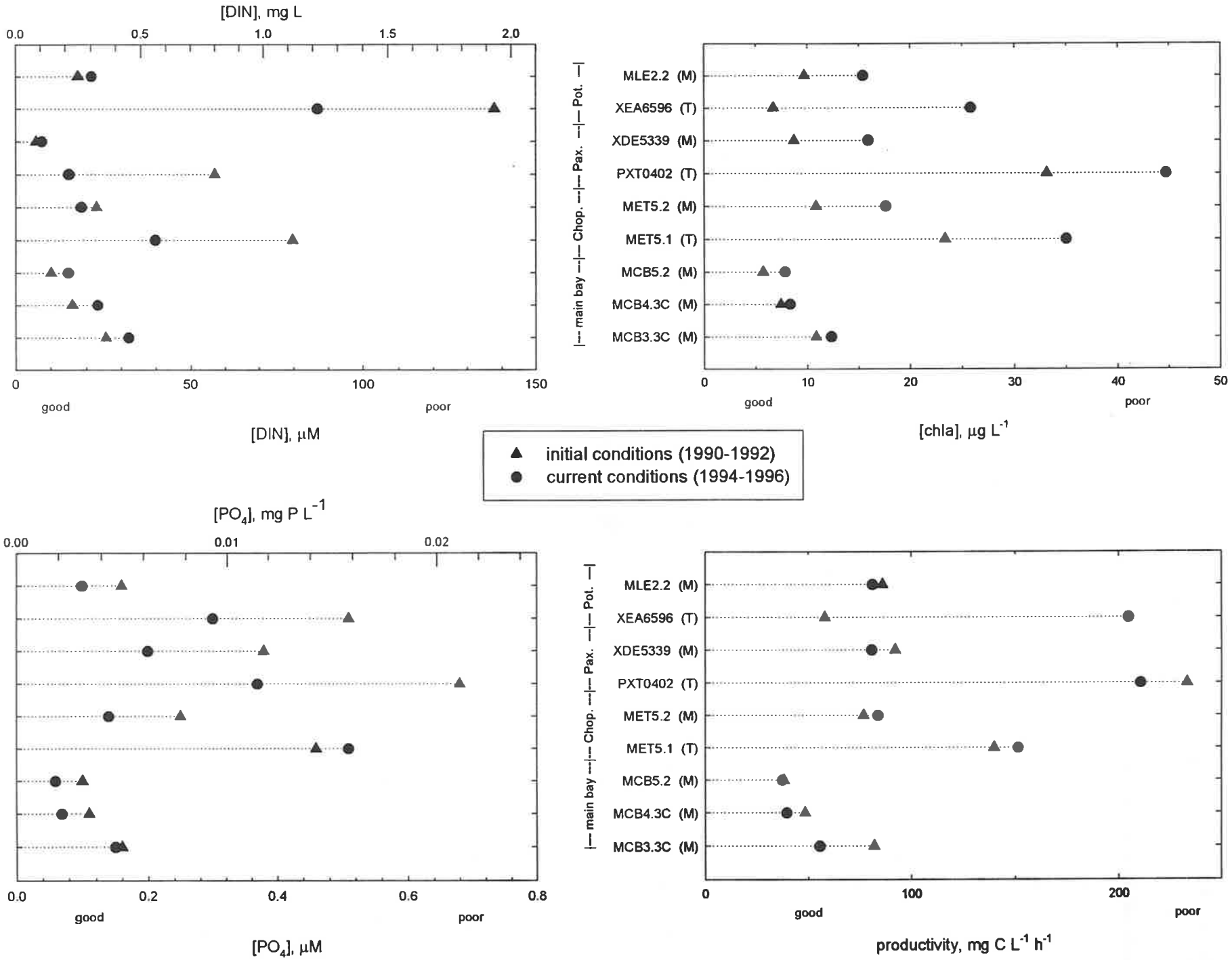

Fig. 18. Status of dissolved inorganic N (DIN = NH_4 + NO_2 + NO_3), phosphate (PO_4), chlorophyll a (chla = indicator of algal biomass) and algal primary productivity at 9 stations in MD waters of Chesapeake Bay. Station types (M=mesohaline, T=tidal fresh) are indicated in parentheses.

light limitation. No stations approached the minimum goal for both nutrients, indicating some nutrient saturation and light limitation during the year.

These same data have also been summarized as average monthly and interannual trends. Average monthly data were computed over the entire data set to show seasonal patterns (e.g., Fig. 20). DIN was usually highest in spring, peaking with river flow at levels well above those required for saturation of growth rates, and minimal in summer following highest algal productivity. Phosphate showed little annual variation (a factor of ~2), and algal biomass peaked in spring at moderate temperatures. Productivity was maximal in summer until DIN was depleted in August. These strong seasonal variations tend to mask interannual variations in these parameters.

Interannual variations were assessed by calendar year. Data were computed as annual averages for each calendar year, except for 1990, for which only partial data exist (Aug. - Dec. 1990). These were excluded from the linear regression analyses used to compute rates of annual change (Δ y-1), as shown in Fig. 21. Graphs for all stations are given in the appendix, and the results of this analysis are summarized in Tables 6 and 7. Over the period of record (CY 1991-1996), there were no significant changes in average DIN concentrations except at the tidal fresh Patuxent (PXT0402) and the tidal fresh Choptank (MET5.1), both of which showed small interannual increases in concentrations of +2 to +9 μM y-1 (+0.03 to +0.11 mg N L^{-1} y^{-1}). Unlike DIN, PO_4 showed

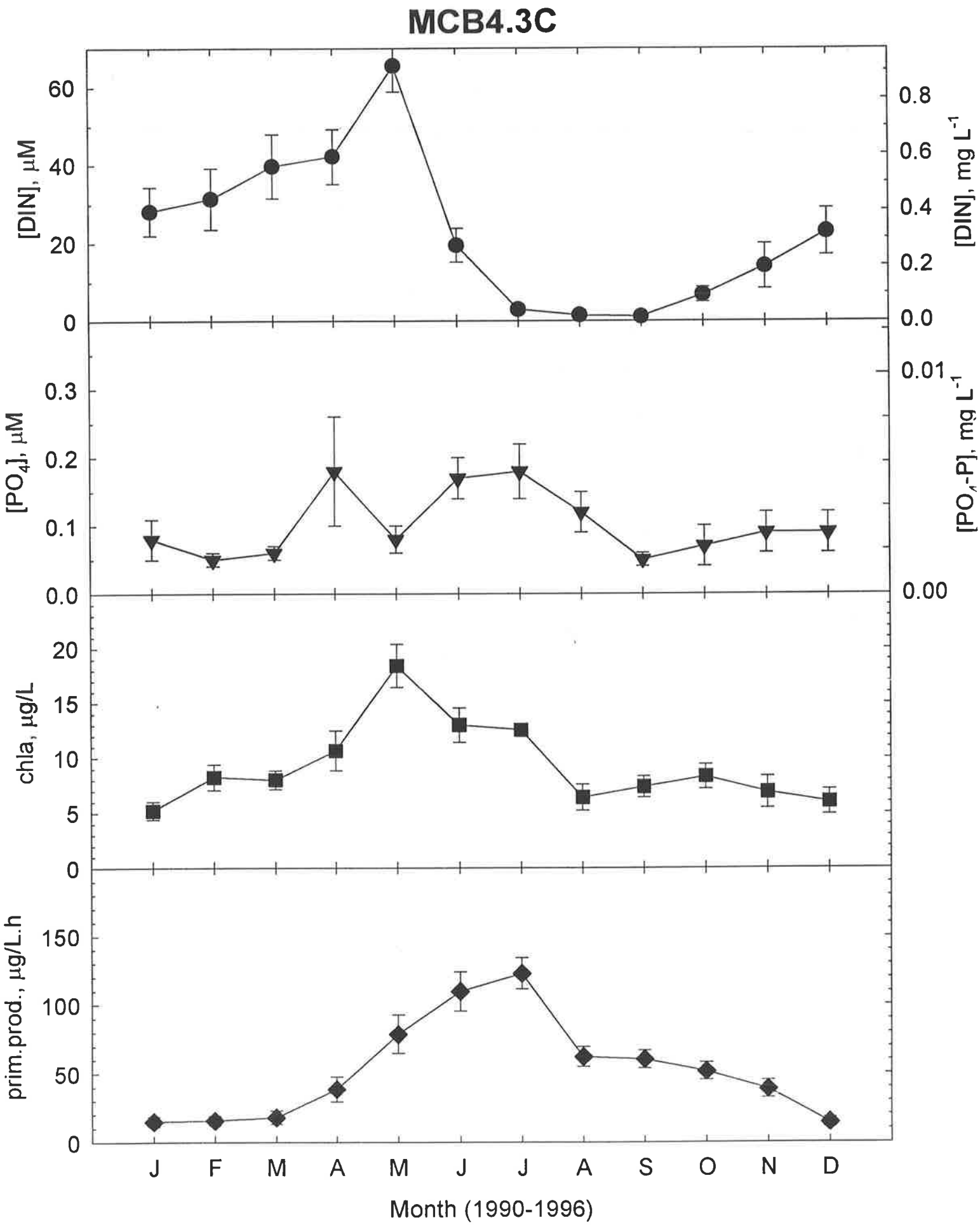

Fig. 20. Average and se of monthly variations in nutrients, chlorophyll a, and productivity at main Bay station MCB4.3C.

Table 7. Status and trends of nutrients and plankton at nine stations in the MD waters of Chesapeake Bay. Station types are mesohaline (meso) or tidal fresh (tf). Initial status was based on the initial two years of data (Aug. 1990 - July 1992); current status was based on the last three calendar years (1994-1996). Interannual linear trends were based on annual values calculated for each calendar year since 1990; the significance of a trend is shown by the symbols following each r^2 term (NS = not significant, $p>0.05$; * = significant, $0.05>p>0.01$; ** = highly significant, $0.01>p$). Units: DIN, μM; PO_4, μM; chla, $\mu g\ L^{-1}$; prod, $\mu g\ L^{-1}\ h^{-1}$. All trends indicate a net decrease in water quality over the period 1990 - 1996.

		initial status (1990-1992)				current status (1994-1996)			
station	type	DIN	PO_4	chla	prod	DIN	PO_4	chla	prod
MCB3.3C	meso	25.7	0.16	10.8	81.8	32.2	0.15	12.3	55.5
CB4.3C	meso	16.3	0.11	7.4	48.3	23.3	0.07	8.3	39.5
MCB5.2	meso	10.3	0.10	5.7	38.1	15.2	0.06	7.8	37.2
XEA6596	tf	138.	0.51	6.7	57.8	87.0	0.26	25.8	205.
MLE2.2	meso	17.8	0.16	9.7	86.0	21.6	0.11	15.4	81.1
PXT0402	tf	57.1	0.68	33.1	233.	15.3	0.37	44.7	211.
XDE5339	meso	5.9	0.38	8.7	92.0	7.6	0.22	15.9	80.7
MET5.1	tf	79.8	0.46	23.3	140.	39.8	0.51	35.0	151.
MET5.2	meso	23.1	0.25	10.8	76.6	18.7	0.14	17.6	83.6

		interannual trends							
station	type	r^2	ΔDIN y^{-1}	r^2	$\Delta PO_4\ y^{-1}$	r^2	Δchla y^{-1}	r^2	Δprod y^{-1}
MCB3.3C	meso	0.23 NS	--	0.27 NS	--	0.35 *	+0.99	0.55 *	-9.3
MCB4.3C	meso	0.21 NS	--	0.44 *	-0.015	0.73 **	+0.40	0.53 *	-4.3
MCB5.2	meso	0.15 NS	--	0.77 *	-0.013	0.17 NS	--	0.26 NS	--
XEA6596	tf	0.28 NS	--	0.04 NS	--	0.33 *	+4.6	0.14 NS	--
MLE2.2	meso	0.10 NS	--	0.07 NS	--	0.44 *	+1.5	0.01 NS	--
PXT0402	tf	0.48 *	+2.4	0.02 NS	--	0.11 NS	--	0.07 NS	--
XDE5339	meso	0.02 NS	--	0.40 *	-0.060	0.55 *	+1.8	0.01 NS	--
MET5.1	tf	0.42 *	+8.6	0.12 NS	--	0.01 NS	--	0.06 NS	--
MET5.2	meso	0.03 NS	--	0.55	-0.032	0.80 **	+2.3	0.10 NS	--

Table 6. Status and trends of resource limitation at nine stations in the MD waters of Chesapeake Bay. Station types are mesohaline (meso) or tidal fresh (tf). Initial status was based on the initial two years of bioassays (Aug. 1990 - July 1992); current status was based on the last three calendar years (1994-1996). Interannual linear trends in N, P, and Light indices were based on annual indices calculated for each calendar year since 1990; the significance of a trend is shown by the symbols following each r^2 term (NS = not significant, $p>0.05$; * = significant, $0.05>p>0.01$; ** = highly significant, $0.01>p$). Positive trends in N and P indices and negative trends in Light indices are associated with increasing water quality.

		initial status (1990-1992)		current status (1994-1996)		interannual trends in indices					
station	type	N index	P index	N index	P index	r^2	$\Delta N\ y^{-1}$	r^2	$\Delta P\ y^{-1}$	r^2	$\Delta L\ y^{-1}$
MCB3.3C	meso	0.27	0.29	0.31	0.49	0.10NS	--	0.57*	+0.049	0.48*	-0.051
MCB4.3C	meso	0.32	0.39	0.41	0.59	0.36*	+0.019	0.68*	+0.066	0.66*	-0.085
MCB5.2	meso	0.37	0.38	0.35	0.48	0.11NS	--	0.68*	+0.044	0.44*	-0.031
XEA6596	tf	0.04	0.39	0.09	0.41	0.02NS	--	0.02NS	--	0.01NS	--
MLE2.2	meso	0.44	0.39	0.35	0.45	0.53*	-0.033	0.31*	+0.034	0.01NS	--
PXT0402	tf	0.34	0.03	0.50	0.07	0.02NS	--	0.01NS	--	0.03NS	--
XDE5339	meso	0.59	0.30	0.51	0.27	0.47*	-0.025	0.05NS	--	0.09NS	--
MET5.1	tf	0.28	0.07	0.59	0.03	0.24NS	--	0.38*	+0.014	0.18NS	--
MET5.2	meso	0.50	0.27	0.53	0.38	0.01NS	--	0.83**	+0.042	0.80**	-0.046

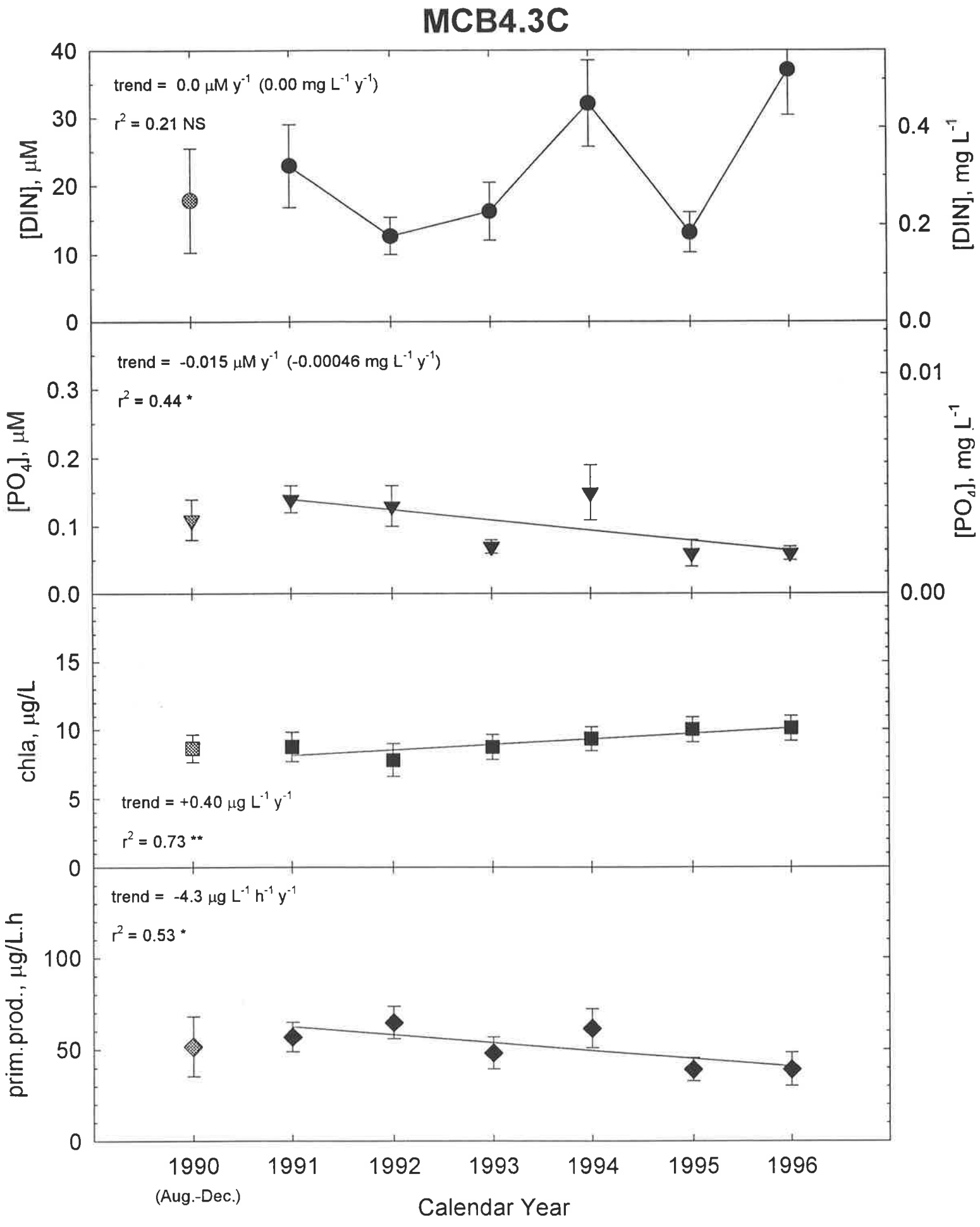

Fig. 21. Average and se of annual variations in nutrients, chlorophyll a, and productivity at main Bay station MCB4.3C.

significant decreases at four stations (two main Bay and two other mesohaline stations) at rates of change of -0.01 to -0.06 μM y^{-1} (-0.0003 to -0.0019 mg P L^{-1} y^{-1}). These declines in PO_4 appeared to be primarily the result of higher algal biomass over the period, and increases in chlorophyll a ranged from +0.4 to +4.6 μg L^{-1} y^{-1} at 6 of the 9 stations. Although biomass showed consistent increases over the period of record, productivity showed only small significant decreases at two of the main bay stations.

The indices of resource limitation showed parallel changes over the period of record (Table 6). The N indices showed no consistent pattern; most stations showed no significant trends, 2 were negative, and one was positive. However, there was a consistent tendency for increasing P limitation. Six of 9 stations were significantly positive (+0.01 to +0.07 y^{-1}), particularly when the index of light limitation decreased. These trends in Table 6 indicate a consistent pattern of decreasing light limitation (perhaps as a result of decreasing turbidity in inputs) and increasing P limitation.

Acknowledgements

We acknowledge the technical support of Ann Barse and Amy Imirie for collecting and transporting water samples and assisting with the bioassays. We also thank the captain and crews of R/V's Aquarius, Orion, and Discovery for expert assistance with the water collections. MDE and DNR provided financial support for years 1990-1994 and 1995-1997, respectively. Rob Magnien, Darcy Austin, Bruce Michaels, Deborah Everitt, and Renee Karrh provided helpful discussions and comments on the research and drafts of this document.

