水域での生物活性連続測定システムの開発

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本報告書は、平成 12-14 年度の科学研究費補助金基盤研究 (B) (2) (課題番号 12555155) により実施された「水域での生物活性連続測定システムの開発」の最終報告書である。以下に、研究の背景と目的、研究の概要、研究組織、研究経費、研究発表をまとめる。

研究背景と目的

地球温暖化、富栄養化、毒性物質などの水界生態系への影響に関しては、いまだ不明な点が多く、また各種対策の効果を定量的に評価する技術をもっていないのが現状である。また、様々な環境改変の影響を調べる場合にも、生態系としての活性を簡易に、定量的に測定することができる手法の確立が望まれてきた。ここでは、水中に吊した DO、pH、水温などのセンサーを定期的に上げ下げし、多くの水深での DO や DIC (アルカリ度と pH から計算) の経時変化を疑似的に連続測定する装置を開発し、湖沼、海域などで利用可能かどうかを調べることを目的としている。

研究の概要

A. 水域生物活性連続測定システムの制作とそれを用いての測定

自動昇降装置付きの水域生物活性連続測定システムを作成した．それを霞ヶ浦湖心に設置し，各季節，それぞれ約 1 週間にわたり DO，pH，クロロフィル a，水温，深度等を連続測定した (研究発表 4, 5)。この結果をもとに，生物活性の時間，空間変化を推測する方法を検討したが，その際に最も問題となるのは上下層間の混合の影響を取り除くことである．すなわち，水温による密度差を考慮して鉛直拡散係数を推定し，鉛直混合量を予測するモデル 1，大気交換の影響が全水深均一に生じるとするモデル 2，最上層と最下層の水温差から成層しているかを判定し，成層している場合にはモデル 1 を，成層していない場合にはモデル 2 を用いるモデル 3，成層破壊時には全層均一の生物現象による変動があるとするモデル 4 を，それぞれ観測結果に当てはめた結果，モデル 4 により滑らかな生物活性変化が得られることを確認した (研究発表 3)．以上にあわせて，屋外実験池における夜間の呼吸量の連続測定結果を研究発表 1 に，霞ヶ浦の富栄養化について研究発表 2 に示す．

B. 箱方式による水域生物活性連続測定システムの試作と運転

海域，観潮域など水の入れ替わりに激しい水域では上述のようなフリーウ

オーター法では誤差が大きい．このため，プラスチック製の箱中に水質センサーを取り付け，定期的に中の水が入れ替わる仕組みを作り，また底面にスターラーを配置しセンサーをゆるやかに撹拌した．こうした装置を屋外実験池に取り付け，システムの動作確認を行い，問題なく動くことを確かめた．

C. ダム湖における水質連続観測データの解析
　山口県佐波川水系島地川ダムの堤体に設置され，上下移動可能な水質センサー（水温，電気伝導度，pH，DO，クロロフィルa，濁度）を年4回，それぞれ1週間にわたり，1m間隔21水深を1時間に1回ごと上下するようにプログラムし，鉛直水質変動を連続観測した．水深2-4mに生物活性の高い層があり，DO，pHの日周変動が大きいこと，また水深15m以深では時間の経過とともに貧酸素化してゆく様子が観察された．こうしたシステムは，ダム湖などの水質管理に極めて重要な情報を提供しうることがわかった．
（発表論文リスト6）

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平成14年度	1,300	0	1,300
総計	10,100	0	10,100

研究発表

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A．水域生物活性連続測定システムの制作とそれを用いての測定

写真 A-1. センサーを上下させる装置

写真 A-2. この装置を霞ヶ浦湖心の観測タワーに取り付けた様子

Takehiko Fukushima · Kazuo Matsushige
Richard S.J. Weisburd

Characteristics of nighttime respiration in outdoor mesocosms

Abstract To better understand the patterns and regulation of nighttime community respiration, dissolved oxygen (DO) and pH were simultaneously measured at 5-min intervals for 37 days in each of three outdoor mesocosms with different fish stocking levels. Nighttime decreases in community respiration rates were estimated fairly well by an exponential function of time and slightly worse by a linear one, irrespective of ecosystem differences, but smaller time coefficients were obtained for dissolved inorganic carbon (DIC) than for DO. Respiratory quotients increased significantly from nightfall to the hour before dawn. To roughly estimate gross productivity from net productivity measurements, we extrapolated nighttime respiration from various parts of the night to the daytime; among the models evaluated, that extrapolating the respiration rate averaged over the whole nighttime to the previous day led to the highest correlation between irradiance and estimated gross productivity. Significant correlations were found between estimated daytime gross production rates and respiration rates just after sunset, whereas respiration before sunrise seemed quite constant and close to minimum metabolic rates of the ecosystems. Nighttime respiration was also affected by the composition and/or metabolic state of the system, expressed here by daily net community productivity. Multiple regression analysis showed that more than 75% of daily and between-pond variation in respiration rates just after sunset was explained by daytime gross productivity, planktonic and detrital carbon concentrations, and daily net community productivity.

Introduction

Dissolved oxygen (DO) is arguably one of the most important components of water quality. The ability to predict minimum nighttime DO levels from measurements in the evening is important in many situations, including management of reservoirs and ponds; toward this end, the patterns of variation in nighttime respiration also must be well understood. Dark respiration usually decreases with time in the dark (Grobbelaar and Soeder 1985; Weger et al. 1989; Watanabe and Kimura 1990; Markager et al. 1992; Szyper et al. 1992). Madenjian et al. (1988) found that a whole-pond respiration–diffusion model fairly accurately predicted dawn DO in freshwater and brackish ponds on the basis of information about water temperature, suggesting that respiration is independent of time after dark. In contrast, Markager and Sand-Jensen (1989) reported that the most common patterns showed a pronounced peak in respiration rate shortly after sunset, but that there were several types of deviation from this pattern. Many variables, including primary productivity, biomass of phytoplankton and/or bacteria, DO, temperature, etc., have been investigated as potential factors that affect nighttime respiration rates (Jensen et al. 1990; Szyper et al. 1992; Sampou and Kemp 1994; Aristegui et al. 1996), but the most influential factors differed among these studies. Thus, we are not able to accurately predict the patterns of nighttime respiration at present.

Since DO is both a product of the photoautotrophic production of organic matter and consumed during aerobic respiration, patterns of DO change provide information about relative rates of net community organic matter production. In fact, when used in mass balance expressions that correct for other fluxes (e.g., gas exchange across the air–water interface), the rate of change in DO can be used to measure net community productivity.

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Aside from being of interest in and of itself, daytime gross community productivity might be a good predictor of nighttime respiration rate. To calculate gross community productivity from measurements of net community production, we must first estimate community respiration rates. If patterns of community respiration, particularly those during daytime, were better known, then we could use measurements of net community productivity to estimate gross productivity accurately.

Respiration is usually estimated by dark-bottle incubations of water with or without plankton and/or by measurement of in situ DO or pH changes (Williams 1984). Incubations have the advantages of a closed system (no fluxes in or out) and ease of replication or manipulation. In situ approaches, often referred to as free-water methods, often involve measurements of DO and/or dissolved inorganic carbon (DIC) and permit frequent automatic collection of data. Both approaches have their drawbacks. Incubations are inaccurate due either to bottle effects (e.g., contamination or growth on the walls of the container, exclusion of large organisms, etc.) that may alter the rates being measured or to poor temporal resolution. On the other hand, with free-water measurement, non-biological influences, e.g., exchange between air and water, advection, etc., must be corrected for. Few papers have reported continuous DIC change over long periods (but see Maberly 1996), and we are aware of no reports that compared simultaneous DO decrease and DIC increase to determine nighttime changes in respiratory quotient (RQ); knowledge of RQ is necessary to convert between carbon- and oxygen-based productivity measurements.

In this study, we simultaneously measured DO and pH (by the free-water method) in three outdoor mesocosms with different biota for 37 days during the summer of 1994 in order to determine the patterns of nighttime respiration and RQ. Both linear and exponential models were applied to the nighttime respiration rates, and the fits of these models were compared. Correlation analysis was applied to the relationships between nighttime respiration rates, biomass in several categories, gross and net productivity, etc., in order to determine the extents to which these factors affected nighttime respiration rates. A similar experiment was conducted during the summer of 1993, and the results were analyzed mainly from the viewpoint of carbon cycles in the ponds (Fukushima et al. 1995c).

Materials and methods

Experimental systems

The experiment was conducted in three artificial outdoor ponds (mesocosms) located near Lake Kasumigaura, 60 km northeast of Tokyo, Japan (Fukushima et al. 1995a; Park et al. 1997). The concrete ponds were lined with nylon sheeting, containing $36 m^3$ of water each (regular hexagonal shapes of 3 m on a side; water depth controlled at 1.55 m), and were filled continuously with sand-filtered water from Lake Kasumigaura at a dilution rate of $0.05 day^{-1}$ for more

than one year (Table 1). Dissolved inorganic nutrients (stock solution containing $2 mg N l^{-1}$ as $NaNO_3$ and $0.2 mg P l^{-1}$ as KH_2PO_4) were added to the water to induce high primary production. A pump ($100 l min^{-1}$), which drew water from near the bottom and brought it to just below the surface, was set in each pond to circulate the water gently. In order to elucidate the influence of fish on nutrient cycles, the dynamics of dissolved organic carbon, and dominant species of phytoplankton, we prepared three different pond ecosystem treatments: pond 1 had no fish, whereas ponds 2 and 3 had been stocked with goldfish (*Carassius auratus*) a year earlier (August 1993). During the summer of 1993, the ecosystems in the ponds changed rapidly and then gradually shifted to steady states (Fukushima et al. 1995c). At the start of this experiment (August 1994), the goldfish densities were 8.1 and $4.7 g Cm^{-3}$, and they remained fairly constant thereafter (Table 1).

Measurement systems

Global solar radiation and wind velocity were measured with a pyranometer (black and white detectors with thermopiles; EKO MS-42; EKO, Tokyo, Japan) and a propeller-type anemometer mounted 10 m above the ground near the ponds. Water temperature, DO, and pH were measured during the summer of 1994 from August 3 to September 9 (37 days) at 50- and 100-cm depths in each pond with t-type thermocouples (Copper-Constantan, rated temperature precision $0.018°C$), Yellow Springs Instruments dissolved oxygen meters (model 58; YSI, OH, USA) and polarographic probes (model M5739) with stirrers, and combination pH electrodes, each with an internal amplifier and temperature-calibration circuit (DKK Model 6430L; DKK, Tokyo, Japan). For each sampling time (5-min intervals), a personal computer stored the mean of seven consecutive sensor readings.

Every week, the sensors were cleaned and, if in poor condition, replaced. At the same time, the oxygen electrodes were calibrated by Winkler titrations of triplicate bottles drawn from a single water sample collected with a Van Dorn sampler from immediately adjacent to each oxygen electrode. The pH electrodes were immersed for more than 10 min each in pH 7 and 9 buffer solution; the resulting data were used to convert raw millivolt values to pH. The alkalinity was determined by Gran titration (Gran 1952) for water collected weekly with a 1.2-m-long column sampler from the middle layer at the center of each pond. Water was also taken daily (at around 1100) from each pond with the 1.2-m-long column sampler and filtered through precombusted, tarred Whatman GF/F filters for determination of other particulate and dissolved properties. The filters were analyzed for particulate dry weight (DW), chlorophyll a (Marker et al. 1980), particulate organic carbon (POC), and particulate organic nitrogen (PON) (Yanagimoto CHN-analyzer MT-5; Yanagimoto, Kyoto, Japan). The filtrates were analyzed for dissolved organic carbon (DOC) (Shimadzu TOC-5000 with purging at pH 2; Shimadzu, Kyoto, Japan; Fukushima et al. 1996), dissolved inorganic nitrogen and phosphorus (NH_4^+, NO_2^-, NO_3^-, and

Table 1. Average biological and chemical conditions (mean ± SD; n = number of samples) of the outdoor ponds during the experiment (August 3–September 9, 1994)

Condition		Pond 1	Pond 3	Pond 2	Inflow[a]
Dominant species of phytoplankton (n = 17)		*Scenedesmus* sp.	*Oscillatoria* sp.	*Oscillatoria* sp.	
Dominant species of zooplankton (n = 38)		Brachionus, Bosmina	Cyclops, Brachionus	Brachionus, Cyclops	
Biomass of zooplankton (n = 38)	(gCm^{-3})	1.60 ± 0.86	0.23 ± 0.12	0.16 ± 0.24	0
Biomass of goldfish (n = 2)	(gCm^{-3})	0	4.7[b], 4.4[c]	8.1[b], 8.2[c]	0
Water quality[d] (n = 38)	Chlorophyll a (mgl^{-1})	79 ± 35	128 ± 46	60 ± 25	1 ± 1
	DOC (mgl^{-1})	5.0 ± 0.2	5.8 ± 0.7	4.1 ± 0.3	3.1 ± 0.2
	POC (mgl^{-1})	9.0 ± 1.7	11.0 ± 2.1	6.1 ± 1.4	0.3 ± 0.0
	NH_4^+-N (mgl^{-1})	0.010 ± 0.007	0.008 ± 0.007	0.010 ± 0.011	0.010 ± 0.010
	NO_2^--N (mgl^{-1})	0.002 ± 0.002	0.002 ± 0.002	0.002 ± 0.002	0.002 ± 0.003
	NO_3^--N (mgl^{-1})	0.013 ± 0.019	0.004 ± 0.003	0.007 ± 0.009	0.490 ± 0.086
	DIN (mgl^{-1})[e]	0.025 ± 0.022	0.014 ± 0.008	0.019 ± 0.016	0.502 ± 0.082
	DTN (mgl^{-1})	0.65 ± 0.07	0.53 ± 0.08	0.48 ± 0.09	0.80 ± 0.14
	PON (mgl^{-1})	1.29 ± 0.27	1.27 ± 0.38	0.73 ± 0.23	0.04 ± 0.01
	TN (mgl^{-1})	1.97 ± 0.28	1.80 ± 0.39	1.22 ± 0.26	0.83 ± 0.14
	PO_4^{3-}-P (mgl^{-1})	0.066 ± 0.023	0.004 ± 0.003	0.003 ± 0.002	0.067 ± 0.013
	DP (mgl^{-1})	0.081 ± 0.023	0.012 ± 0.003	0.012 ± 0.003	0.061 ± 0.015
	TP (mgl^{-1})	0.138 ± 0.0030	0.086 ± 0.010	0.051 ± 0.010	0.052 ± 0.016