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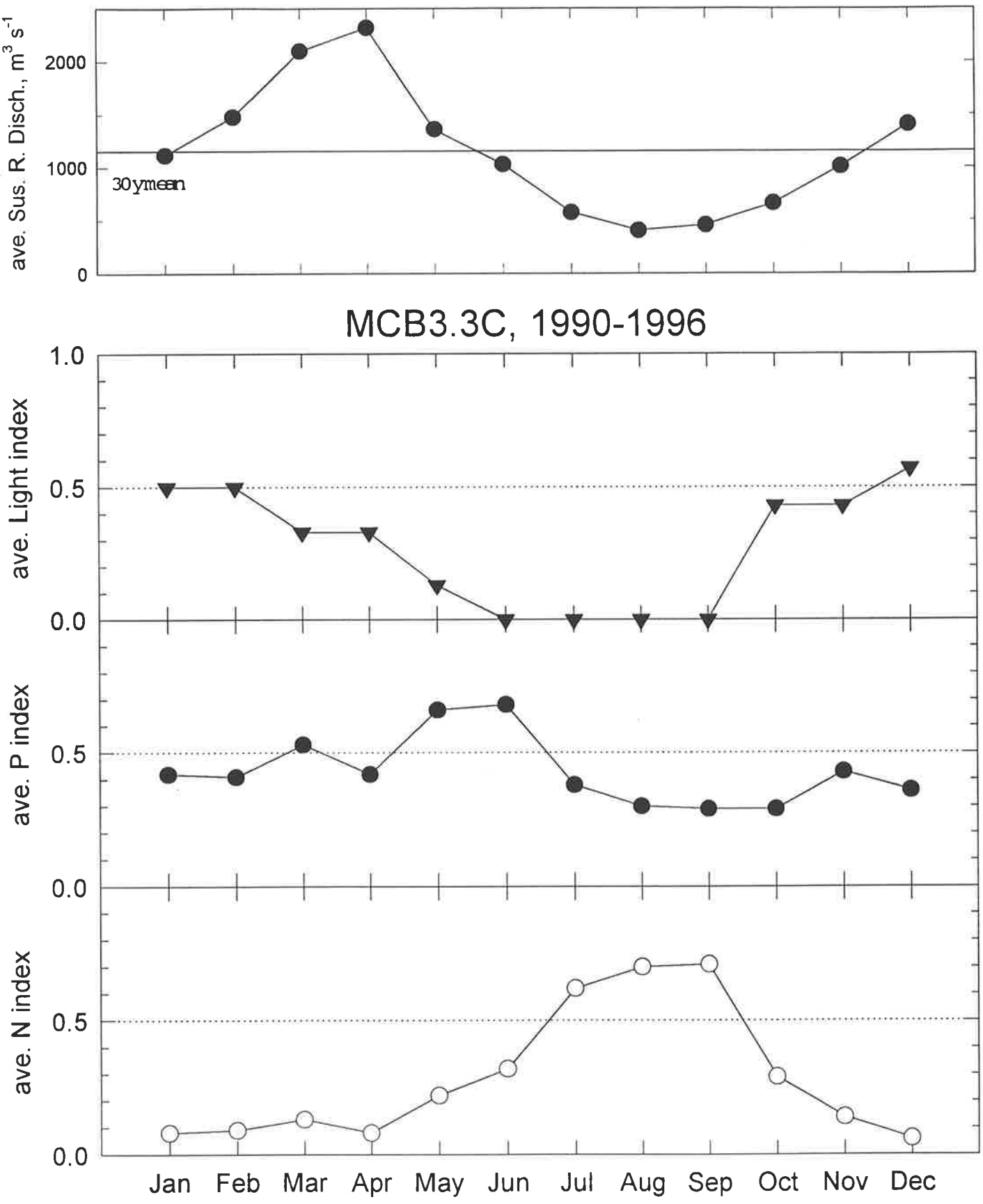
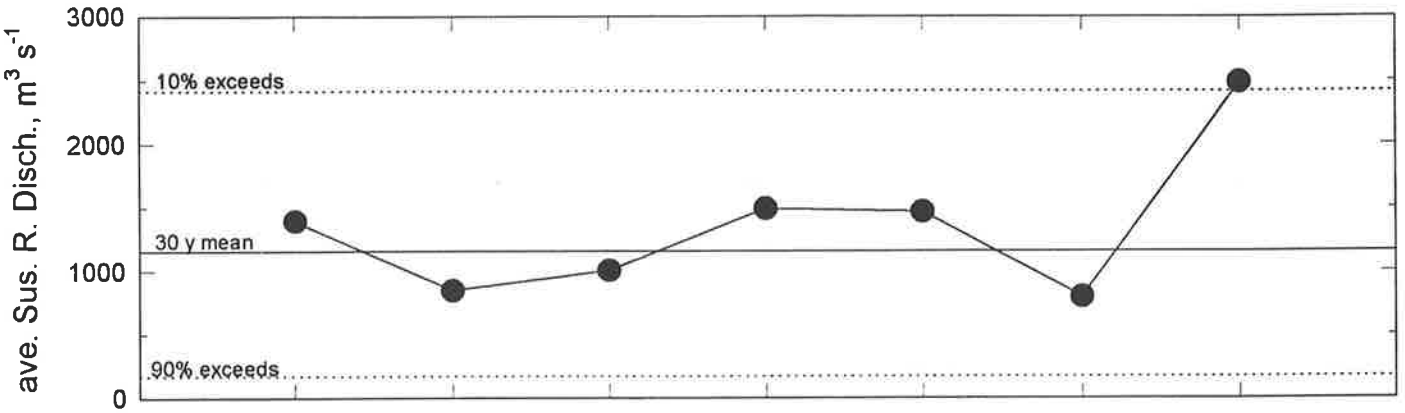
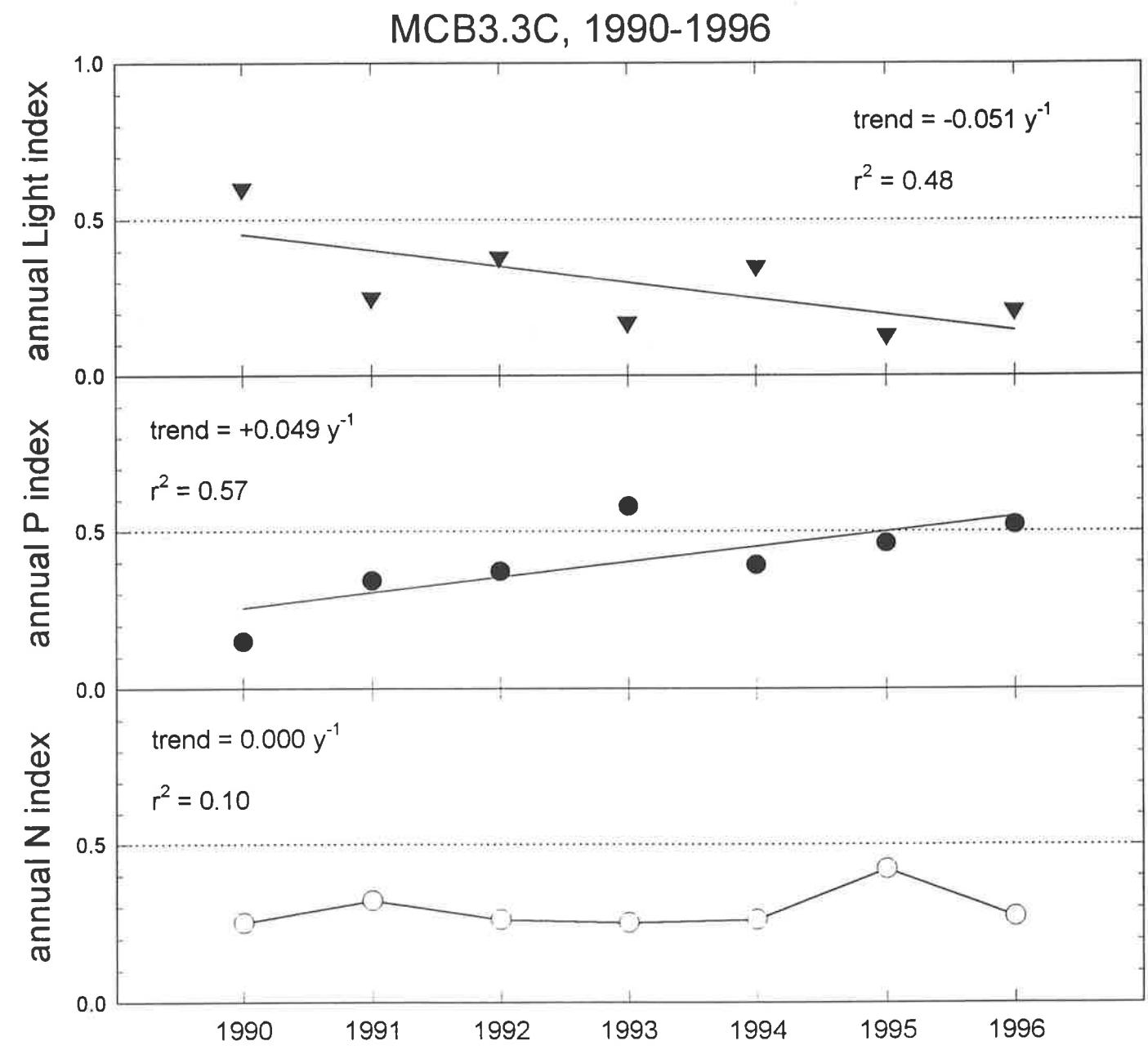
APPENDIX

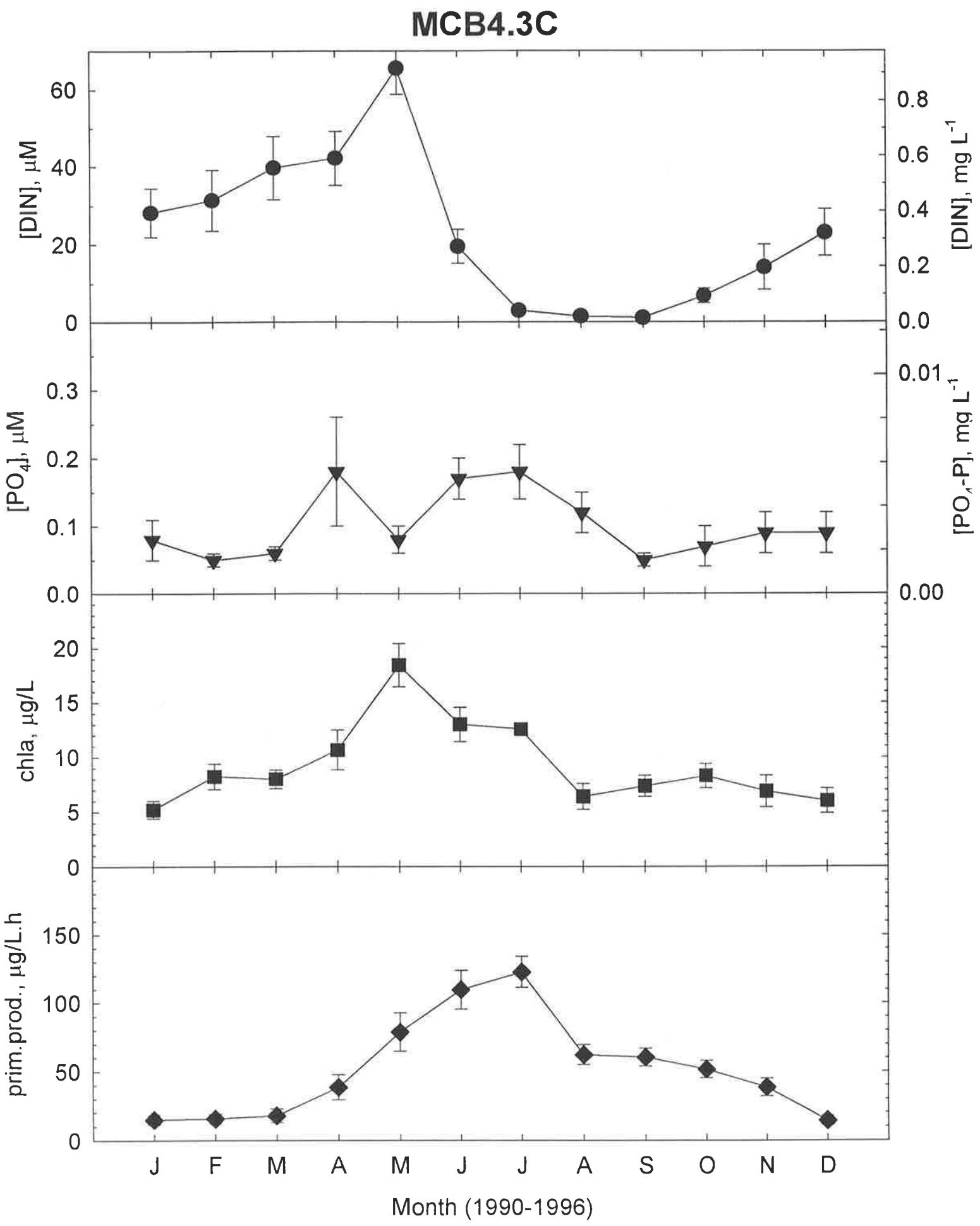
MONTHLY and INTERANNUAL TREND ANALYSIS

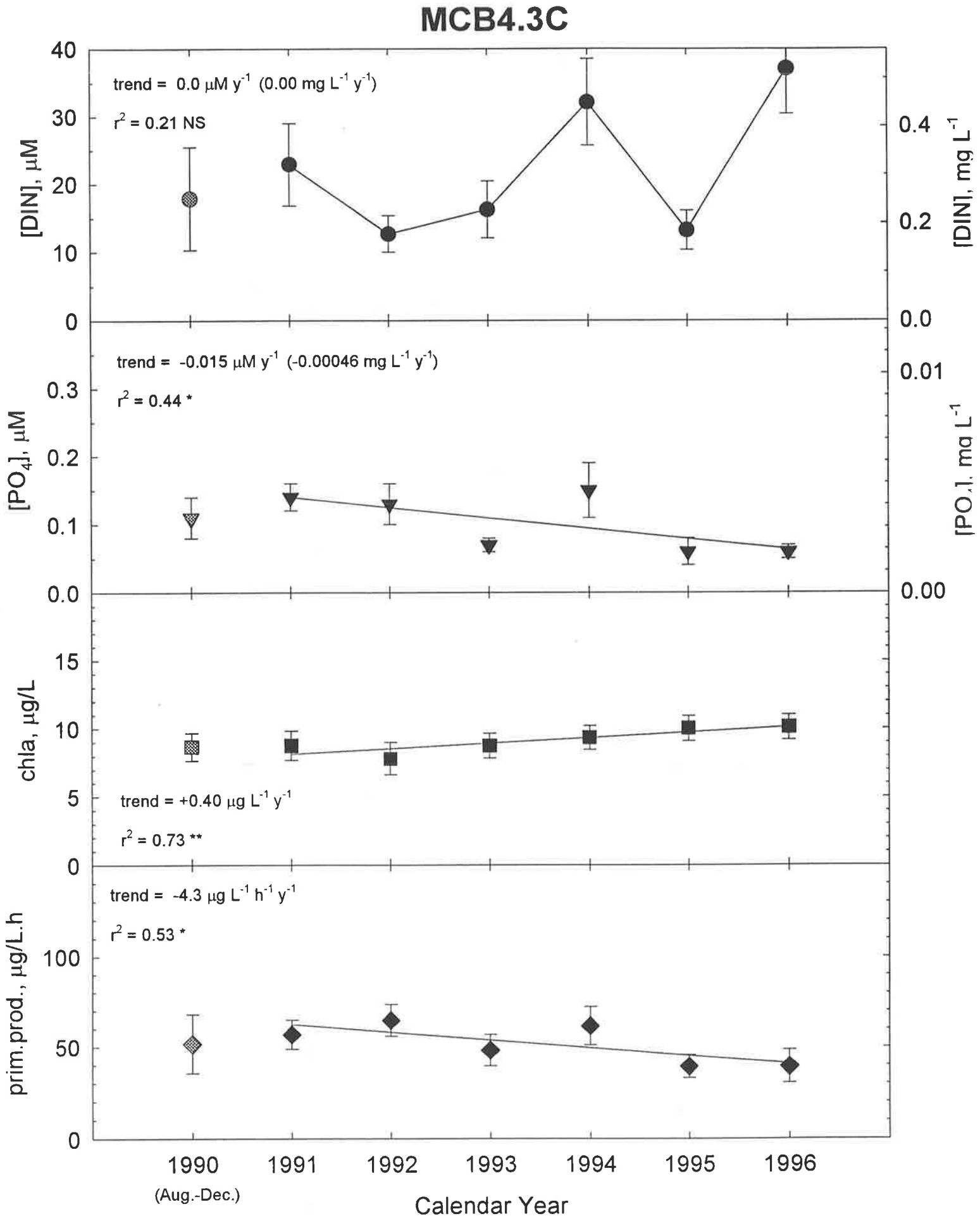
1. NUTRIENTS
2. CHLOROPHYLLa
3. PRODUCTIVITY
4. BIOMASS
5. N INDEX
6. P INDEX
7. LIGHT INDEX

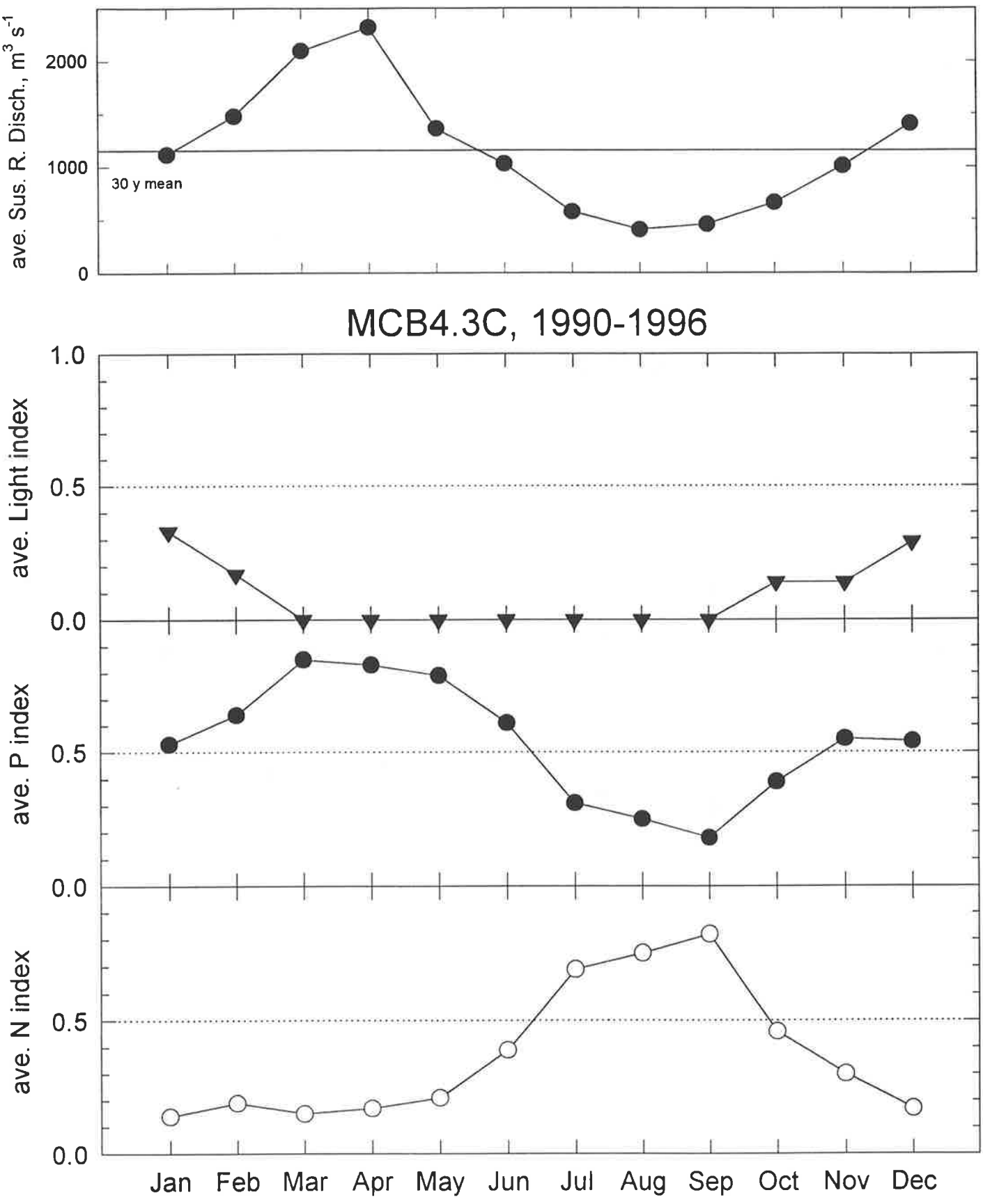

ave. Sus. R. Disch., m3 s-1
2000
1000
0
30ymean
MCB3.3C, 1990-1996
ave. Light index
1.0
0.5
0.0
ave. P index
0.5
0.0
ave. N index
0.5
0.0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

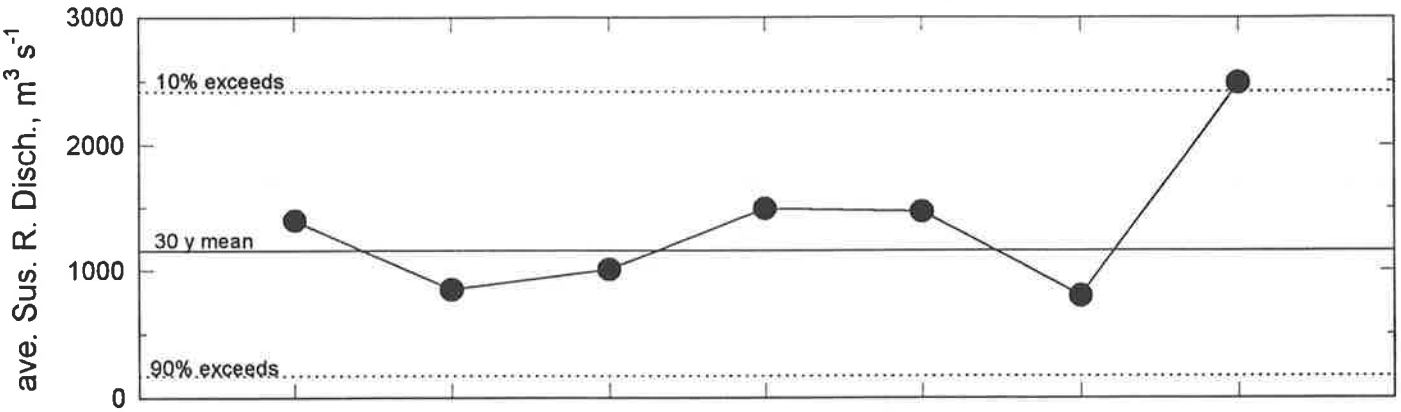

ave. Sus. R. Disch., $m^3 s^{-1}$
3000
2000
1000
0
10% exceeds
30 y mean
90% exceeds