DOC, Dissolved organic carbon; POC, particulate organic carbon; DIN, dissolved inorganic nitrogen; DTN, dissolved total nitrogen; PON, particulate organic nitrogen; TN, total nitrogen; DP, dissolved phosphorus; TP, total phosphorus

[a] Before addition of nutrients
[b] Aug. 2 1994
[c] Sep. 10 1994
[d] Sampled every day at around 1100
[e] NH_4^+-N + NO_2^--N + NO_3^--N

PO_4^{3-}; Bran + Luebbe, Traacs 800 autoanalyzer; Brand Luebbe, Norderstedt, Germany), dissolved total nitrogen and phosphorus, and total nitrogen and phosphorus (DTN, DTP, TN, TP, respectively; after digestion with persulfate).

Plankton numbers were determined by direct microscopic counts of samples either fixed with Lugol's iodine solution for phytoplankton or filtered through a 75-μm mesh net and then fixed with formalin for zooplankton. The carbon concentration of zooplankton was estimated as the sum of the products of the numbers of each zooplankton species multiplied by species-specific mean volumes (T. Hanazato, Suwa Hydrobiological Station, Shinshu University, Japan, personal communication) and volumetric carbon contents (mean of several samples $0.464 \mathrm{g\,C\,cm^{-3}}$). Five goldfish were weighed, dried, and pooled; their average carbon content was determined to be 7.1% of wet weight. The phytoplanktonic carbon concentration was estimated by multiplying the chlorophyll a concentration by the carbon:chlorophyll a ratios (49 mg $POC\cdot mg^{-1}$ chlorophyll a for the green algae-dominated pond 1 and 43 mg $POC\cdot mg^{-1}$ chlorophyll a for the cyanobacteria-dominated ponds 2 and 3) (Fukushima et al. 1995a). The bacterial and fungal carbon concentrations were assumed to be negligible (bacterial biomass $<0.2 \mathrm{mg\,C\,l^{-1}}$) (Fukushima et al. 1995a). Detrital carbon concentration was calculated as POC minus the phytoplanktonic and zooplanktonic carbon concentrations.

Calculation of dissolved inorganic carbon

Concentrations of DIC were calculated from our measurements of titration alkalinity, pH, and temperature, based on the dissolution and dissociation reactions of the aqueous carbonate system [Stumm and Morgan (1981) and DOE (1994) present excellent summaries]. Carbonate alkalinity (Alk) was estimated as titration alkalinity plus hydrogen ion concentration minus hydroxide ion concentration. We assumed that other weak acids and bases had no quantitatively important effects on alkalinity. Carbonate dissociation constants ($K_1 = [H^+][HCO_3^-]/[H_2CO_3^*]$; $K_2 = [H^+][CO_3^{2-}]/[HCO_3^-]$) were calculated with algorithms from temperature and chlorinity ($g\,kg^{-1}$) based on the data of Gieskes (1974), and the dissociation constant for water was calculated ($K_w = [H^+][OH^-]$) based on that of Harned and Owen (1958).

Measurement precision

To evaluate the imprecision of sensor measurements of DIC and DO, we sampled pond pH and DO continuously for 651 measurements. The maximum sample standard deviations of all 93 consecutive sets of seven measurements of DIC and DO were 4.0×10^{-4} and $7.7 \times 10^{-4} \mathrm{mM}$, with coefficients of variation of 0.04% and 0.24%, respectively. These standard deviations correspond to standard errors of differences between consecutive DIC and DO determinations (as used in net community productivity measurements) of 2.2×10^{-4} and $4.1 \times 10^{-4} \mathrm{mM}$, respectively.

Measurement accuracy

Our DO measurements were accurate to within $\pm 0.006 \mathrm{mM}$, as estimated from the standard error of a linear regression line between the sensor outputs and Winkler titration values. The calculated DIC concentrations were occasionally compared with direct determinations on a nondispersive infrared spectrometer-based instrument, the Shimadzu TOC-5000 (Weisburd et al. 1995). For the pH-alkalinity-derived [DIC] and maximum hourly DIC change we observed, the implied error in the difference between consecutively measured concentrations of, for example, 0.97 and 1.00 mM would be only 0.0014 mM (Fukushima et al. 1995b); furthermore, because this implied error was calculated with the maximum observed hourly DIC change, it represents an upper bound on the actual errors that would have arisen due to such inaccuracies in [DIC].

Calculation of air–water gas exchange

The air–water exchange flux (F) was calculated as follows:

$$F = k_L (C_{sat} - C_w) \tag{1}$$

where k_L is the gas exchange coefficient ($\mathrm{cm\,h^{-1}}$), C_{sat} is the gas concentration in water at equilibrium with ambient air ($= p\,K_H$; p is the partial pressure and K_H is the Henry's law constant), and C_w is the gas concentration in the water just below the interface. In the case of DIC, C_w can be approximated by $[H_2CO_3^*]$, which we can calculate with the values of DIC, K_1, K_2, and pH. We used the concentrations of DO and DIC measured with the upper probes as the values of C_w, because the water they sampled was closer to the air–water interface than that sampled by the lower probes. Saturation DO and DIC concentrations were calculated with K_H; we estimated K_H from temperature by fitting a cubic polynomial to the DO solubility data of Benson and Krause (1980) and the DIC solubility data of Buch (1951). In addition, we assumed that the carbon dioxide and oxygen partial pressures were unchanged with time, e.g., the air CO_2 concentration was constant at 350 ppm, a reasonable approximation based on data collected by Ibaraki Prefecture (Department of Living Environment; 1-5-38, Mito, Ibaraki, Japan) at Mt. Tsukuba, 20 km from our mesocosms.

To empirically evaluate the effect of wind speed on gas exchange (the gas exchange coefficient, k_L) during seven different 3-h periods, we compared temporal changes in DO and DIC concentrations between open and closed boxes (20 × 20 × 20 cm, made of 5-mm-thick clear acrylic sheets) that were set in a pond with their upper faces just above the water surface [details are presented in Fukushima et al. (1995b)]. That study found k_L to be approximately proportional to the 1.5 power of wind velocity for both gases. This exponent of 1.5 on the gas exchange coefficient is consistent with the gas exchange coefficient (k_L) formulation proposed by Hartman and Hammond (1985):

$$k_L = Xa Rv(D m_{20})^{0.5}(U_{10})^{1.5} \tag{2}$$

where Xa is a constant ($144 \mathrm{s^2 m^{-1.5} h^{-1}}$), Rv is the ratio of the kinematic viscosity of pure water at 20°C to that at the

measured temperature, Dm_{20} is the molecular diffusivity of the gas of interest at 20°C in cm^2s^{-1}, and U_{10} is the wind velocity 10m above the surface in ms^{-1}. We adopted this formulation but empirically determined the value of Xa for our system with data from Fukushima et al. (1995b); k_L values were regressed on the 1.5 power of wind speed. The slope of that regression, Xa, was calculated to be $49.2 s^2 m^{-1.5} h^{-1}$. We attribute the difference in Xa between our study and that of Hartman and Hammond (1985) to the difference in openness between our ponds and San Francisco Bay.

In addition, we calculated the chemical enhancement of CO_2 exchange with the formulation proposed by Smith (1985):

$$Z = 0.072 \exp(-0.215 U_{10}) \tag{3}$$

$$r = ((K_{12}[H^+] + K_{13}K_w[H^+])/Dm[H^+])^{0.5} \tag{4}$$

where K_{12} is the rate constant for the hydration reaction of CO_2 $(0.037 s^{-1})$, K_{13} is that for combination of CO_2 and OH^- $(8500 lmol^{-1}s^{-1})$, z is the thickness of the surface stagnant boundary layer, r is the factor expressing the effect of pH on the kinetics of CO_2 ionization (cm^{-1}), and Dm is the molecular diffusivity (cm^2s^{-1}). We recast this calculation as an enhancement factor (EF) following Weisburd and Laws (1990):

$$EF = rz \coth(rz) \tag{5}$$

k_L for DIC was estimated with the following equation:

$$k_L = Xa\ Rv(Dm_{20})^{0.5} EF(U_{10})^{1.5} \tag{6}$$

k_L for DO was estimated with an equation of the same form, but without the enhancement factor EF.

Data processing and exclusion of noisy data

After exclusion of times with no output or constant data, and smoothing of the DO and DIC data by application of a moving average of five successive outputs (data for the 20 min from 10 min before to 10 min after each hour), we calculated the change in these dissolved gases for each 1-h interval. These changes in gas concentrations ($d[DO]/dt$, $d[DIC]/dt$) are the result of several fluxes; for example, in the case of DO we can write the following mass balance equation: $Vd[DO]/dt = A(F_{in\ situ} + F_{advection} + F_{gas\ invasion})$, where V is the volume of the pond, A is the surface area, $F_{in\ situ}$ is the areal rate of biochemical change explained below, $F_{advection}$ is the net flux through water exchange, and $F_{gas\ invasion}$ is the net flux through gas exchange. We solved for the in situ flux by difference: $F_{in\ situ} = (V/A) d[DO]/dt - F_{advection} - F_{gas\ invasion}$, where $F_{advection}$ was calculated as the difference between influx and outflux through water exchange and rainfall, and $F_{gas\ invasion}$ was calculated by eq. (1).

A similar expression can be written for DIC $((V/A)d[DIC]/dt = -F_{in\ situ} + F_{advection} + F_{gas\ invasion})$. We assume that productivity is responsible for essentially all of the DO and DIC changes occurring in the water column and henceforth refer to these terms ($F_{in\ situ}$ for DO and for DIC) as the rates of net productivity.

Table 2. Number of sets of measurements after exclusion (see text)

Pond	DO		DIC	
	Upper	Lower	Upper	Lower
1	27	20	4	14
2	23	25	20	30
3	16	14	31	29

DO, Dissolved oxygen; DIC, dissolved inorganic carbon

We also removed apparently noisy data for which the difference in hourly productivity exceeded half of the daily maximum productivity (the difference between the maximum and the minimum of DO or DIC in a day calculated after removing the advection and gas-exchange fluxes). Upon exclusion of any data for a day, we excluded the entire data set for that day (from 0500 to 0500). More than half of the data series were excluded for the upper and lower DO sensors in pond 3 and the DIC data for pond 1 (Table 2), because these sensors did not perform well, although they were replaced with new ones several times. The beginning of the day for analysis was set at 0500, because during this period the irradiance started between 0510 (in the beginning of August), and 0530 (in the beginning of September). In addition, night fell between 1740 (in the beginning of September) and 1800 (in the beginning of August), and hence we defined "night" as the period between 1800 and 0500.

Results

Contributions of $F_{gas\ invasion}$ and $F_{advection}$

The relative contributions of gas exchange ($F_{gas\ invasion}$) and advection ($F_{advection}$) to total DO and DIC changes during the nights were calculated. Net productivity ($F_{in\ situ}$) was generally the most dominant factor influencing the temporal changes in DO and DIC in our mesocosms, and the errors in estimating $F_{gas\ invasion}$ were minor in our evaluation of $F_{in\ situ}$ (Fig. 1).

Hourly DO and DIC productivities

Hourly DO production became positive between 0600 and 0800 and turned negative between 1400 and 1700; the reverse was observed for DIC production (Fig. 2). The morning transition period was more than 1h after sunrise, and the evening transition was more than 1h before sunset. The beginning time of positive net production varied little, but the ending time varied due to the light conditions (see the standard deviations in Fig. 2). In the daytime, the pattern of change looked like half of a sine curve; the maximum DO usually occurred between 0900 and 1200, whereas an approximately mirror-image pattern was observed for DIC (with a minimum usually between 1000 and 1300). During the nighttime, the peak of respiration rate occurred be-

tween 1800 and 2000, and then decreases in respiration gradually slowed and stopped.

Pattern of nighttime respiration and respiratory quotient

We averaged the rates of in situ DO consumption and DIC production for each sensor for each nighttime hour of all days and applied both linear and exponential models (Table 3). Except for two cases (DIC pond 1, upper and lower), the decrease in nighttime respiration was expressed slightly better by the exponential model than by the linear model, very similar to the results of Markager and Sand-Jensen (1989), suggesting regulation with a storage pool of carbohydrates built up by photosynthesis during the previous day. Adjusting the results for a Q_{10} of 2.0 (Grobbelaar and Soeder 1985) – the change in respiration for a 10°C temperature change –

did not improve, and often worsened, the fit of the models to the data. The squares of the regression coefficients for both models were rather lower for DIC than for DO. This difference was not due to the degree of variation (coefficients of variation for six sensors: DO, 34 ± 6%, and DIC, 29 ± 10%, for 1800 to 1900; DO, 23 ± 6%, and DIC, 15 ± 5% for 0400 to 0500).