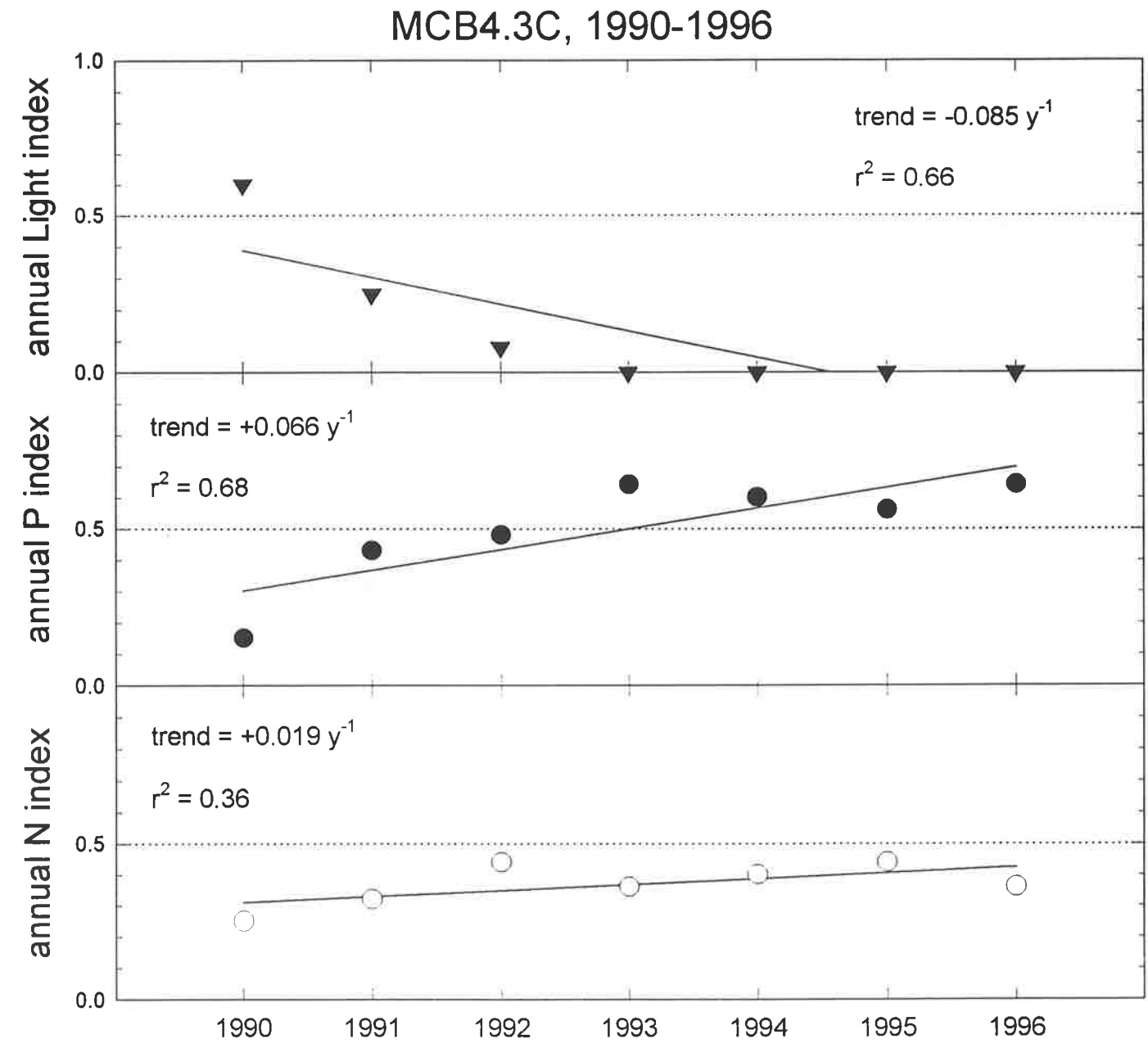

MCB3.3C, 1990-1996
annual Light index
trend = -0.051 y^{-1}
r^2 = 0.48
annual P index
trend = +0.049 y^{-1}
r^2 = 0.57
annual N index
trend = 0.000 y^{-1}
r^2 = 0.10
1.0
0.5
0.0
1990
1991
1992
1993
1994
1995
1996

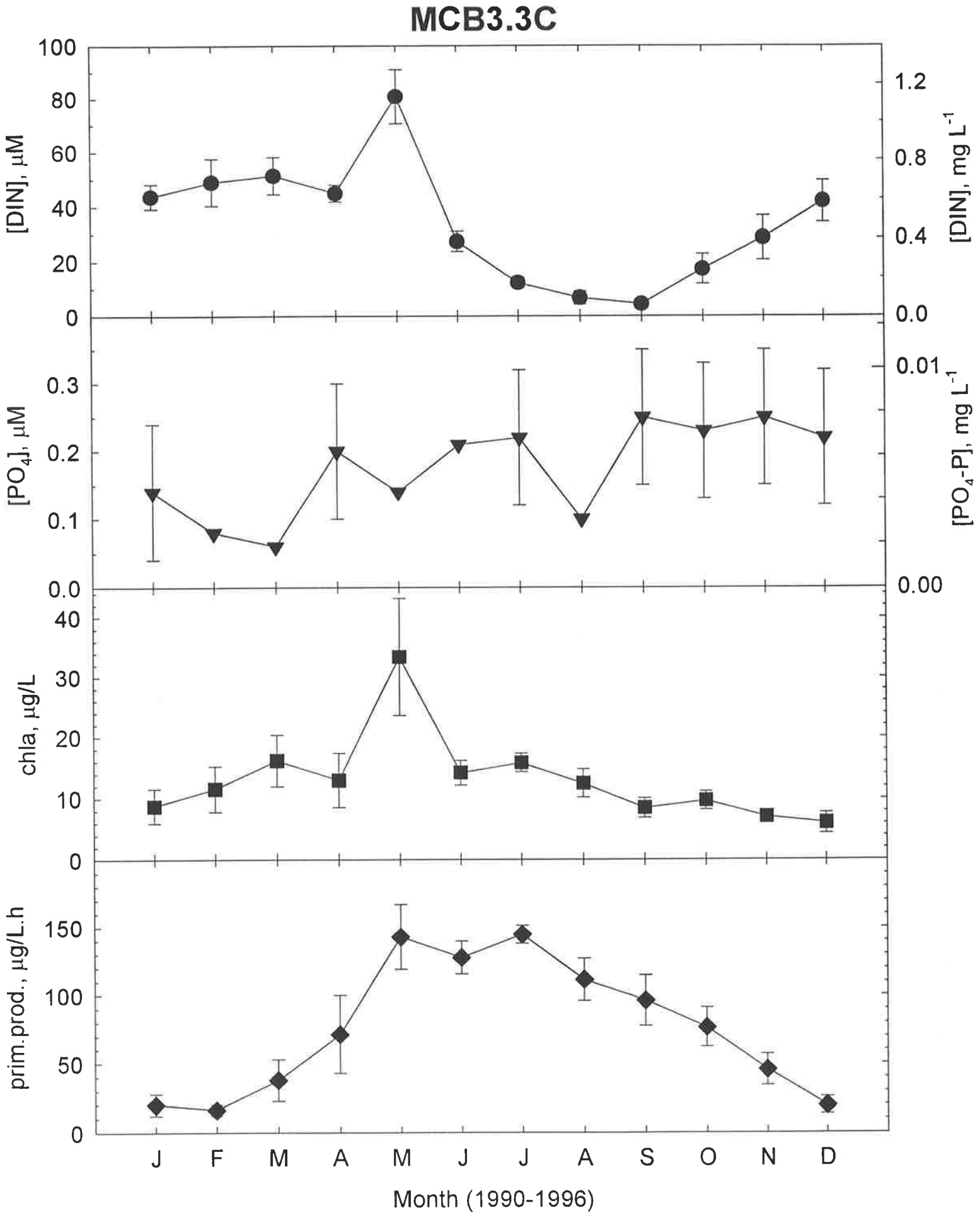

MCB4.3C
[DIN], µM
[DIN], mg L-1
[PO4], µM
[PO4-P], mg L-1
chla, µg/L
prim.prod., µg/L.h
J F M A M J J A S O N D
Month (1990-1996)

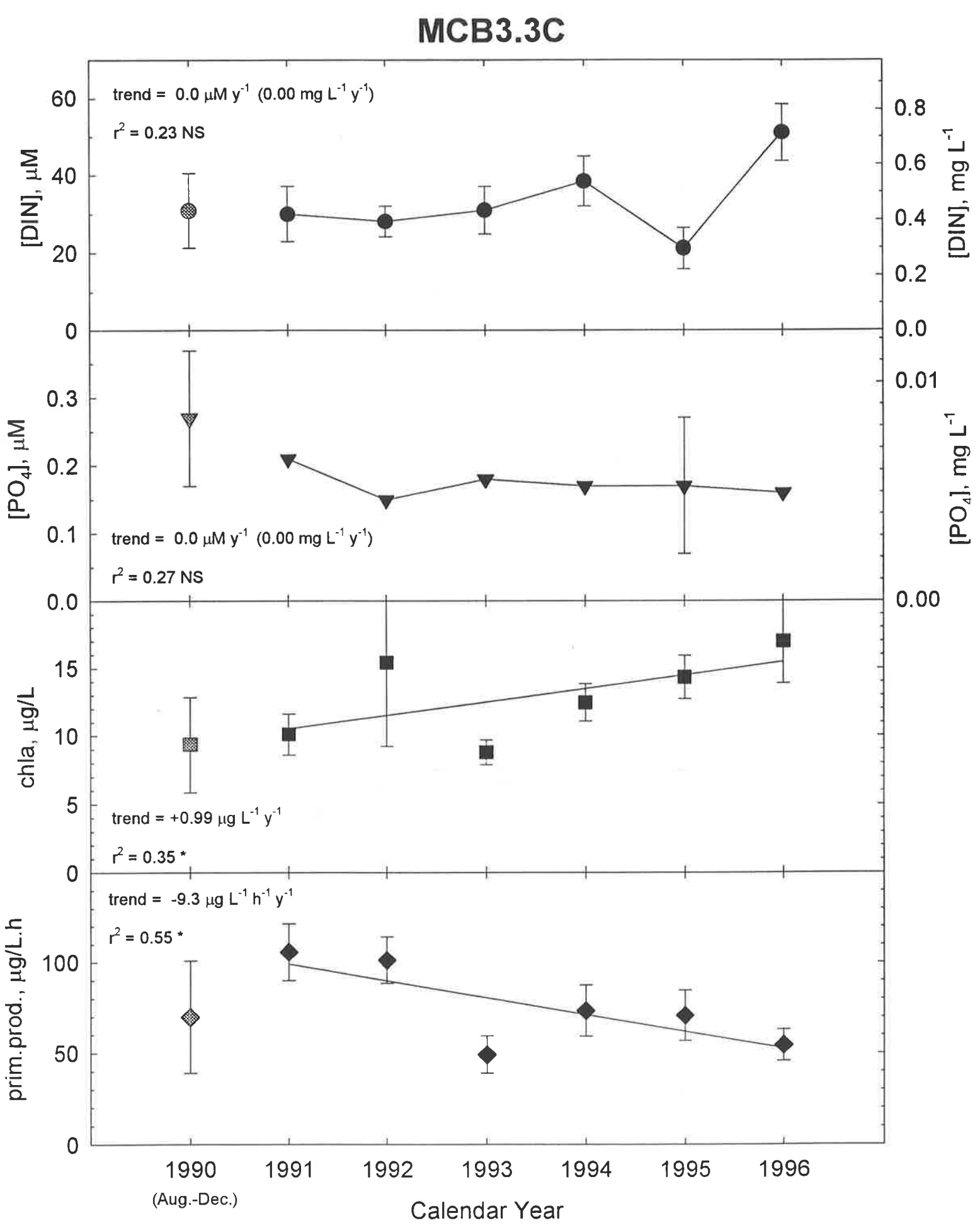

MCB4.3C
trend = 0.0 µM y-1 (0.00 mg L-1 y-1)
r2 = 0.21 NS
[DIN], µM
[DIN], mg L-1
trend = -0.015 µM y-1 (-0.00046 mg L-1 y-1)
r2 = 0.44 *
[PO4], µM
[PO4], mg L-1
chla, µg/L
trend = +0.40 µg L-1 y-1
r2 = 0.73 **
trend = -4.3 µg L-1 h-1 y-1
r2 = 0.53 *
prim.prod., µg/L.h
1990
(Aug.-Dec.)
1991
1992
1993
1994
1995
1996
Calendar Year

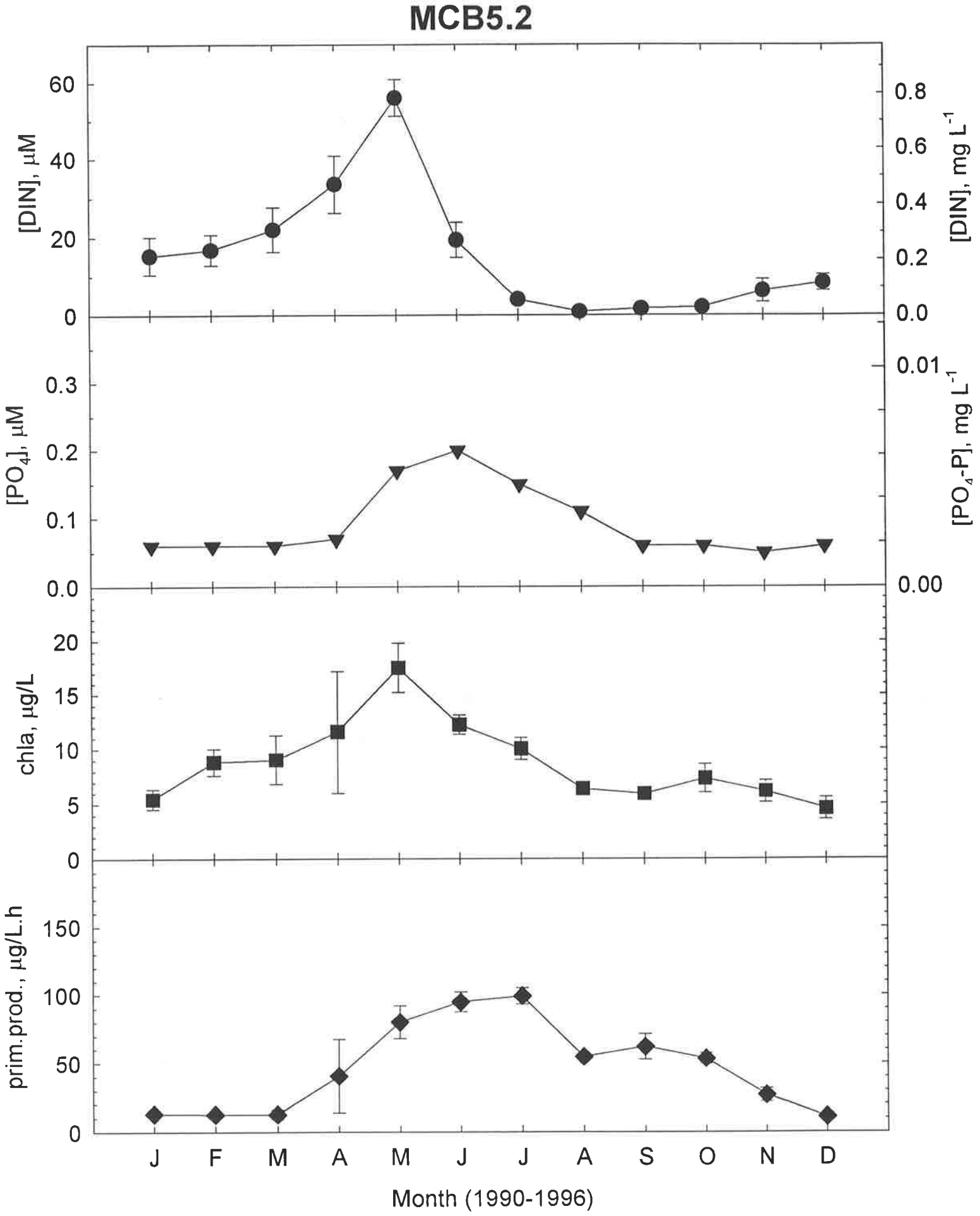

ave. Sus. R. Disch., m3 s-1
2000
1000
0
30 y mean
MCB4.3C, 1990-1996
ave. Light index
1.0
0.5
0.0
ave. P index
0.5
0.0
ave. N index
0.5
0.0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

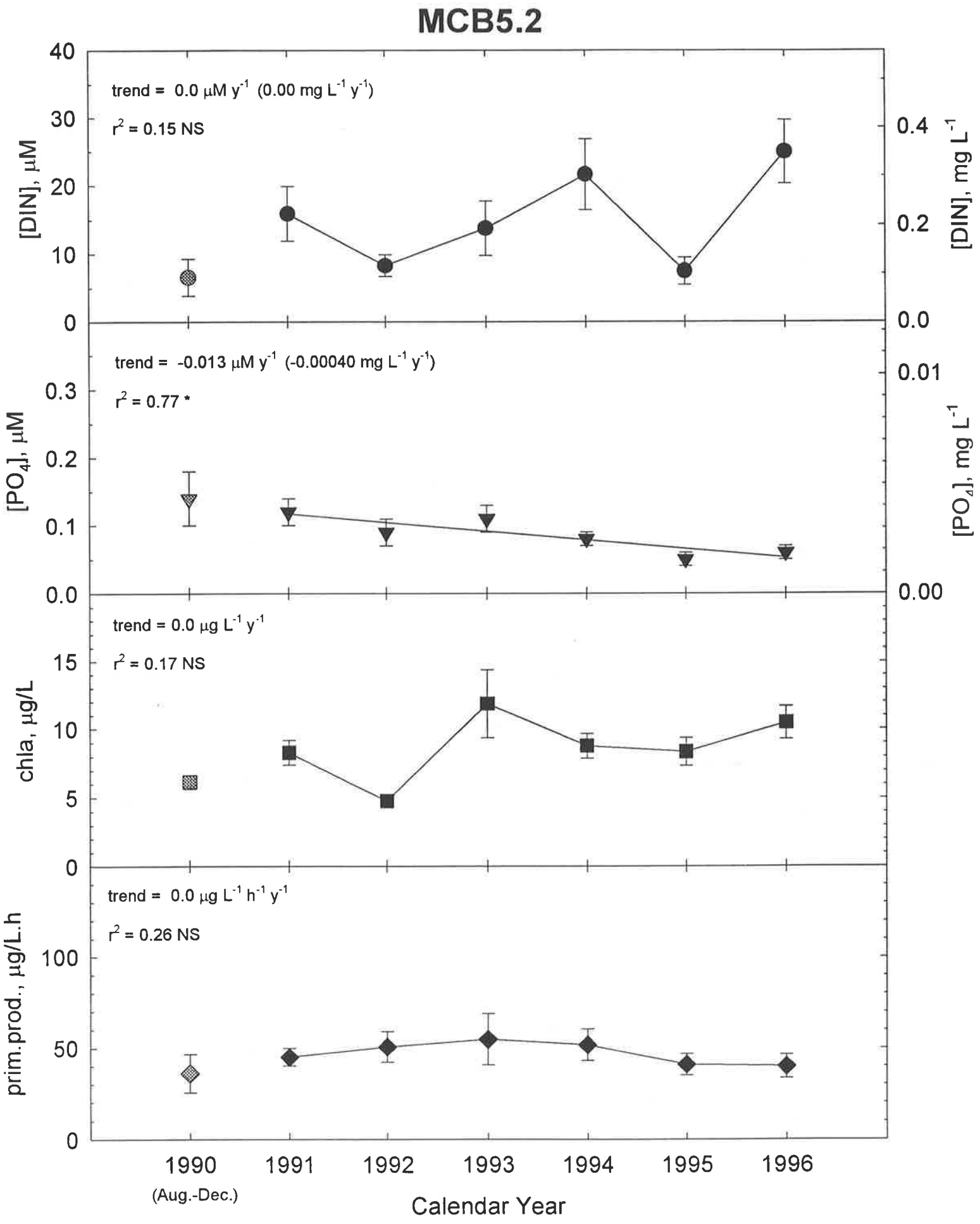

ave. Sus. R. Disch., $m^3 s^{-1}$
3000
2000
1000
0
10% exceeds
30 y mean
90% exceeds

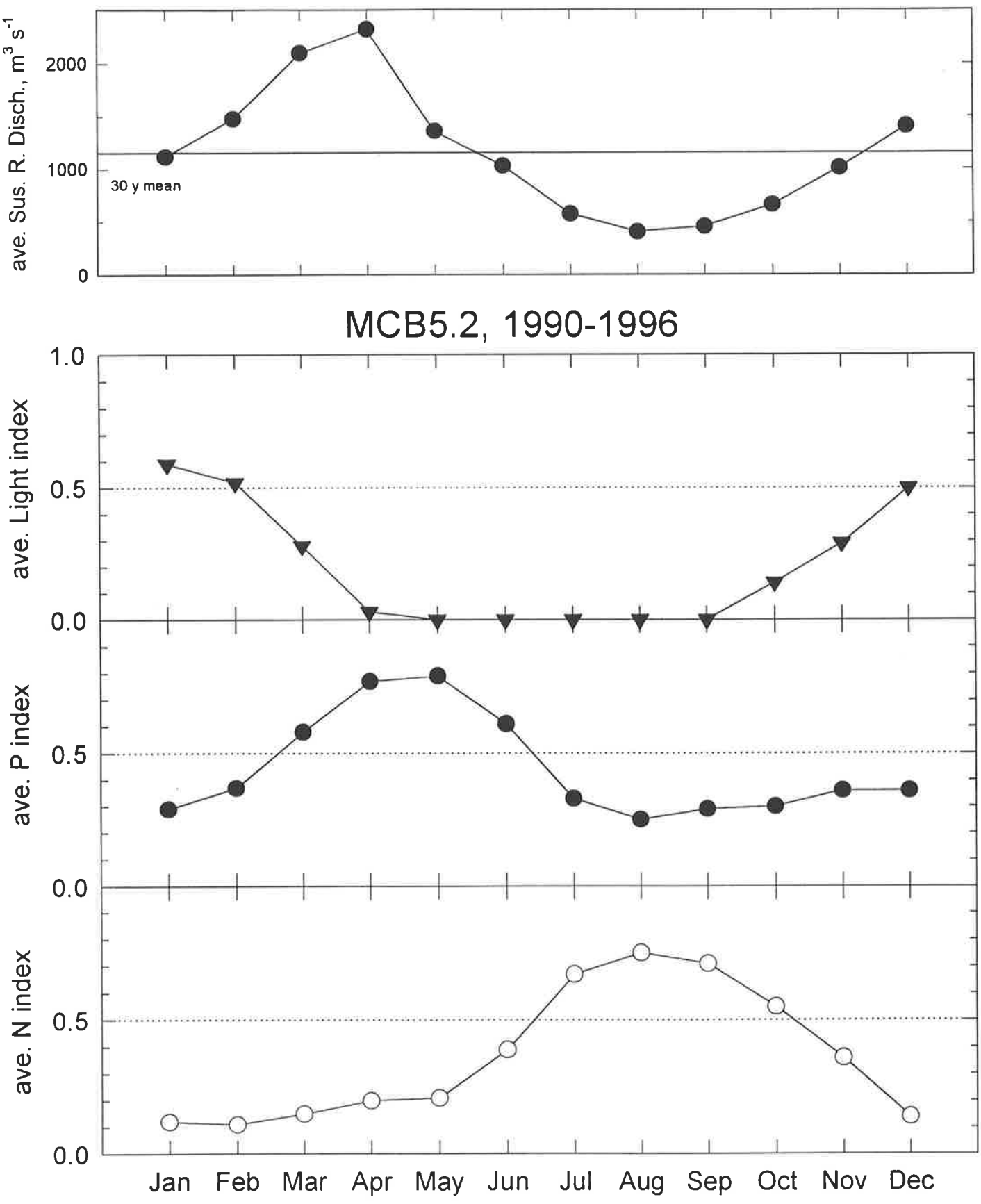

MCB4.3C, 1990-1996
annual Light index
trend = -0.085 y^{-1}
r^2 = 0.66
annual P index
trend = +0.066 y^{-1}
r^2 = 0.68
annual N index
trend = +0.019 y^{-1}
r^2 = 0.36
1.0
0.5
0.0
1990
1991
1992
1993
1994
1995
1996