Smaller time coefficients α for DIC than for DO (Table 3) corresponded to the ratio of respiration from 1800 to 1900 to that from 0400 to 0500 (R18-19/R4-5) for DIC (1.3 ± 0.3), being closer to unity than that for DO (1.7 ± 0.2). There were no clear differences in α and/or the suitability of the models between ponds. RQ changed with time from 0.53 to 0.69 for the period between 1800 and 1900 to 0.72 to 0.92 for the period between 0400 and 0500 (Fig. 3; $P < 0.05$, except for the upper sensor in pond 1, due to the small number of samples (four) for that pond; paired sample t-test and Wilcoxon two-sample test).
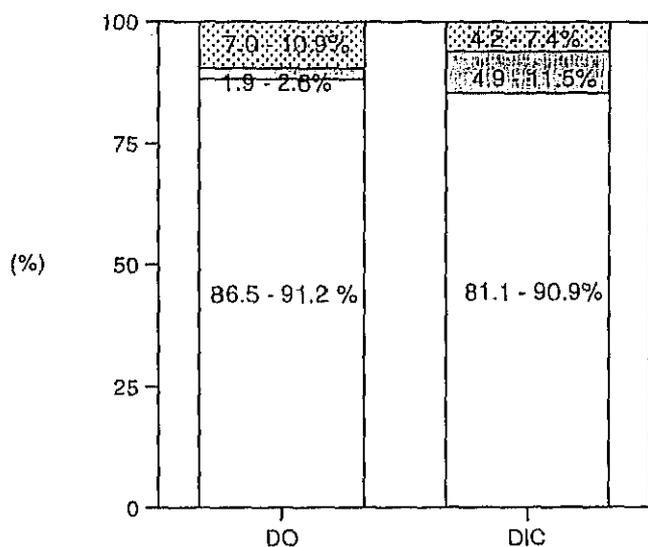
Fig. 1. Contributions of absolute value of each flux to the sum; average of the three ponds for all sampled days. The figures indicate the ranges of the values in all three ponds. White, $F_{in situ}$; shaded, $F_{advection}$; stippled, $F_{gas invasion}$. DO, Dissolved oxygen; DIC, dissolved inorganic carbon
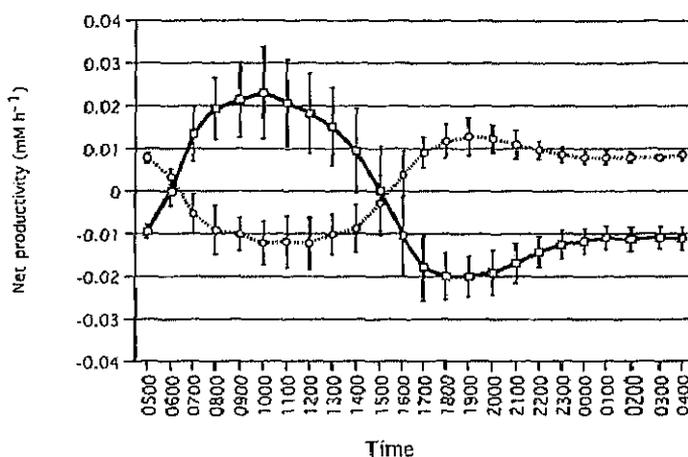

Fig. 2. Example of averages and standard deviations of hourly biotic DO and DIC change (net productivity for DO and −1 times net productivity for DIC) (pond 2 upper sensors). The times on the horizontal axis correspond to the starting times of each 1-h measurement period. Bars indicate standard deviations. Open squares, DO (23 days); open circles, DIC (20 days)

Table 3. Squared regression coefficients when a linear model ($R = a + bt$) and an exponential model [$R = R_0\exp(-\alpha t)$] are applied to the nighttime respiration (hourly average for all nights with data sets for each sensor) and time coefficients (α) (t: time; a, b, R_0: constants)

Measurement	Pond		Linear model		Exponential model		
			Raw data	Tem. correction	Raw data	Tem. correction	α (h⁻¹)
DO	1	Upper	0.88***	0.87***	0.93***	0.92***	0.058
		Lower	0.86***	0.81***	0.88***	0.83***	0.039
	2	Upper	0.87***	0.86***	0.89***	0.87***	0.073
		Lower	0.91***	0.89***	0.93***	0.91***	0.072
	3	Upper	0.93***	0.93***	0.97***	0.96***	0.066
		Lower	0.84***	0.80***	0.87***	0.84***	0.047
DIC	1	Upper	0.63**	0.57**	0.60**	0.53**	0.050
		Lower	0.42*	0.07	0.42*	0.07	0.012
	2	Upper	0.77***	0.73***	0.78***	0.74***	0.052
		Lower	0.56*	0.42*	0.58**	0.43*	0.030
	3	Upper	0.64**	0.48*	0.64**	0.47*	0.026
		Lower	0.48*	0.15	0.48*	0.14	0.013

$*P < 0.05$; $**P < 0.01$; $***P < 0.001$; $n = 11$. DO, Dissolved oxygen; DIC, dissolved inorganic carbon
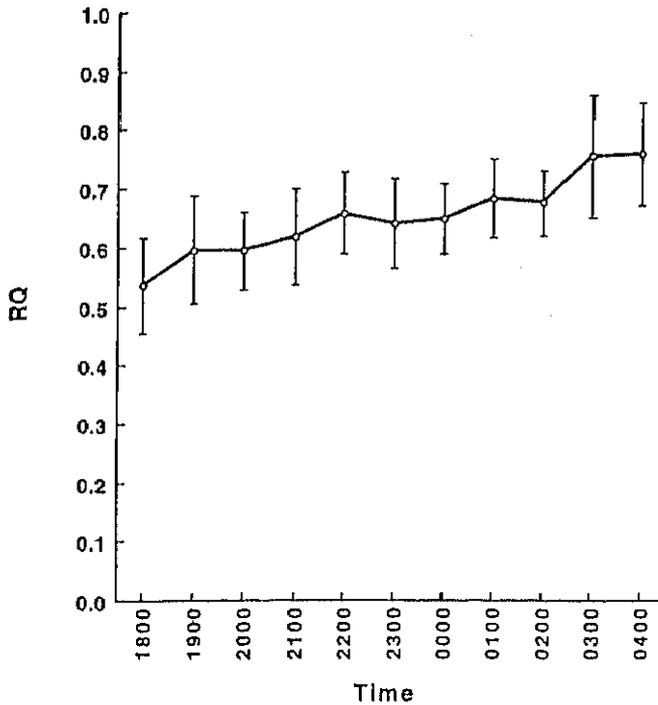
Fig. 3. Respiratory quotient (RQ) during nighttime averaged for all sensors. *Bars* indicate standard deviations of pond 1 lower. The times on the horizontal axis correspond to the starting times of each 1-h measurement period. RQ = (DIC increase)/(DO decrease)

Estimation of gross production

Although our free-water measurements yielded only estimates of net community productivity, we suspected that daytime gross productivity might be more closely related to nighttime respiration. To test this hypothesis, we estimated gross productivity from the net productivity measurements corrected with estimates of daytime respiration derived from our nighttime respiration measurements for the preceding or following nights (six models). We evaluated the suitability of each of these models by correlating the resulting daily gross productivity estimates from each model divided by biomass (GP/B) with irradiance corrected for light extinction with depth and integrated over time (I_{corre}); gross productivities derived with the respiration model producing the best GP/B vs. I_{corre} fit were selected for further use.

Daytime respiration was modeled on the assumption that daytime respiration was equivalent to respiration during different periods of the preceding or following night (A): in model 1, the respiration rate from 1800 to 1900 (A) was assumed to have prevailed during the preceding day from 0500 until 1800; in model 2, A was replaced by the average rate from 1800 to 2000; in model 3, A was replaced by the average rate from 1800 to 2200; in model 4, A was replaced by the average rate from 1800 to 0500; in model 5, A was replaced by the rate from 0400 to 0500; in model 6, the respiration rate from 0400 to 0500 was assumed to continue during the subsequent period from 0500 to 1800.

We assumed that the photosynthetic rate increased with increasing irradiance up to a saturating intensity, beyond

which it remained constant. Thus irradiance driving gross production was expressed as a function, f_{light}, in a simplified form of Smith's formula (Smith 1936):

$$f_{light} = 1; \quad I > I_0$$
$$f_{light} = I/I_0; \quad I < I_0 \tag{7}$$

where I is irradiance and I_0 is the saturation light intensity. We used $0.18\,MJ\,m^{-2}\,h^{-1}$ as the saturation irradiance; this value was calculated with the irradiation saturation level observed at several points in Lake Kasumigaura, $200\,\mu E\,m^{-2}\,s^{-1}$ (Matsuoka 1984), and mean wavelength of irradiation 450 nm.

The influence of light on photosynthetic rate integrated over depth and time was calculated with a series of equations. The extinction of light in water was expressed as follows (Matsuoka 1984):

$$I(t, z) = I(t, 0)\,exp(-k_z z) \tag{8}$$
$$k_z = 0.02\,Chla + 1.1 \tag{9}$$

where t is the time of day; z is depth (m); k_z is the light extinction coefficient (m^{-1}); and Chla is the chlorophyll a concentration ($\mu g\,l^{-1}$). Consequently, the productivity-driving irradiance integrated over depth and time, I_{corre}, can be calculated as follows:

$$I_{corre} = \int_{t_{ini}}^{t_{end}}\int_0^{z_{pond}} f_{light}\,dz\,dt \tag{10}$$

where t_{ini} is the starting time of irradiance, t_{end} is the ending time of irradiance, and z_{pond} is the depth of the pond (m). We then compared I_{corre} with daily gross primary production normalized to chlorophyll a concentration, because we assumed that gross primary production was the product of the standing stock of phytoplankton and the time- and depth-integrated irradiance (I_{corre}). The daily gross primary production was calculated as the sum of daytime in situ DO or DIC change and each of the six types of respiration rates in turn.

Here, we did not consider the influence of temperature and nutrient concentrations on primary productivity, because the levels of these variables did not vary much from day to day (daily average temperature, $29.7 \pm 1.6°C$; nutrients, DTN and DP in Table 1).

Of the six models, the use of model 4, which extrapolated nighttime respiration rates for the whole night period to the preceding daytime, resulted in the highest GP/B vs. I_{corre} correlation coefficients in almost all cases [average $\pm$ standard deviation of regression coefficients: model 1, 0.70 ± 0.18; model 2, 0.73 ± 0.17; model 3, 0.77 ± 0.16; model 4, 0.81 ± 0.12; model 5, 0.72 ± 0.15; model 6, 0.77 ± 0.16 ($n = 12$)]. Although there seems to have been a positive intercept on the axis of irradiance, the regression coefficients were fairly high (Fig. 4). Even when the value of I_0 was raised enough to eliminate the light-saturated range (always $I < I_0$) or lowering it to $0.09\,MJ\,m^{-2}\,h^{-1}$(half of the observed value), the superiority of model 4 was not changed (data not shown). When the regression line with no intercept was applied, the highest correlation coefficients between the observed and predicted respiration rates were also obtained

for model 4 (data not shown). Hence,.we assumed that daytime respiration could be best estimated by model 4. The ratios of gross production predicted by use of other models to that predicted by model 4 ranged from 0.8 (models 5 and 6) to 1.2 (models 1 and 2).

Comparison of respiration and production differences between the upper and lower parts of the water column

We compared respiration and production measured at the 50-cm-deep sensors (upper water column) with those measured at the 100-cm-deep sensors (lower water column); whereas almost all the ratios between upper versus lower

Influence of light on photosynthetic rate
(I_{light}) Integrated over depth and time (m·h)
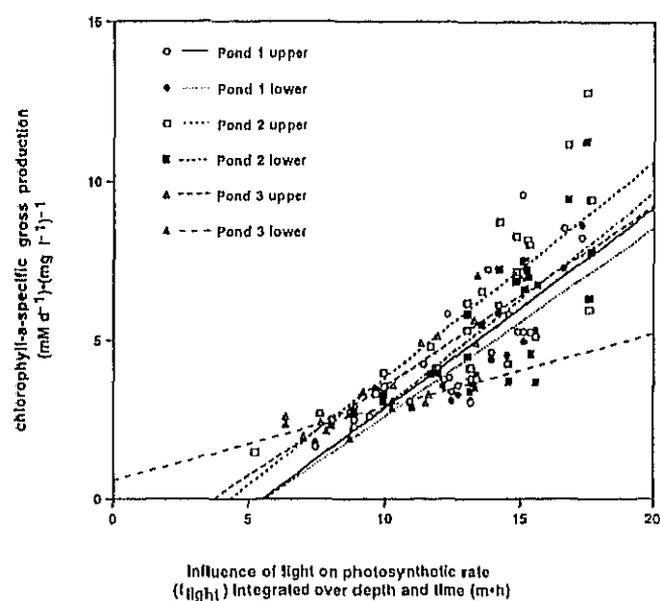
Fig. 4. Linear regressions of biomass normalized gross production estimated with the respiration rates of model 4, on depth- and time-integrated irradiance corrected for the influence of light extinction on productivity (I_{corr}) (see eq. 10 in text). Each line indicates the linear regression for the individual sensor

parts of the water columns for respiration and production in the same pond were above unity, the ratios were usually very close to unity, and the differences among them were usually insignificant (Table 4). In addition, the upper and lower activities were highly correlated; thus, the mixing of these ponds posed no problem.

Factors regulating nighttime respiration

Influence of primary production

Significant correlations were found for daytime gross production and respiration rates during the subsequent 1800 to 2200 period for both DO and DIC, irrespective of depth (Table 5; significant correlations with gross production were also obtained for the respiration rates during the periods from 1800 to 1900 from 1800 to 0500). In contrast, there were rather fewer significant correlations, in particular for DIC, between daytime gross production rates and respiration rates from 0400 to 0500. In addition, considerably fewer significant correlations with respiration rates were observed for daily net production rates compared with daily gross production rates.

Correlations between nighttime respiration and various organic carbon fractions

To assess whether nighttime respiration was related to the abundance of different carbon stocks in the water column, we conducted a correlation analysis between the daily respiration data of each sensor for five nighttime periods (1800 to 1900, 1800 to 2000, 1800 to 2200, 1800 to 0500, and 0400 to 0500) and several organic carbon fractions [POC, DOC, zooplanktonic C, phytoplanktonic C, detrital C, and total organic C] for each pond. For pond 1, the no-fish pond, all respiration rates except the one during 0400 to 0500 usually were significantly correlated with POC and phytoplanktonic C [e.g., respiration rates during 1800 to 0500 vs. POC: DO upper 0.52, $P < 0.01$; DO lower 0.55, $P < 0.05$;

Table 4. Comparison of respiration and gross production between upper and lower sensors

Measurement			Pond 1	Pond 2	Pond 3
Respiration 1800–0500	DO	r^2	0.71***	0.81***	0.65*
		Ratio	1.02 ± 0.08	1.19*** ± 0.10	1.15* ± 0.16
		n	20	21	7
	DIC	r^2	0.74	0.95***	0.91***
		Ratio	0.99 ± 0.04	1.02* ± 0.03	1.05*** ± 0.05
		n	4	18	26
Gross production 0500–1800	DO	r^2	0.80***	0.86***	0.98***
		Ratio	1.02 ± 0.09	1.15*** ± 0.10	1.07* ± 0.04
		n	20	21	7
	DIC	r^2	0.95*	0.98***	0.97***
		Ratio	0.99 ± 0.06	1.02* ± 0.04	1.04** ± 0.07
		n	4	18	26