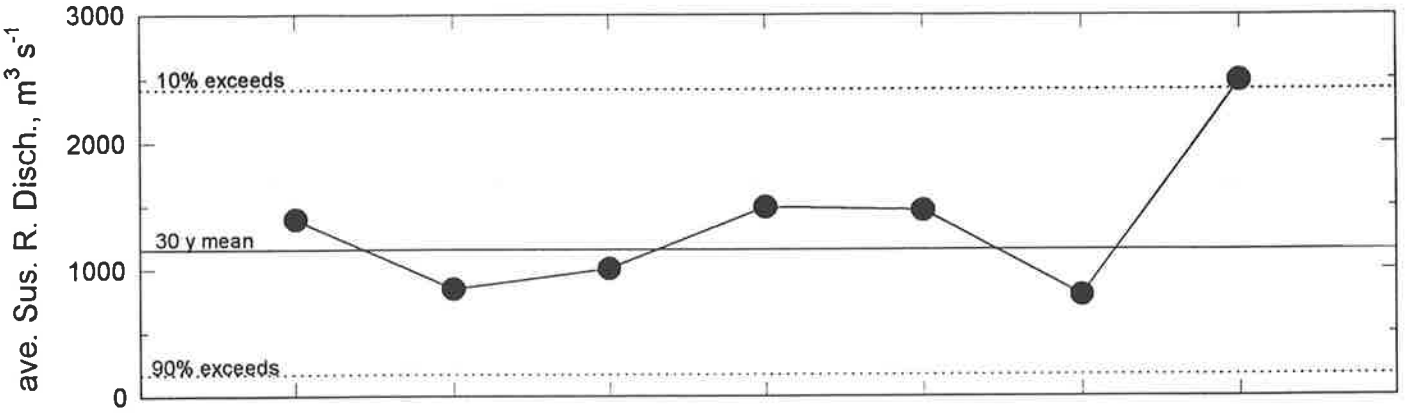

MCB3.3C
[DIN], µM
[DIN], mg L-1
[PO4], µM
[PO4-P], mg L-1
chla, µg/L
prim.prod., µg/L.h
J F M A M J J A S O N D
Month (1990-1996)

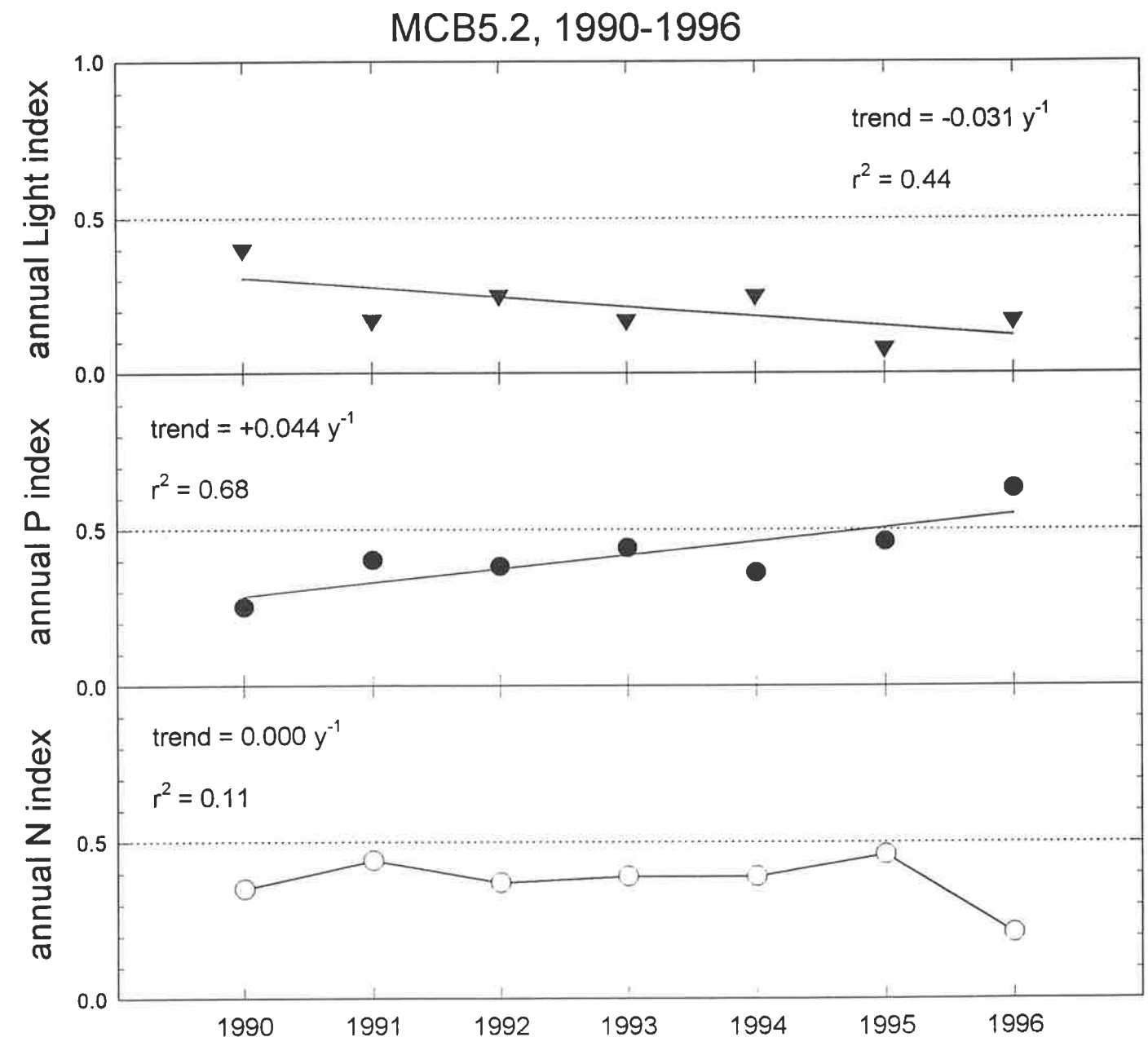

MCB3.3C
trend = 0.0 µM y-1 (0.00 mg L-1 y-1)
r2 = 0.23 NS
[DIN], µM
[DIN], mg L-1
trend = 0.0 µM y-1 (0.00 mg L-1 y-1)
r2 = 0.27 NS
[PO4], µM
[PO4], mg L-1
trend = +0.99 µg L-1 y-1
r2 = 0.35 *
chla, µg/L
trend = -9.3 µg L-1 h-1 y-1
r2 = 0.55 *
prim.prod., µg/L.h
1990
(Aug.-Dec.)
1991
1992
1993
1994
1995
1996
Calendar Year

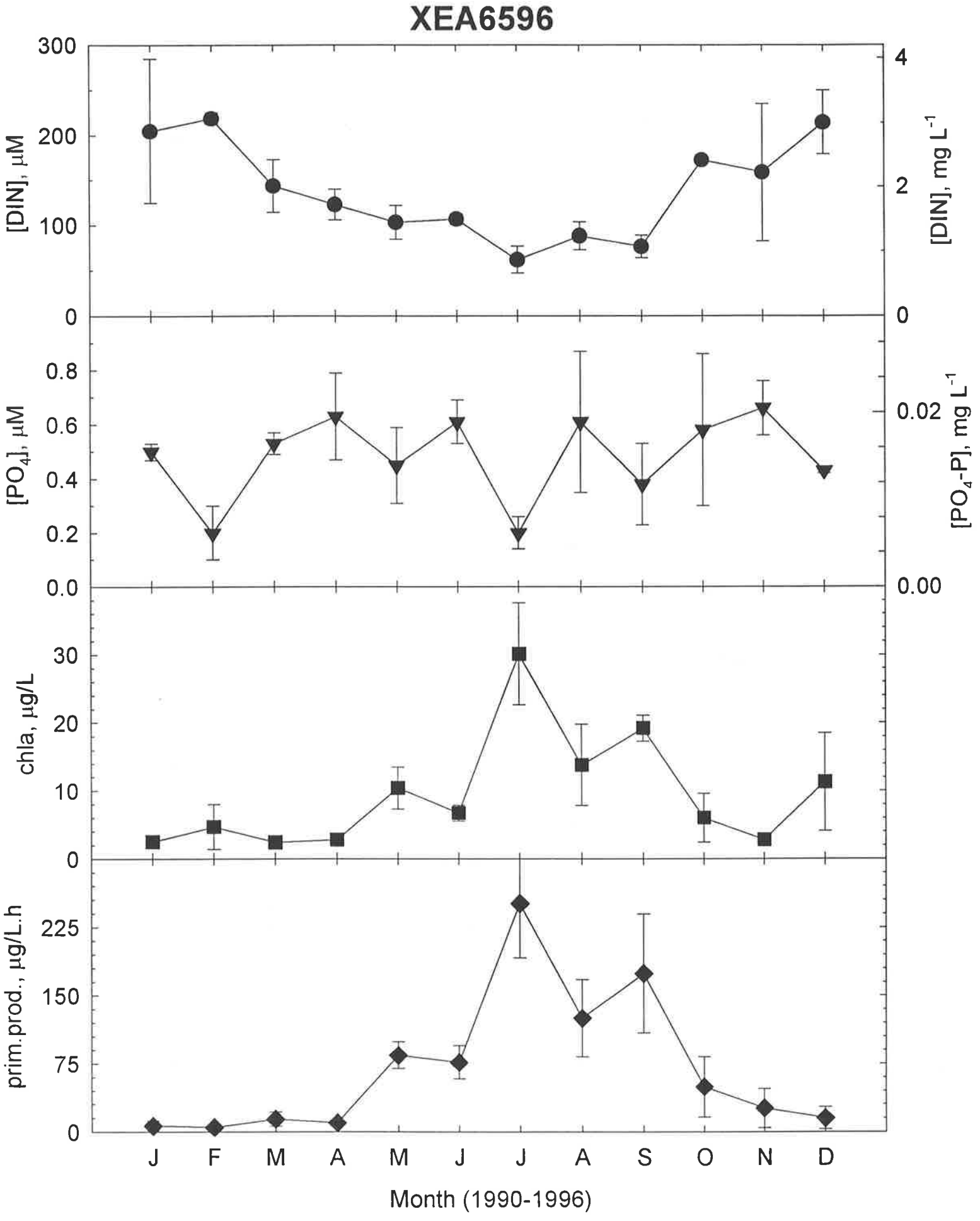

MCB5.2
[DIN], µM
[DIN], mg L-1
[PO4], µM
[PO4-P], mg L-1
chla, µg/L
prim.prod., µg/L.h
J F M A M J J A S O N D
Month (1990-1996)

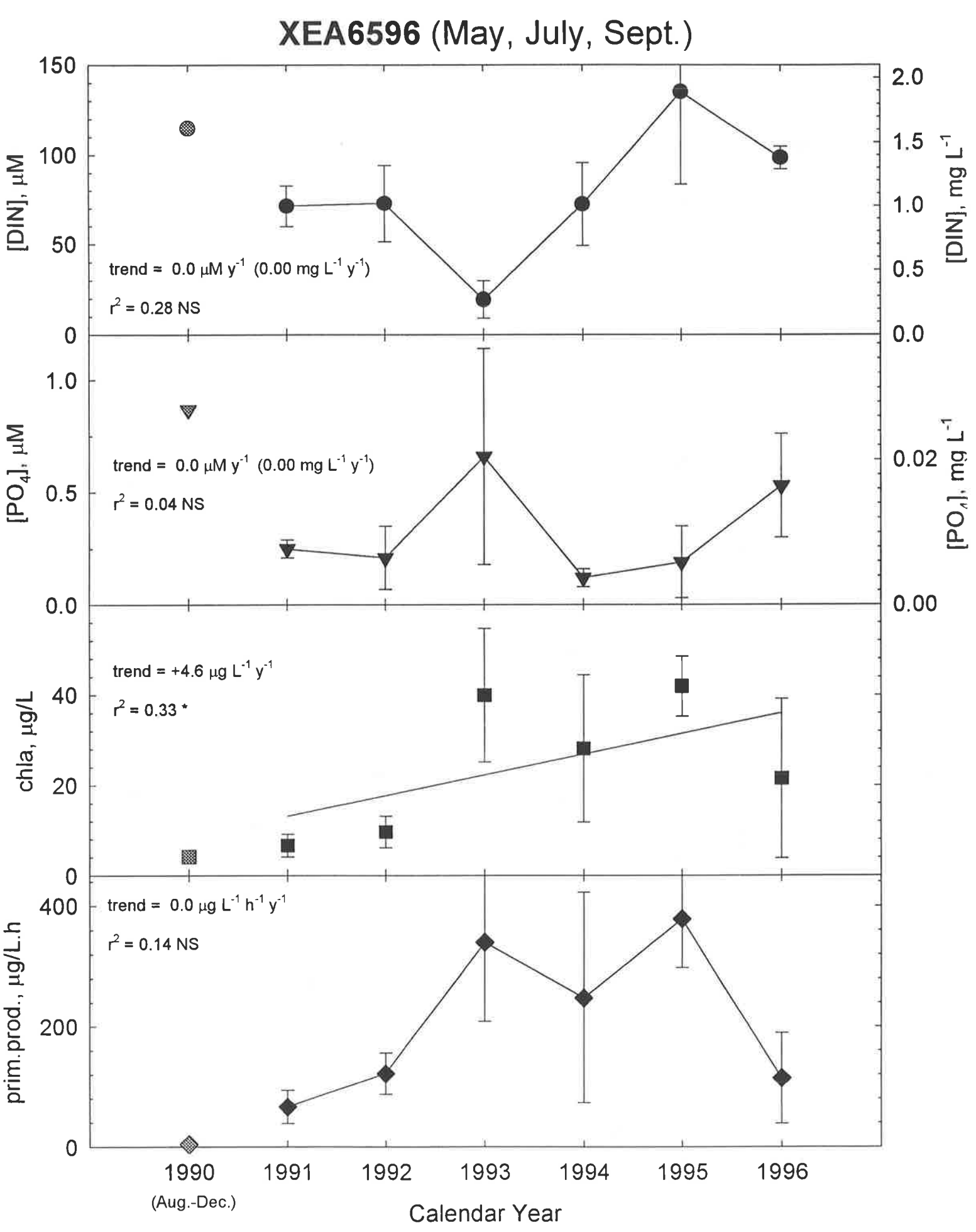

MCB5.2
trend = 0.0 µM y-1 (0.00 mg L-1 y-1)
r2 = 0.15 NS
[DIN], µM
[DIN], mg L-1
trend = -0.013 µM y-1 (-0.00040 mg L-1 y-1)
r2 = 0.77 *
[PO4], µM
[PO4], mg L-1
trend = 0.0 µg L-1 y-1
r2 = 0.17 NS
chla, µg/L
trend = 0.0 µg L-1 h-1 y-1
r2 = 0.26 NS
prim.prod., µg/L.h
1990
(Aug.-Dec.)
1991
1992
1993
1994
1995
1996
Calendar Year

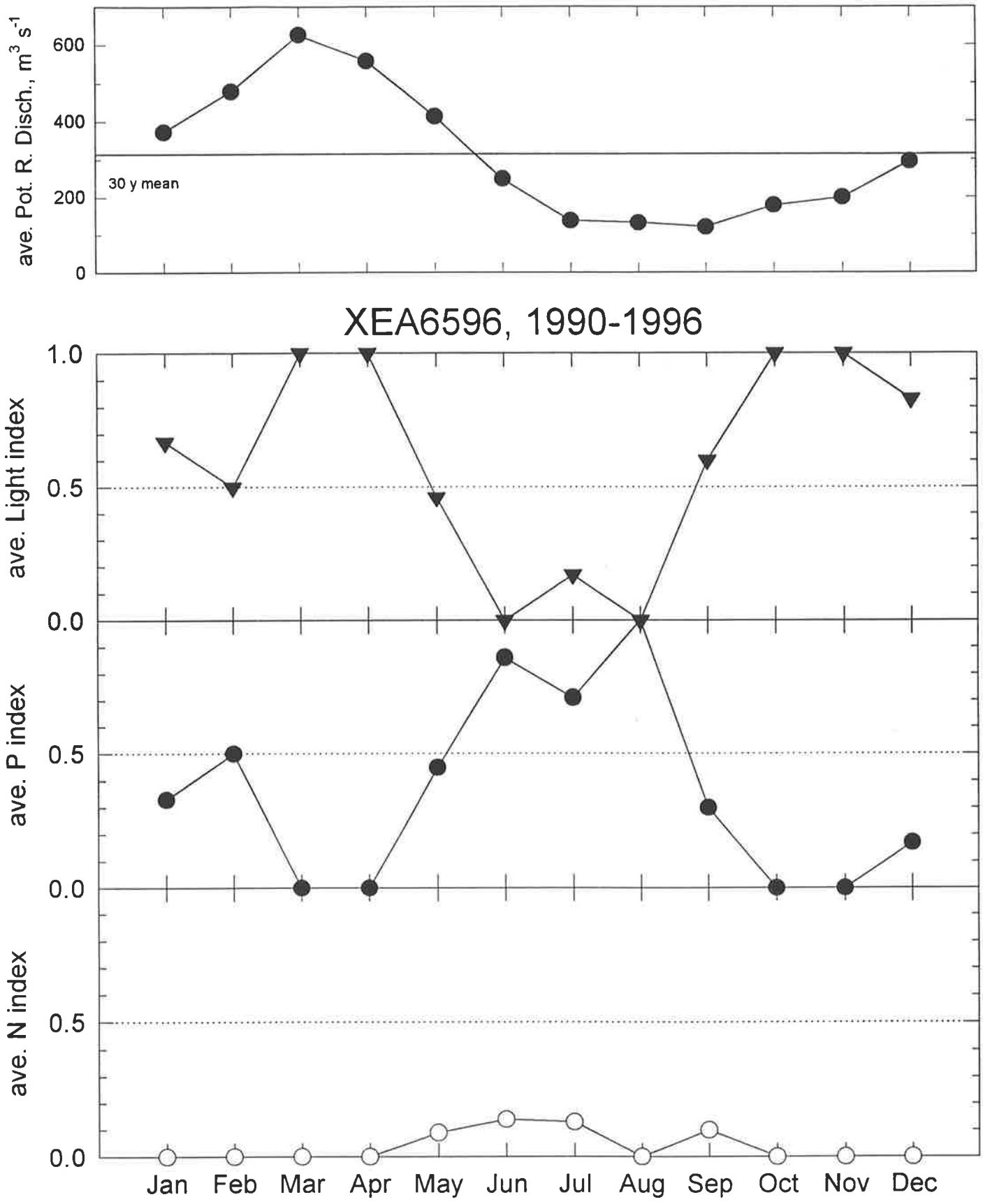

ave. Sus. R. Disch., $m^3 s^{-1}$
2000
1000
0
30 y mean
MCB5.2, 1990-1996
ave. Light index
1.0
0.5
0.0
ave. P index
0.5
0.0
ave. N index
0.5
0.0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