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ significance; correlation analysis and paired sample t-test, respectively. r^2, Square of correlation coefficient; ratio = upper sensor output : lower sensor output (ratio calculated for each day and then averaged for all days); n, days of data used. DO, Dissolved oxygen; DIC, dissolved inorganic carbon

Table 5. Correlation coefficients between daily gross production (0500-1800) vs. respiration (I) and daily net production (0500-1800) vs. respiration (II)

Measurement			DO		DIC	
			Upper	Lower	Upper	Lower
(I)	(A)	Pond 1	0.78***	0.63***	0.68	0.67**
		Pond 2	0.82***	0.64***	0.88***	0.84***
		Pond 3	0.60*	0.69**	0.93***	0.81***
	(B)	Pond 1	0.26	0.58**	0.10	0.17
		Pond 2	0.61**	0.61**	0.19	0.71***
		Pond 3	0.44	0.79***	0.24	0.02
(II)	(A)	Pond 1	0.40*	0.10	0.58	0.27
		Pond 2	0.47*	0.08	0.78***	0.74***
		Pond 3	0.20	0.05	0.84***	0.67***
	(B)	Pond 1	0.27	0.32	0.05	−0.07
		Pond 2	0.20	0.19	0.15	0.61***
		Pond 3	0.09	0.50	0.09	−0.07

Respiration for 1800-2200 (A); respiration for 0400-0500 (B); *** $P < 0.001$; ** $P < 0.01$; * $P <$ 0.05. DO, Dissolved oxygen; DIC, dissolved inorganic carbon
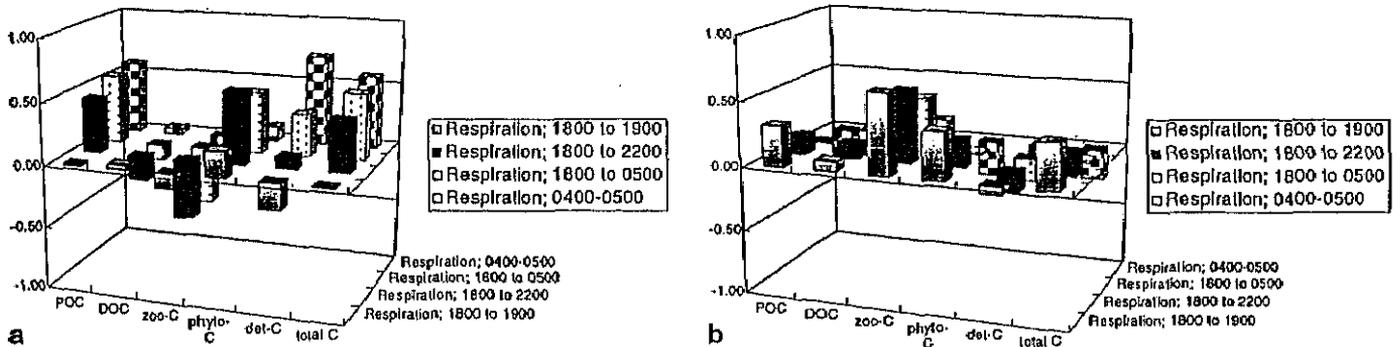
Fig. 5. Correlation coefficients between respiration rates and organic carbon fractions. a Pond 1 DO lower ($n = 20$); b Pond 2 DO upper ($n = 23$)

Fig. 5a]. This indicates that planktonic biomass influenced pond respiration.

In contrast to the no-fish pond, zooplanktonic C was significantly correlated with all types of respiration rates in fish ponds [e.g., respiration rates during 1800 to 0500 vs. zooplanktonic carbon (pond 2, upper sensor): DO 0.42, $P <$ 0.05; DIC 0.65, $P < 0.01$; Fig. 5b]. Zooplanktonic C could not explain the between-pond differences in respiration rates; moreover, the biomass of zooplankton was so much smaller than that of phytoplankton, detritus, and fish as to be negligible (Table 1). Zooplankton biomass in the ponds with fish in the earlier part of the experiment (August 3 to 20, 1994) differed significantly from that in the latter part (August 21 to September 8, 1994) (pond 2, 0.04 vs. $0.23\,\mathrm{mg\,Cl^{-1}}$, $P < 0.01$; pond 3, 0.12 vs. $0.32\,\mathrm{mg\,Cl^{-1}}$, $P <$ 0.001; unpaired sample t-test). While these zooplankton populations were increasing, the daily net community production increased significantly from the former to the latter period, in particular for DIC (Table 6), indicating a change in the composition and/or metabolic state of the biotic community in the ponds. Corresponding to this increase, the organic carbon (POC + DOC) specific respiration rates rose by 3% to 30%. Therefore, we can expect a close rela-

tionship between the composition and/or metabolic state of the pond community and its respiration rate.

Discussion

Although the considerable variability in the productivity data derived from our open-water measurements makes the reliability of any individual measured rate rather low, taken together, the extensive data set demonstrates the outline of carbon cycles in the ponds (Fukushima et al. 1995c) and several consistent patterns of diel change in respiration rates. Gathering a data set of this size by incubation methods would not be practical. Our results shed light on diel patterns of net community respiration rates and suggest several directions for further research.

The clear decreases in respiration rates with time at night that we observed agreed well with those reported by others (Grobbelaar and Soeder 1985; Weger et al. 1989; Watanabe and Kimura 1990; Markager et al. 1992; Szyper et al. 1992). The ratio of respiration rates at the beginning and end of the dark period (R18-19/R4-5: 1.7 ± 0.2 for DO, 1.3 ± 0.3

Table 6. Comparison of net community production and organic carbon (POC + DOC) specific respiration rates between earlier and later halves of the experiment

Measurement		Pond 2						Pond 3				
		DO		DIC				DO		DIC		
		Period 1	Period 2	Period 1	Period 2			Period 1	Period 2	Period 1	Period 2	
Net community production	upper	−90	−41	* −100	−35	***		−74	−61	−89	−50	***
(μM day^{-1})	lower	−62	−18	* −101	−35	***		−71	−52	−87	−45	***
Resp18-22*/(POC + DOC)	upper	7.62	8.09	3.55	4.98	*		5.22	6.50	2.32	3.08	***
(μM 4h^{-1})·(mgCl^{-1})$^{-1}$	lower	6.30	6.51	3.36	4.59	**		4.46	4.81	2.16	2.79	***

*Respiration rate during 1800-2200
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; unpaired-samples t-test. DO, Dissolved oxygen; DIC, dissolved inorganic carbon; POC, particulate organic carbon; DOC, dissolved inorganic carbon

for DIC) was comparable with values obtained by DO measurement in previous studies [1.5 to 3 (Grobbelaar and Soeder 1985); 1.4 (Weger et al. 1989); 1.7 (Watanabe and Kimura 1990); 1.3 to 1.9 (Sampou and Kemp 1994)]. As for DO, our values of time coefficients for the exponential model (0.059 ± 0.013 h^{-1}) were fairly close to those reported by Markager et al. (1992) for the period from 2 to 10 h after the onset of darkness (0.042 h^{-1}), but they were rather smaller than their coefficients of around 0.3 h^{-1} and 0.1 to 0.2 h^{-1} for the initial 2 h of darkness in their daytime and nighttime incubations, respectively.