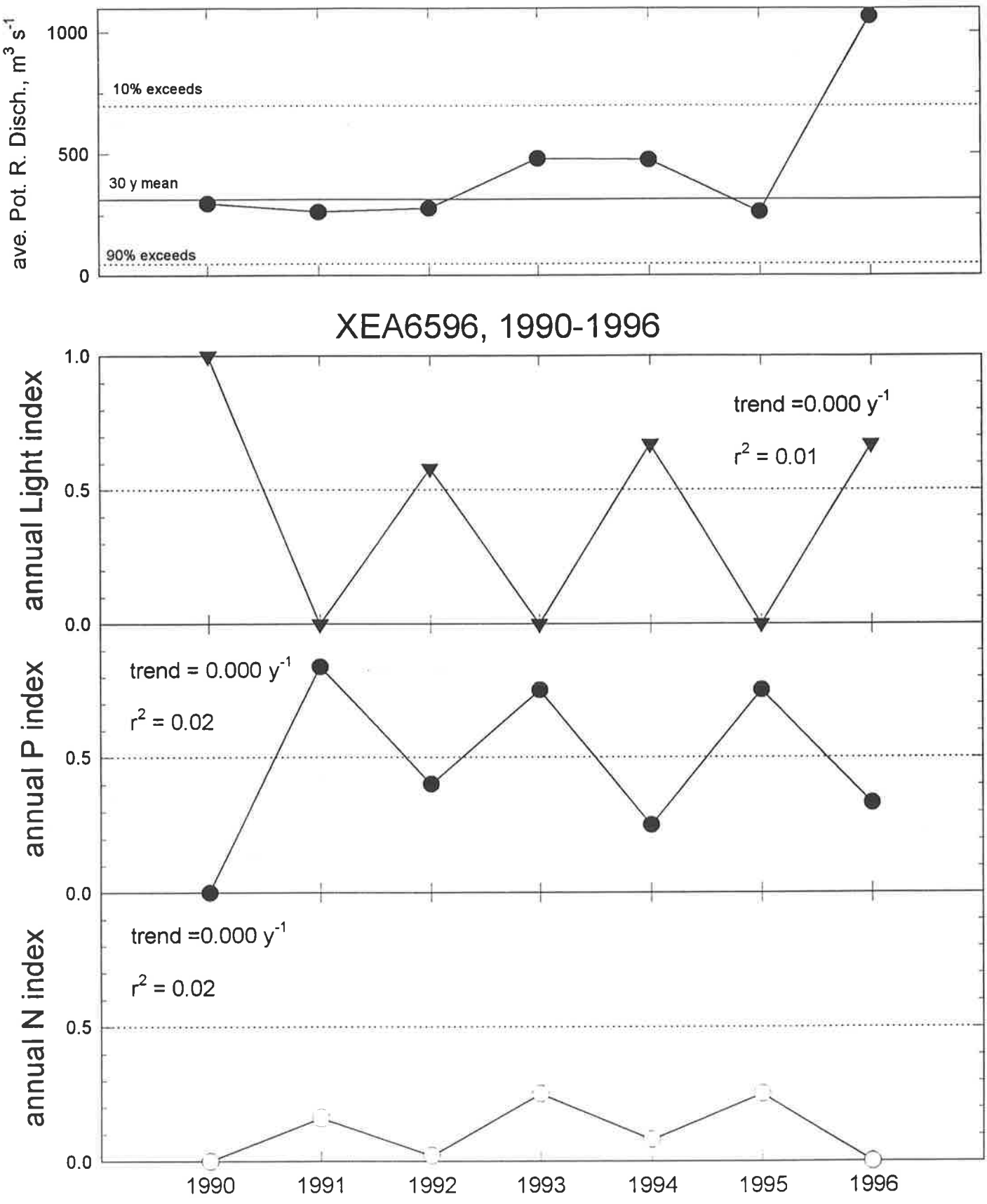

ave. Sus. R. Disch., m3 s-1
3000
2000
1000
0
10% exceeds
30 y mean
90% exceeds

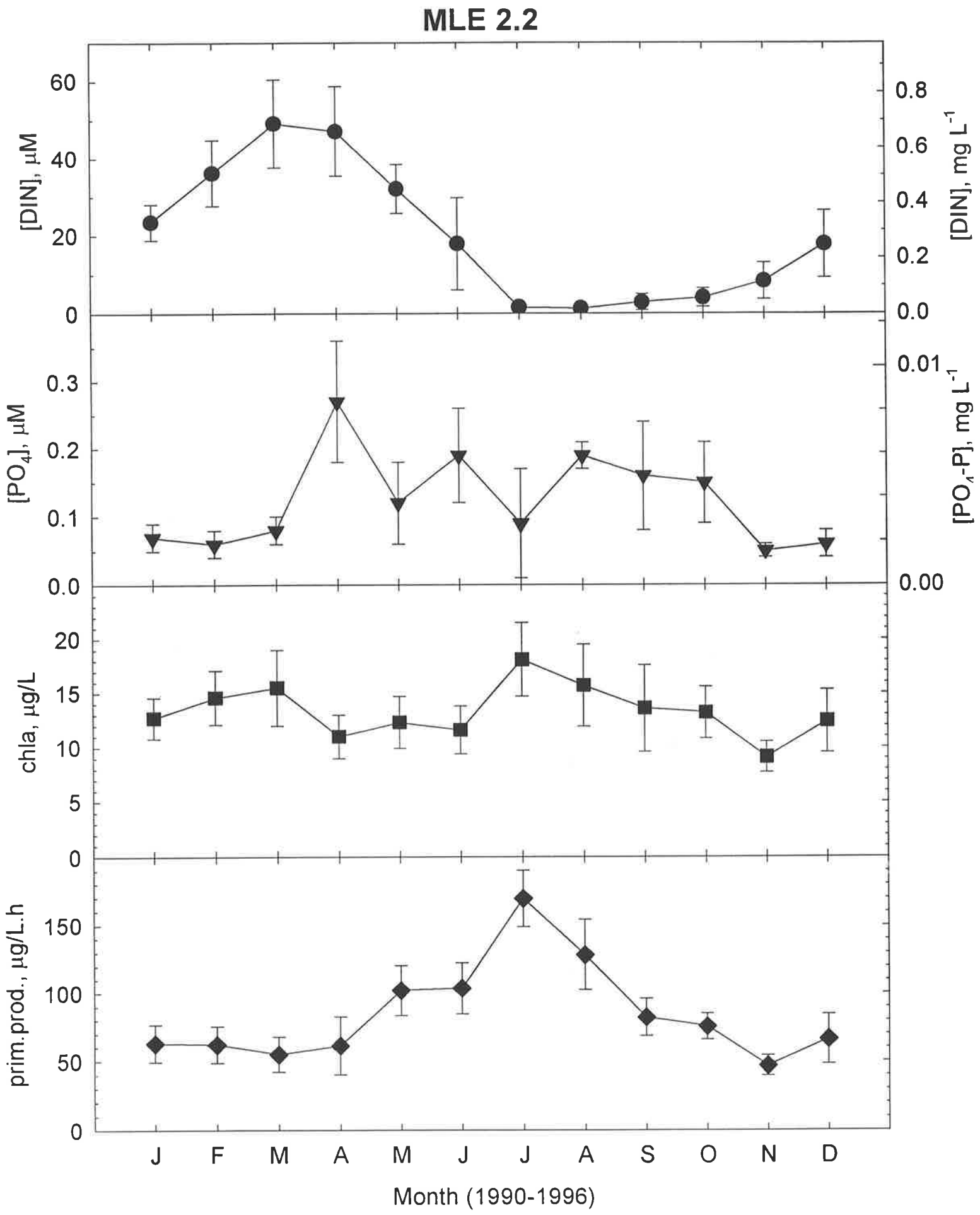

MCB5.2, 1990-1996
annual Light index
trend = -0.031 y-1
r2 = 0.44
annual P index
trend = +0.044 y-1
r2 = 0.68
annual N index
trend = 0.000 y-1
r2 = 0.11
1.0
0.5
0.0
1990
1991
1992
1993
1994
1995
1996

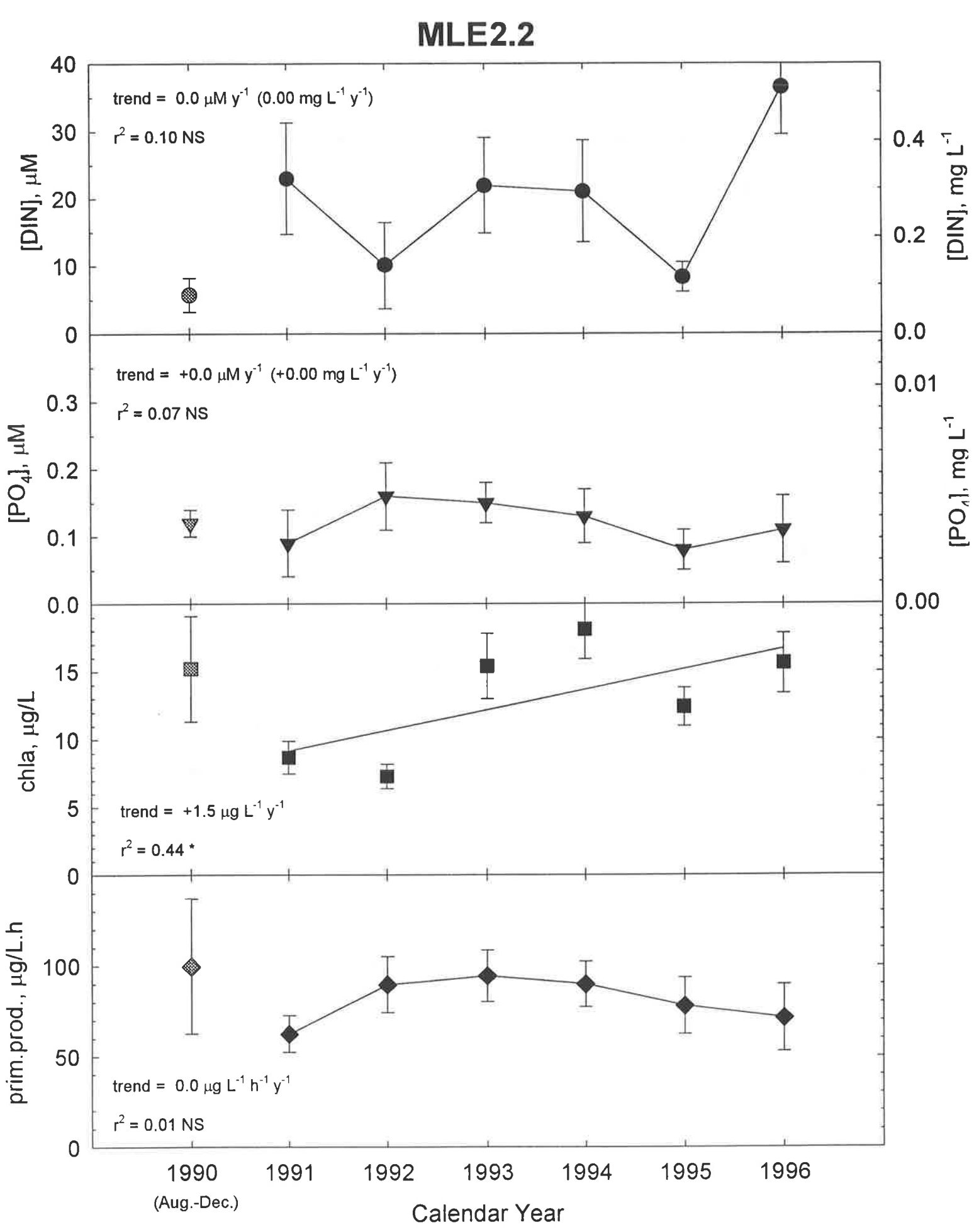

XEA6596
[DIN], µM
[DIN], mg L-1
[PO4], µM
[PO4-P], mg L-1
chla, µg/L
prim.prod., µg/L.h
J F M A M J J A S O N D
Month (1990-1996)

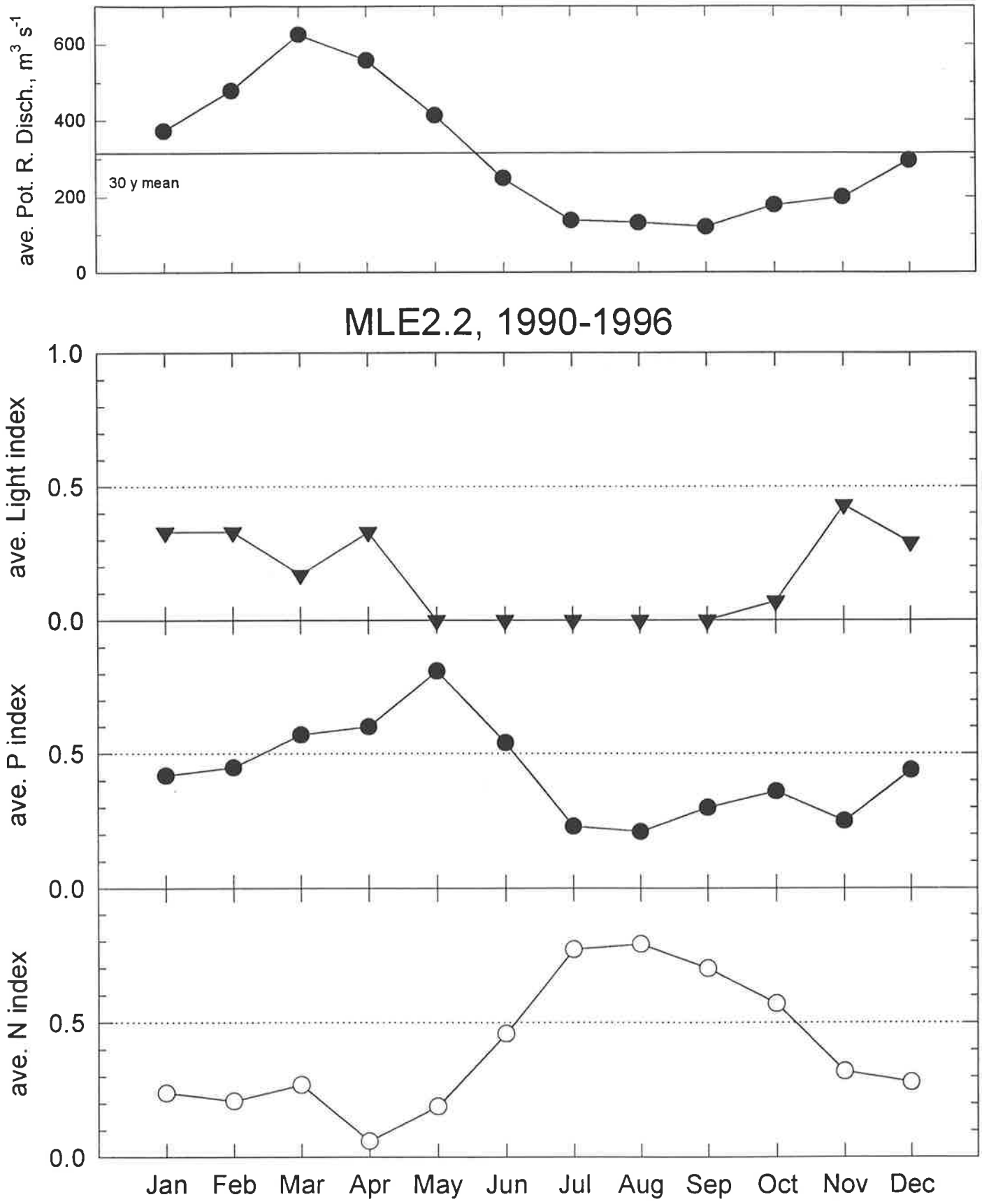

XEA6596 (May, July, Sept.)
[DIN], µM
[DIN], mg L-1
trend = 0.0 µM y-1 (0.00 mg L-1 y-1)
r2 = 0.28 NS
[PO4], µM
[PO4], mg L-1
trend = 0.0 µM y-1 (0.00 mg L-1 y-1)
r2 = 0.04 NS
chla, µg/L
trend = +4.6 µg L-1 y-1
r2 = 0.33 *
prim.prod., µg/L.h
trend = 0.0 µg L-1 h-1 y-1
r2 = 0.14 NS
1990
(Aug.-Dec.)
1991
1992
1993
1994
1995
1996
Calendar Year

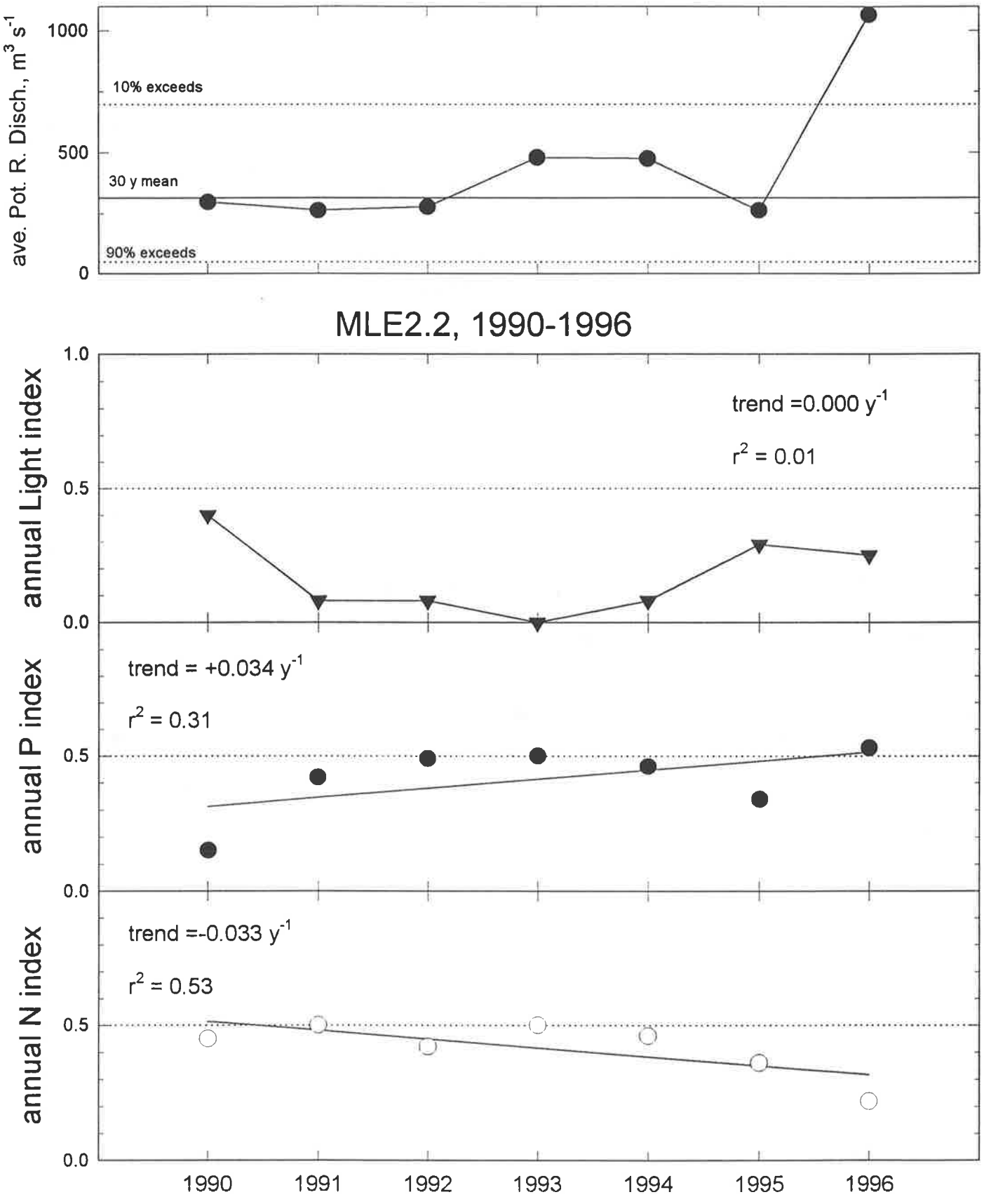

ave. Pot. R. Disch., m3 s-1
600
400
200
0
30 y mean
XEA6596, 1990-1996
ave. Light index
1.0
0.5
0.0
ave. P index
0.5
0.0
ave. N index
0.5
0.0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

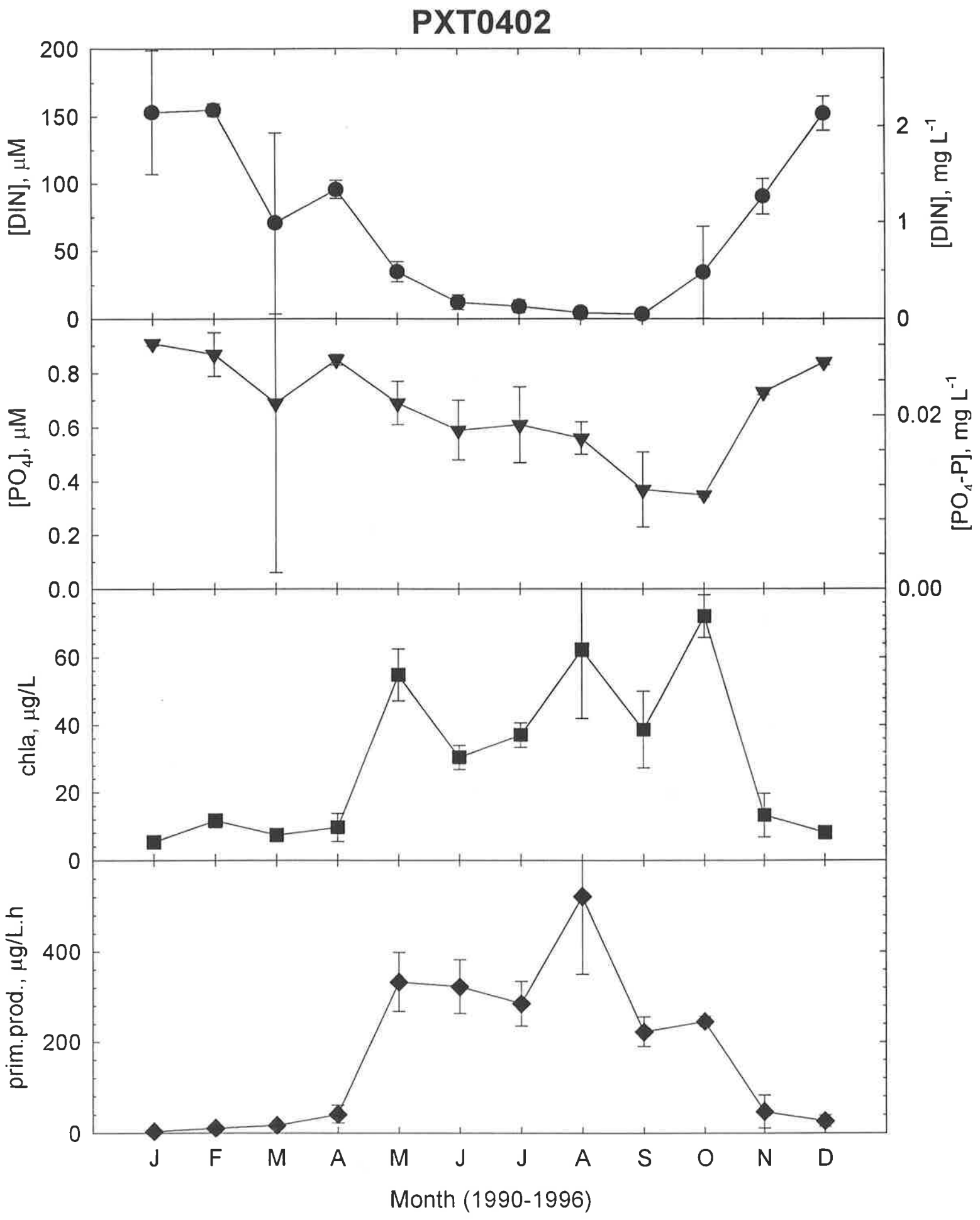

ave. Pot. R. Disch., m3 s-1
1000
500
0
10% exceeds
30 y mean
90% exceeds
XEA6596, 1990-1996
annual Light index
1.0
0.5
0.0
trend =0.000 y-1
r2 = 0.01
annual P index
trend = 0.000 y-1
r2 = 0.02
annual N index
trend =0.000 y-1
r2 = 0.02
1990
1991
1992
1993
1994
1995
1996

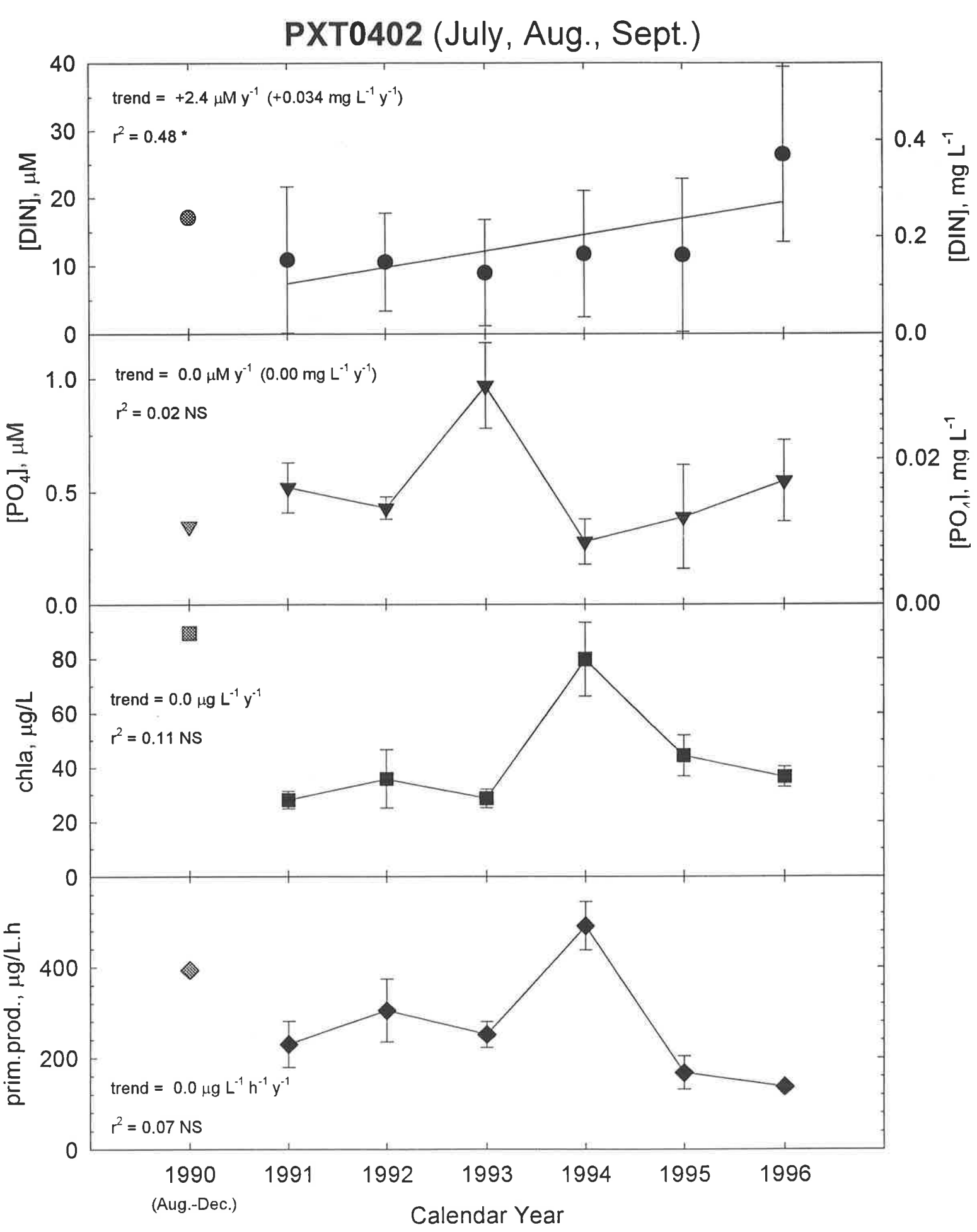

MLE 2.2
[DIN], µM
[DIN], mg L-1
[PO4], µM
[PO4-P], mg L-1
chla, µg/L
prim.prod., µg/L.h
J F M A M J J A S O N D
Month (1990-1996)

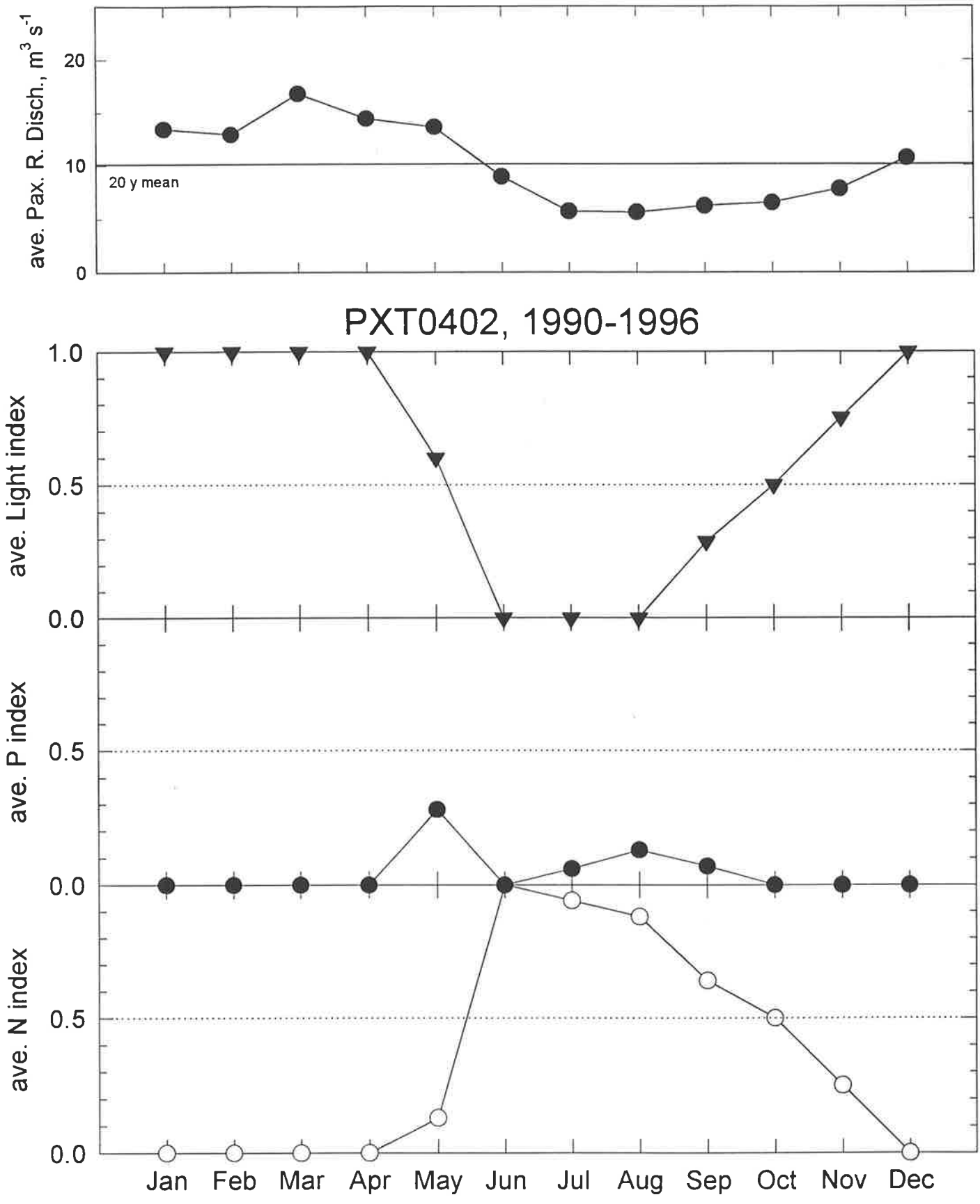

MLE2.2
trend = 0.0 µM y-1 (0.00 mg L-1 y-1)
r2 = 0.10 NS
[DIN], µM
[DIN], mg L-1
trend = +0.0 µM y-1 (+0.00 mg L-1 y-1)
r2 = 0.07 NS
[PO4], µM
[PO4], mg L-1
chla, µg/L
trend = +1.5 µg L-1 y-1
r2 = 0.44 *
prim.prod., µg/L.h
trend = 0.0 µg L-1 h-1 y-1
r2 = 0.01 NS
1990
(Aug.-Dec.)
1991
1992
1993
1994
1995
1996
Calendar Year

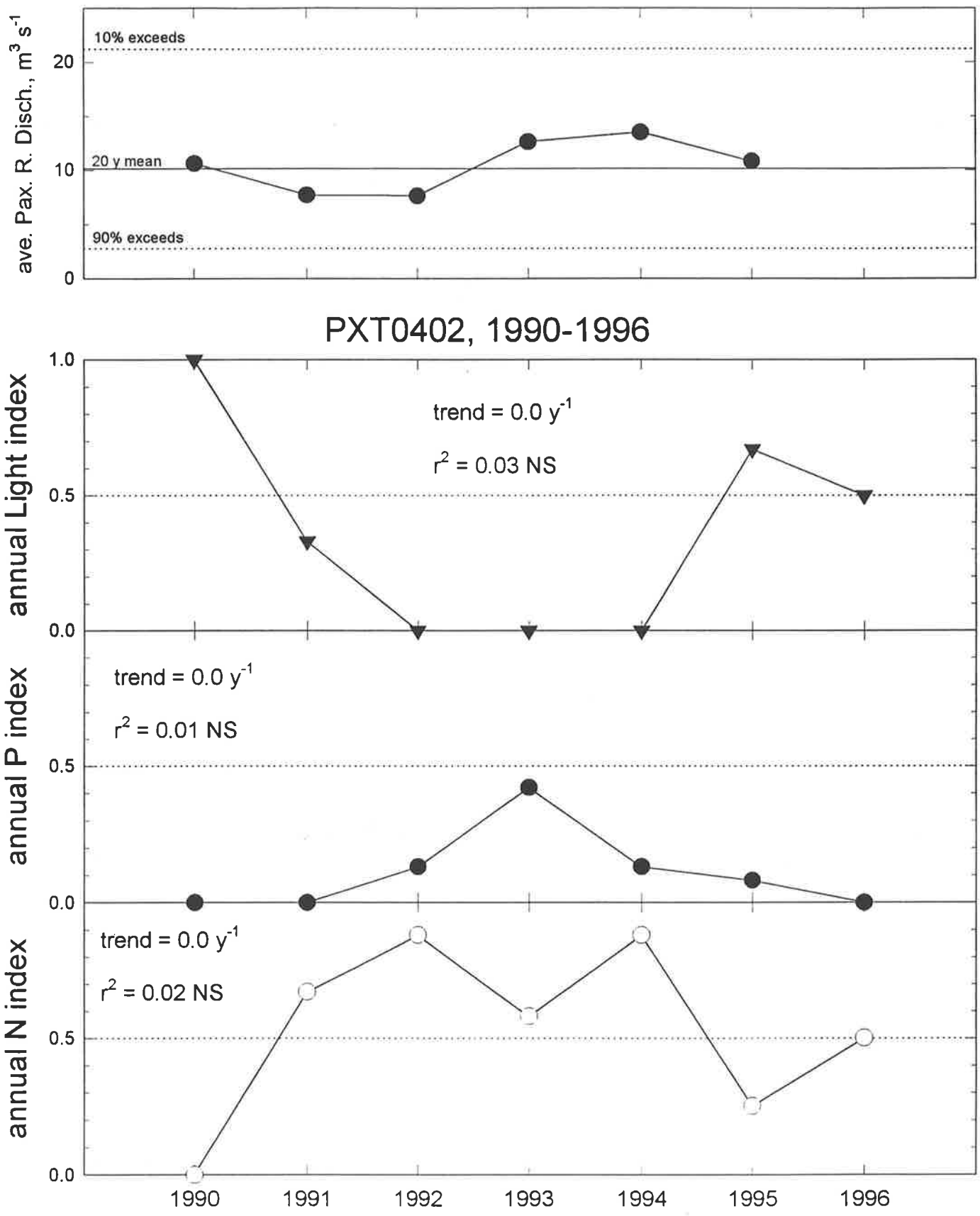

ave. Pot. R. Disch., m3 s-1
600
400
200
0
30 y mean
MLE2.2, 1990-1996
ave. Light index
1.0
0.5
0.0
ave. P index
0.5
0.0
ave. N index
0.5
0.0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

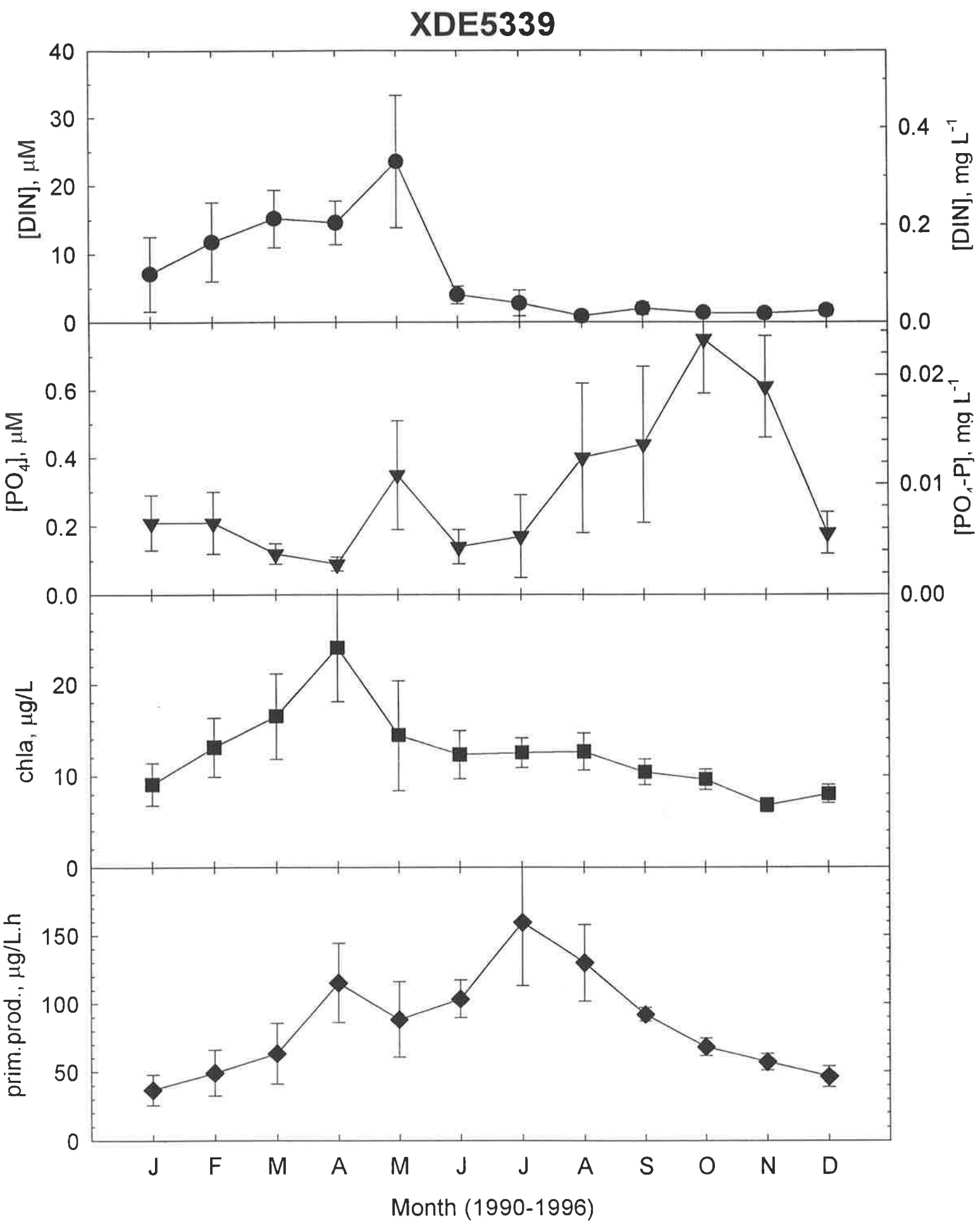

ave. Pot. R. Disch., m3 s-1
1000
500
0
10% exceeds
30 y mean
90% exceeds
MLE2.2, 1990-1996
annual Light index
1.0
0.5
0.0
trend =0.000 y-1
r2 = 0.01
annual P index
trend = +0.034 y-1
r2 = 0.31
annual N index
trend =-0.033 y-1
r2 = 0.53
1990
1991
1992
1993
1994
1995
1996


PXT0402
[DIN], µM
[DIN], mg L-1
[PO4], µM
[PO4-P], mg L-1
chla, µg/L
prim.prod., µg/L.h
J F M A M J J A S O N D
Month (1990-1996)

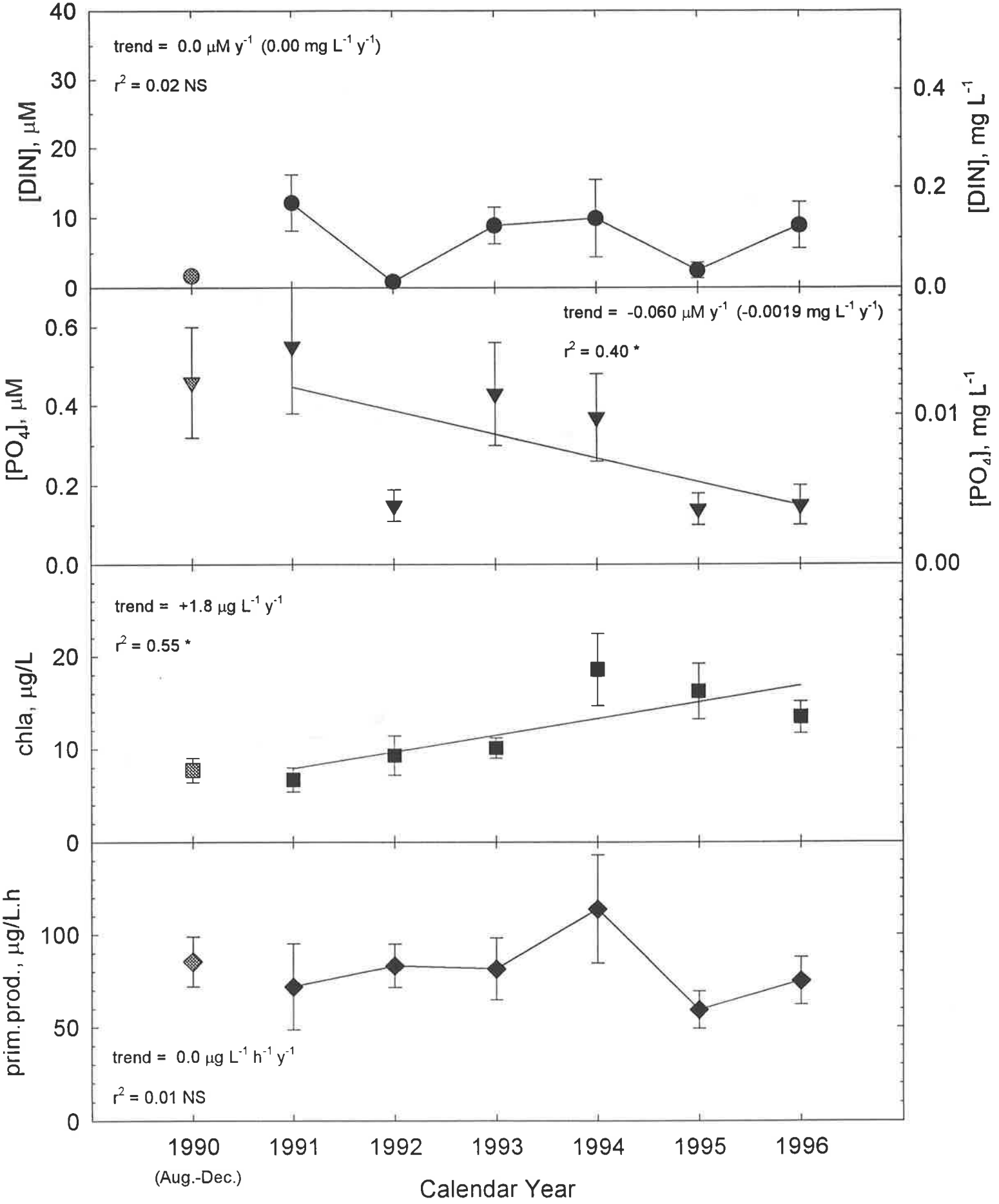

PXT0402 (July, Aug., Sept.)
trend = +2.4 µM y-1 (+0.034 mg L-1 y-1)
r2 = 0.48 *
[DIN], µM
[DIN], mg L-1
trend = 0.0 µM y-1 (0.00 mg L-1 y-1)
r2 = 0.02 NS
[PO4], µM
[PO4], mg L-1
trend = 0.0 µg L-1 y-1
r2 = 0.11 NS
chla, µg/L
trend = 0.0 µg L-1 h-1 y-1
r2 = 0.07 NS
prim.prod., µg/L.h
1990
(Aug.-Dec.)
1991
1992
1993
1994
1995
1996
Calendar Year

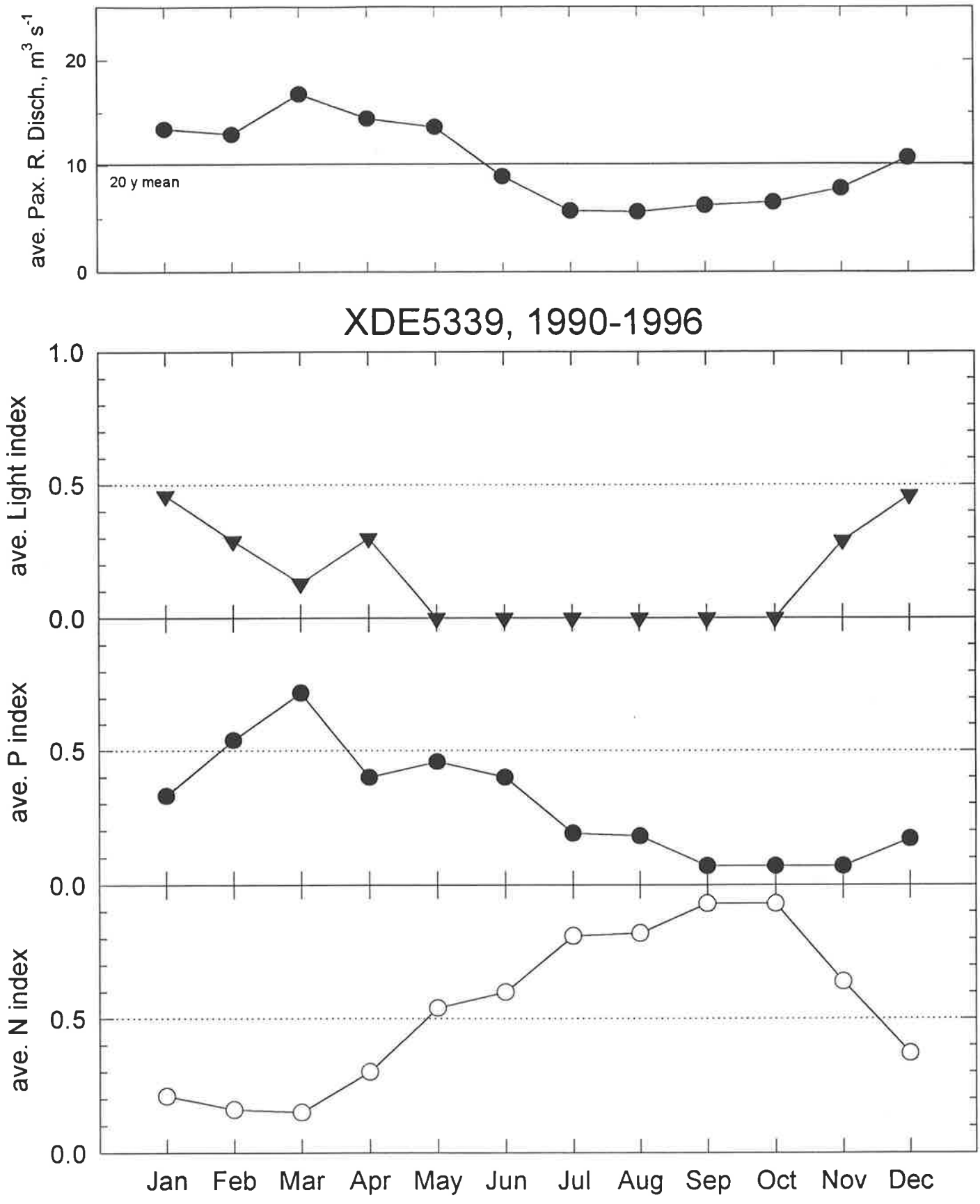

ave. Pax. R. Disch., m3 s-1
20
10
0
20 y mean
PXT0402, 1990-1996
ave. Light index
1.0
0.5
0.0
ave. P index
0.5
0.0
ave. N index
0.5
0.0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

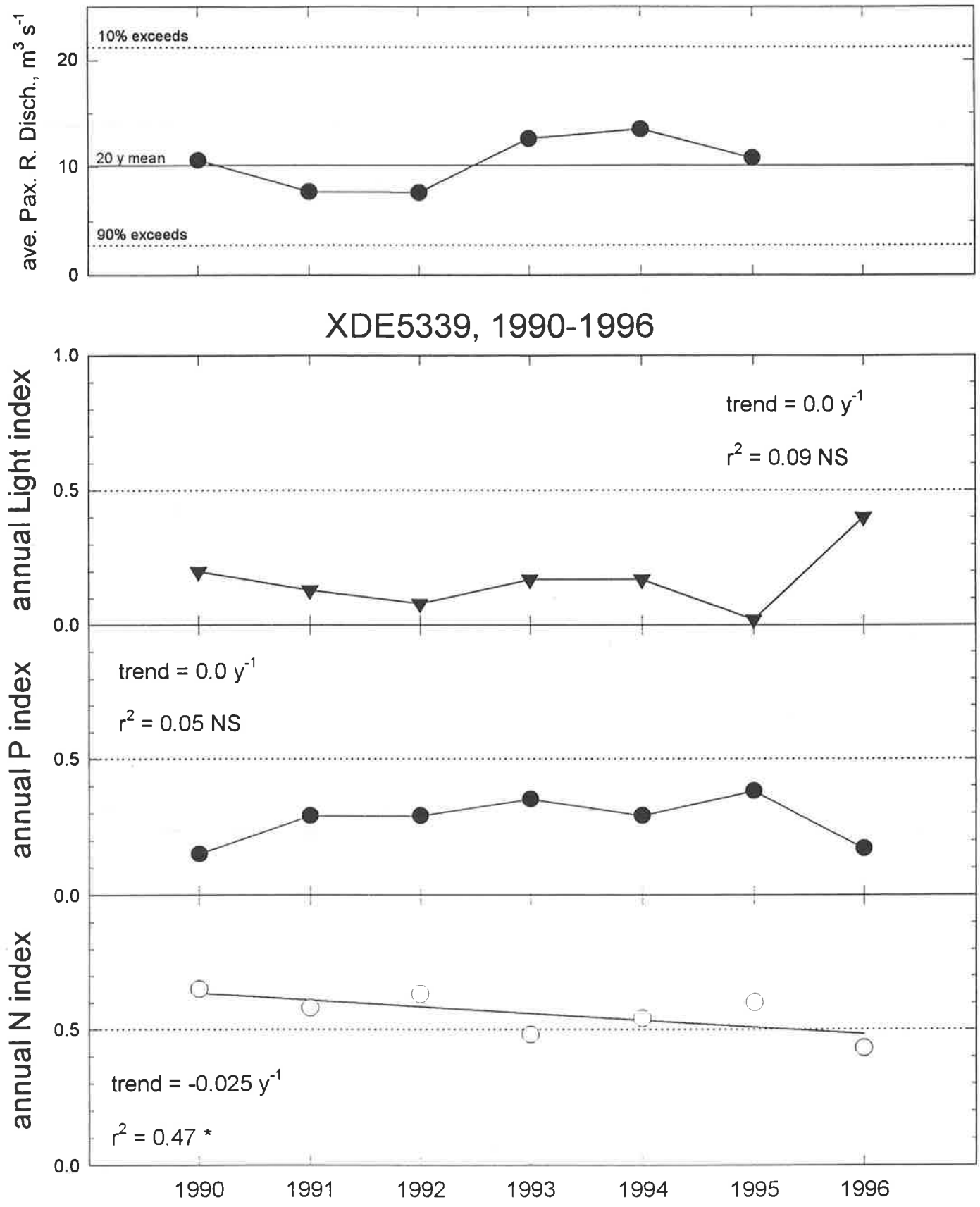

ave. Pax. R. Disch., m3 s-1
10% exceeds
20 y mean
90% exceeds
20
10
0
PXT0402, 1990-1996
annual Light index
trend = 0.0 y-1
r2 = 0.03 NS
1.0
0.5
0.0
annual P index
trend = 0.0 y-1
r2 = 0.01 NS
0.5
0.0
annual N index
trend = 0.0 y-1
r2 = 0.02 NS
0.5
0.0
1990
1991
1992
1993
1994
1995
1996

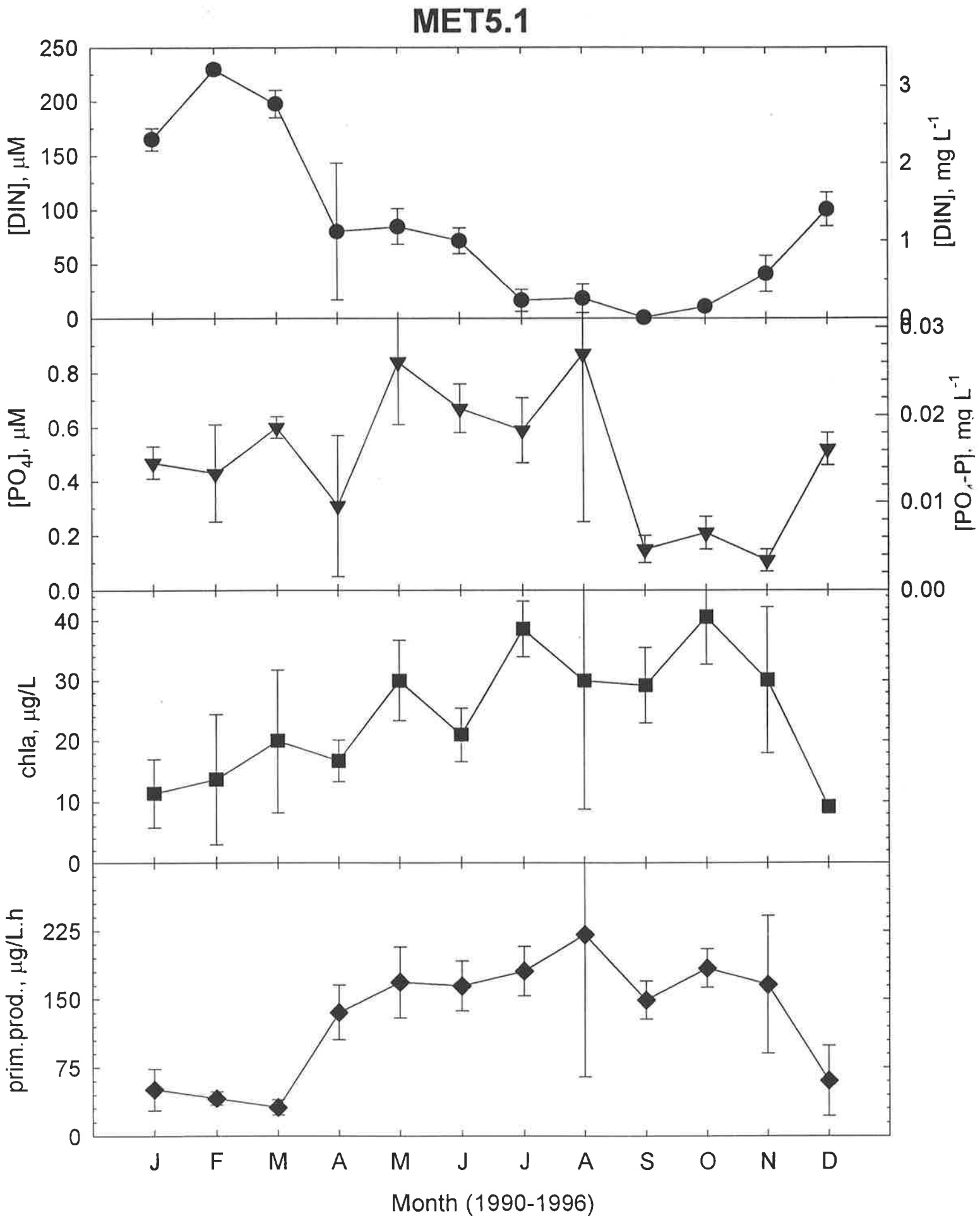

XDE5339
[DIN], µM
[DIN], mg L-1
[PO4], µM
[PO4-P], mg L-1
chla, µg/L
prim.prod., µg/L.h
J F M A M J J A S O N D
Month (1990-1996)

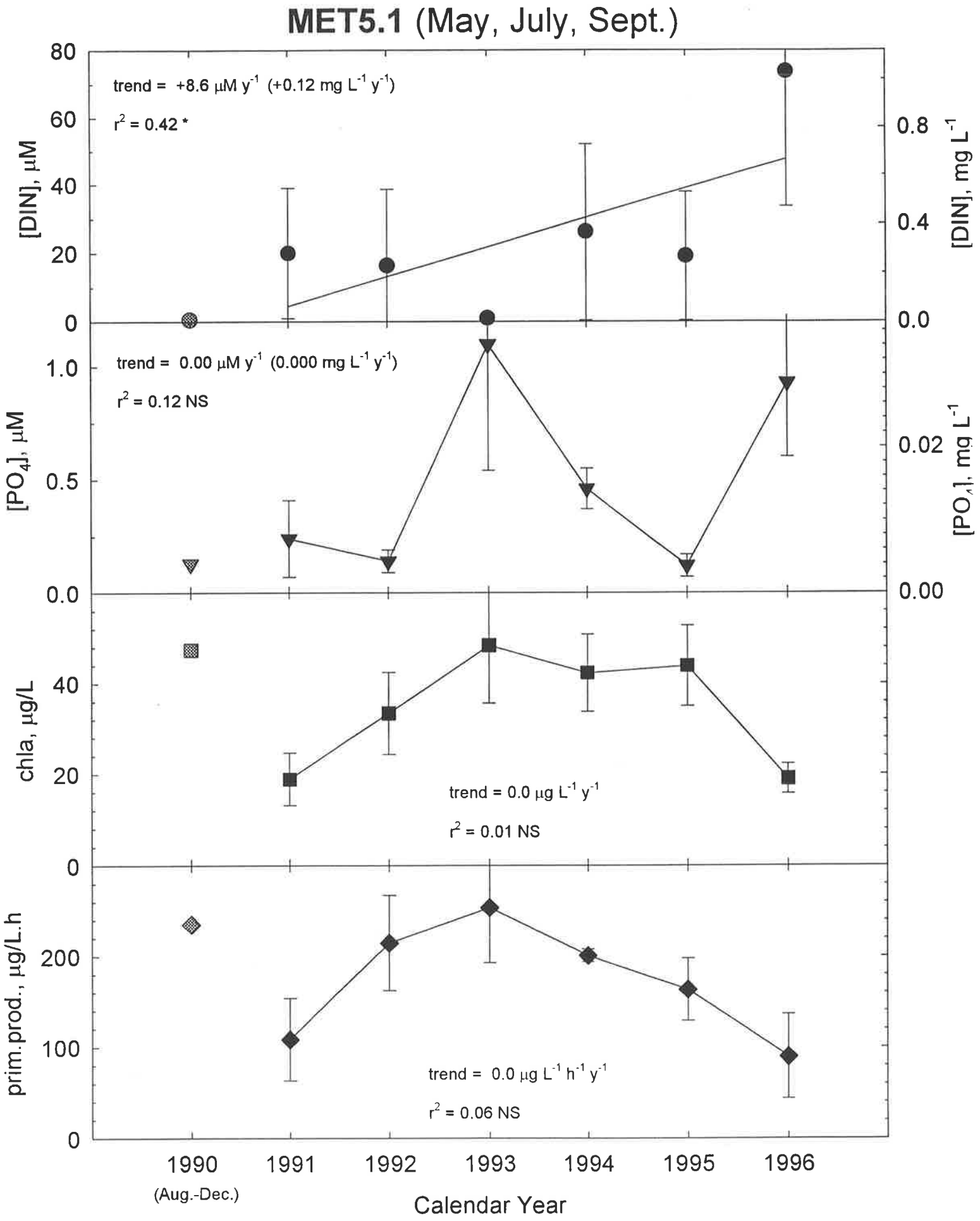
XDE5339

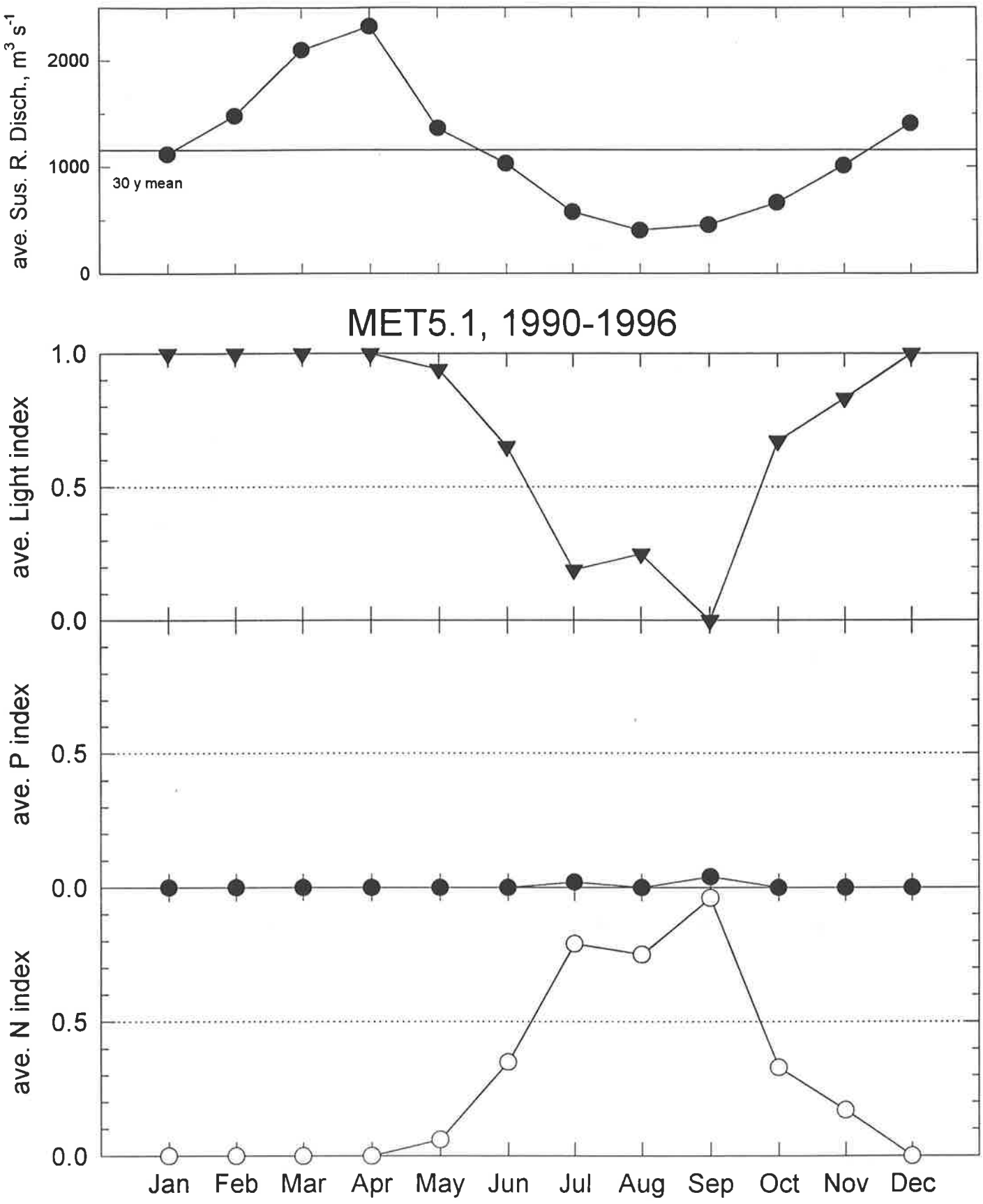

trend = 0.0 µM y-1 (0.00 mg L-1 y-1)
r2 = 0.02 NS
[DIN], µM
[DIN], mg L-1
trend = -0.060 µM y-1 (-0.0019 mg L-1 y-1)
r2 = 0.40 *
[PO4], µM
[PO4], mg L-1
trend = +1.8 µg L-1 y-1
r2 = 0.55 *
chla, µg/L
trend = 0.0 µg L-1 h-1 y-1
r2 = 0.01 NS
prim.prod., µg/L.h
1990
(Aug.-Dec.)
1991
1992
1993
1994
1995
1996
Calendar Year

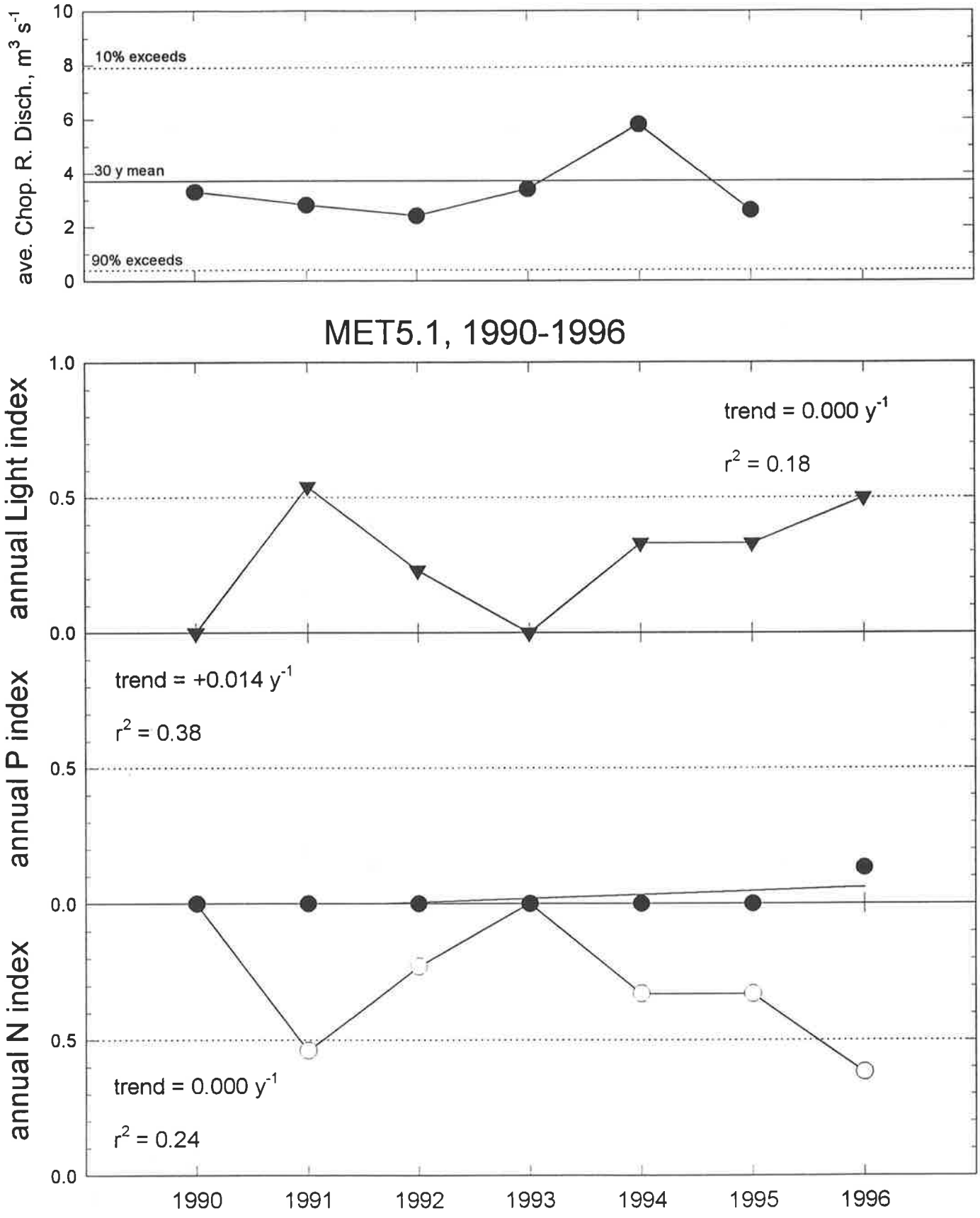

ave. Pax. R. Disch., m3 s-1
20
10
0
20 y mean
XDE5339, 1990-1996
1.0
0.5
0.0
ave. Light index
ave. P index
ave. N index
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

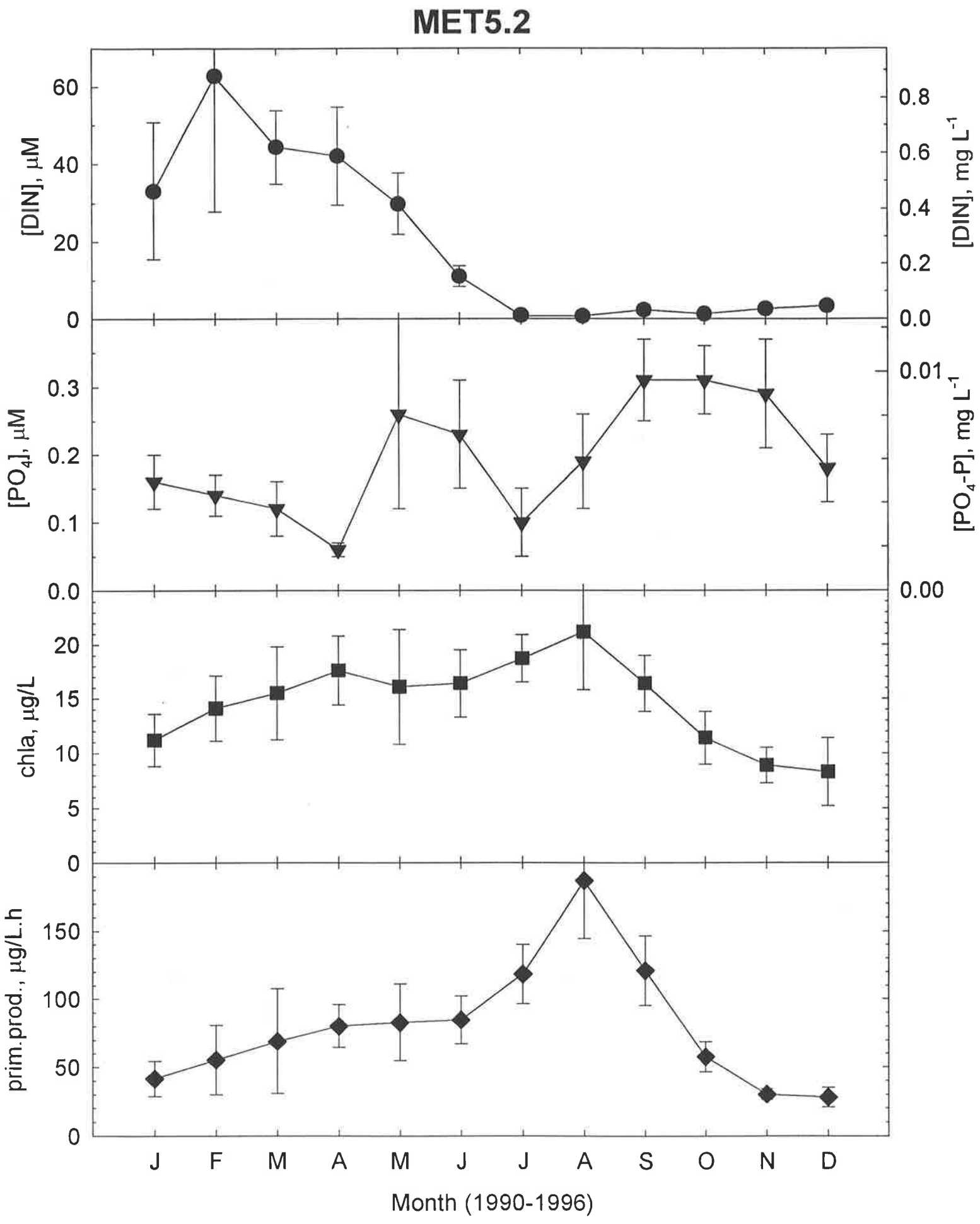

ave. Pax. R. Disch., m3 s-1
10% exceeds
20 y mean
90% exceeds
20
10
0
XDE5339, 1990-1996
annual Light index
trend = 0.0 y-1
r2 = 0.09 NS
annual P index
trend = 0.0 y-1
r2 = 0.05 NS
annual N index
trend = -0.025 y-1
r2 = 0.47 *
1.0
0.5
0.0
1990
1991
1992
1993
1994
1995
1996

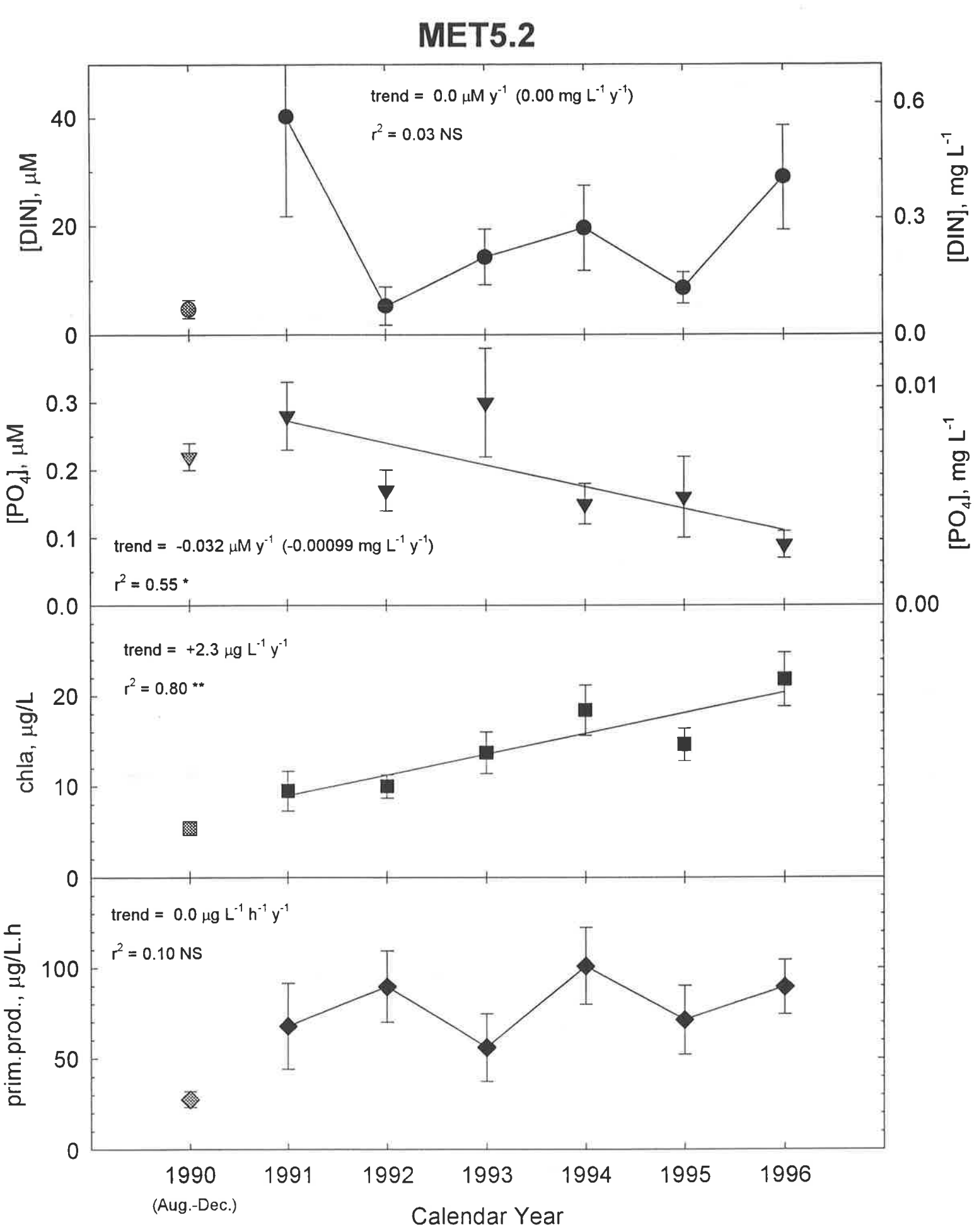

MET5.1
[DIN], µM
[DIN], mg L-1
[PO4], µM
[PO4-P], mg L-1
chla, µg/L
prim.prod., µg/L.h
J F M A M J J A S O N D
Month (1990-1996)

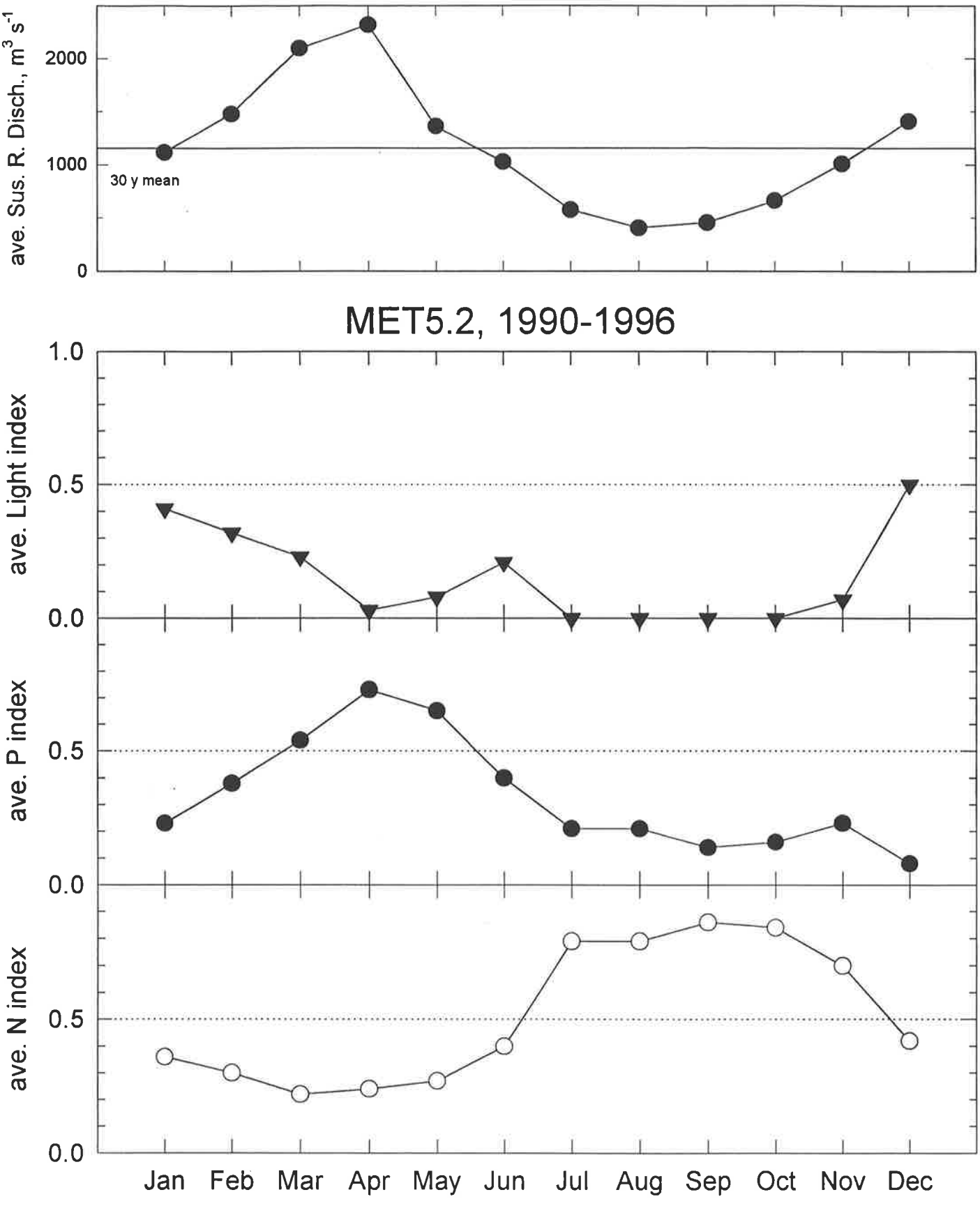

MET5.1 (May, July, Sept.)
trend = +8.6 µM y-1 (+0.12 mg L-1 y-1)
r2 = 0.42 *
[DIN], µM
[DIN], mg L-1
trend = 0.00 µM y-1 (0.000 mg L-1 y-1)
r2 = 0.12 NS
[PO4], µM
[PO4], mg L-1
chla, µg/L
trend = 0.0 µg L-1 y-1
r2 = 0.01 NS
prim.prod., µg/L.h
trend = 0.0 µg L-1 h-1 y-1
r2 = 0.06 NS
1990
(Aug.-Dec.)
1991
1992
1993
1994
1995
1996
Calendar Year

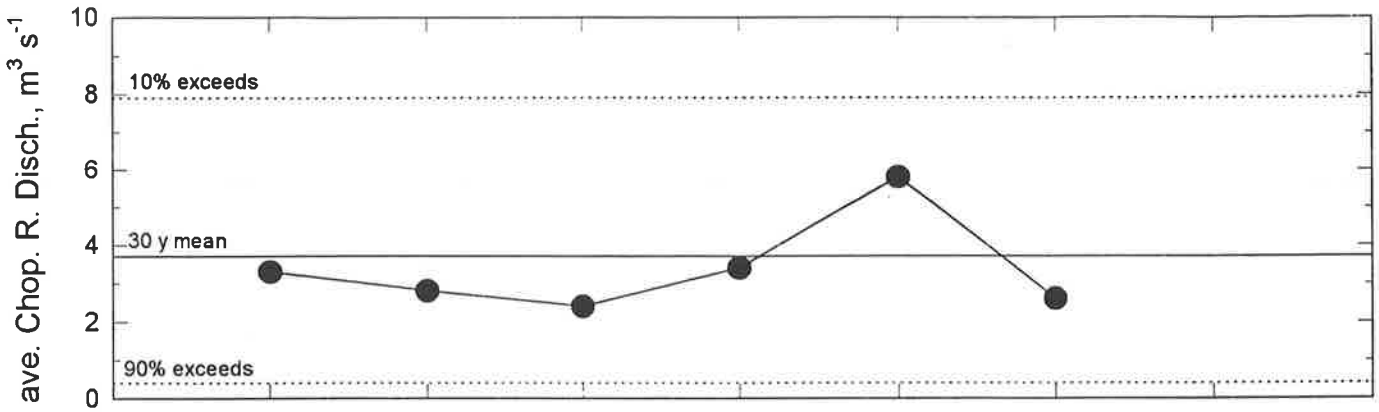
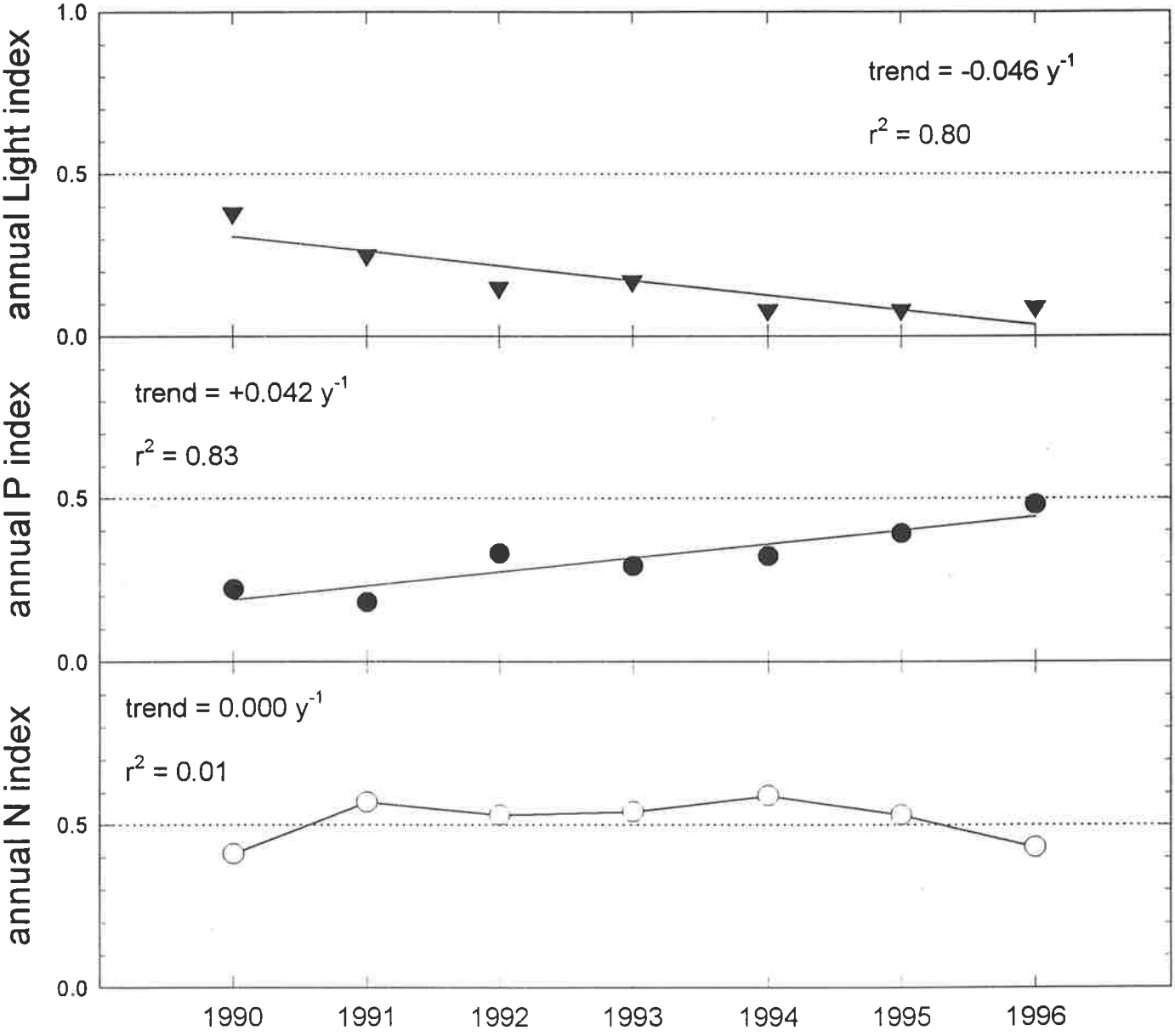

ave. Sus. R. Disch., m3 s-1
2000
1000
0
30 y mean
MET5.1, 1990-1996
ave. Light index
1.0
0.5
0.0
ave. P index
0.5
0.0
ave. N index
0.5
0.0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec


ave. Chop. R. Disch., m3 s-1
10
8
6
4
2
0
10% exceeds
30 y mean
90% exceeds
MET5.1, 1990-1996
annual Light index
1.0
0.5
0.0
trend = 0.000 y-1
r2 = 0.18
annual P index
0.5
0.0
trend = +0.014 y-1
r2 = 0.38
annual N index
0.5
0.0
trend = 0.000 y-1
r2 = 0.24
1990
1991
1992
1993
1994
1995
1996


MET5.2
[DIN], µM
[DIN], mg L-1
[PO4], µM
[PO4-P], mg L-1
chla, µg/L
prim.prod., µg/L.h
J F M A M J J A S O N D
Month (1990-1996)


MET5.2
trend = 0.0 µM y-1 (0.00 mg L-1 y-1)
r2 = 0.03 NS
[DIN], µM
[DIN], mg L-1
trend = -0.032 µM y-1 (-0.00099 mg L-1 y-1)
r2 = 0.55 *
[PO4], µM
[PO4], mg L-1
trend = +2.3 µg L-1 y-1
r2 = 0.80 **
chla, µg/L
trend = 0.0 µg L-1 h-1 y-1
r2 = 0.10 NS
prim.prod., µg/L.h
1990
(Aug.-Dec.)
1991
1992
1993
1994
1995
1996
Calendar Year


ave. Sus. R. Disch., m3 s-1
2000
1000
0
30 y mean
MET5.2, 1990-1996
ave. Light index
1.0
0.5
0.0
ave. P index
0.5
0.0
ave. N index
0.5
0.0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec



MET5.2, 1990-1996