Model 4, which extrapolated nighttime respiration rates to the preceding daytime, yielded the highest coefficient for the correlation between the influence of light on photosynthetic rate integrated over depth and time and chlorophyll a-specific gross productivity. Weger et al. (1989) reported O_2 consumption in the light averaging 54 μmol (mg Chla)$^{-1}$ h^{-1}, declining to 40 μmol (mg Chla)$^{-1}$ h^{-1} just after darkness and to 29 μmol (mg Chla)$^{-1}$ h^{-1} at the end of the dark period, and then increasing to 52 μmol (mg Chla)$^{-1}$ h^{-1} upon subsequent illumination in a diatom culture (*Thalassiosira weisflogii*). Higher respiration rates during the daytime (44.1 μmol l^{-1} h^{-1}) than the nighttime (23.1 μmol l^{-1} hr^{-1}) have also been determined for samples obtained from a fertile earthen pond (Szyper et al. 1992). In these cases, the ratios of daytime to nighttime respiration rates were calculated to be around 1.5 to 1.9. Watanabe and Kimura (1990) measured low respiration in the morning in a *Microcystis* population blooming in a natural pond, and respiration there increased during daytime. The negative y intercept on our GP/B versus I_{corr} curves suggests that light stimulated daytime respiration and that all of the six models we evaluated may have underestimated daytime respiration.

The relationships between estimated daytime gross production and respiration rates suggest that respiration just after sunset is regulated by the preceding gross production, but that respiration long after nightfall approaches the minimum metabolic rate of the community. This agrees with experimental results showing that the respiration rates of planktonic cyanobacteria (Gibson 1975) and green algae (Grobbelaar and Soeder 1985) became steady after 8 h in

the dark. Jensen et al. (1990) reported that community respiration was significantly correlated with gross productivity of phytoplankton and net production of bacterioplankton in a shallow, very eutrophic estuary. Thus, gross productivity greatly affects respiration at the beginning of the night, and this influence declines with time.

The nighttime increase in RQ we observed suggests a temporal change in the composition of respiratory substrates or the final product of nitrogen catabolism, and/or temporal decoupling between DO consumption and DIC release. None of these possibilities seems particularly likely. An increase in RQ due to a change in respiratory substrates could result from a decrease in the rates of oxidation of nitrogen-rich organic substrates in the ponds (Laws 1991; Williams and Robertson 1991). However, fixed carbohydrates, containing no nitrogen, may be a primary respiratory substrate following the onset of darkness (Watanabe and Kimura 1990; Markager et al. 1992); if so, then the nighttime RQ should decrease with time due to increasing oxidation of more nitrogen-rich substrates as these carbohydrates are depleted.

Gallegos et al. (1983) reported an asynchrony between the rates of oxygen production and DIC uptake in a mixed culture of phytoplankton grown outdoors in natural light, indicating a "CO_2 concentrating mechanism" of phytoplankton growing under CO_2-depleted conditions. However, it is hard to imagine such an uncoupling of oxygen and carbon metabolism being maintained by phytoplankton cells over extended periods in the dark. Some studies of RQ evaluated it in axenic or monospecific cultures. In contrast, our measurements were conducted in a more complex and open system with diverse biota and various microenvironments. The range of conditions and reactions in our system was probably wider than those for the culture experiments. In any case, further research is necessary to understand the nighttime increases in RQ we observed.

As shown above, the nighttime respiration rates correlated well with gross production rates, biomass of several categories, and daily net community production (daily, both for all ponds together and for each pond). We applied multiple regression analysis to examine how the respiration rates could be explained by all of the following factors

Table 7. Most influential variables affecting nighttime respiration rates A (1800 to 2200) and B (0400 to 0500) and squares of multiple regression coefficients (adjusted by degrees of freedom) by stepwise multiple regression with the variables down to the seventh most influential

Rank of influence	DO		DIC	
	Respiration A	Respiration B	Respiration A	Respiration B
1	GP: 0.173	GP: 0.236	GP: 0.678	GP: 0.097
2	Fish C: 0.446	Detritus C: 0.338	NCP: 0.831	NCP: 0.256
3	NCP: 0.673	Zooplankton C: 0.372	Fish C: 0.868	DOC: 0.284
All items	All 7 items: 0.781	All 7 items: 0.500	All 7 items: 0.874	All 7 items: 0.296

Number of observations: 125 for DO, 127 for DIC; GP, gross production; NCP, net community production; DO, dissolved oxygen; DIC, dissolved inorganic carbon; DOC, dissolved organic carbon

irrespective of pond, depth, and day (independent variables: daytime gross production rate, phytoplanktonic C, zooplanktonic C, detrital C, fish C, DOC, and daily net community production; number of observations: DO 125, DIC 127). Because the proportions of variation explained by the variables (as expressed by the squares of the regression coefficients) (Table 7) were fairly high (DO 78%, DIC 87%) for the respiration rates from 1800 to 2200, the influence of other factors on respiration during that period must be relatively unimportant. In contrast, the squared coefficients for the rates from 0400 to 0500 were rather low (DO 50%, DIC 30%); thus, we need to seek other factors influencing the minimum respiration rate at night. The gross production rate always explained more of the variability in nighttime respiration rates than any other factor, but the second most predictive factor varied (Table 7).

Conclusions

We have demonstrated the usefulness of continuous free-water measurements of DO and pH assessment of community productivity and respiration. Nighttime respiration decreased with time, but the time coefficients for DO and DIC differed. Respiratory quotients increased with time during the night. Although the cause(s) of nighttime respiratory quotient rises are unclear, the analysis of differences between DO and DIC dynamics can provide new insights into the functioning of aquatic systems.

Of the many factors evaluated, gross production had the greatest effect on respiration rates after nightfall; in fact, the factors we evaluated could account for most of the observed between-pond and day-to-day variability in evening respiration. However, predawn respiration was not well explained by the factors we tested; further research will be necessary to identify factors controlling basal community respiration rates. Knowledge of respiration-regulating factors should facilitate development of a respiration model that can predict nighttime DO decline in aquatic environments from easily monitored water quality data.

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Nutrient dynamics and the eutrophication of shallow lakes Kasumigaura (Japan), Donghu (PR China), and Okeechobee (USA)

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"Capsule": *Complex nutrient dynamics in shallow lakes require that caution be used when applying simple eutrophication models.*

Abstract

We compared the nutrient dynamics of three lakes that have been heavily influenced by point and non-point source pollution and other human activities. The lakes, located in Japan (Lake Kasumigaura), People's Republic of China (Lake Donghu), and the USA (Lake Okeechobee), all are relatively large (> 30 km^2), very shallow (< 4 m mean depth), and eutrophic. In all three lakes we found strong interactions among the sediments, water column, and human activities. Important processes affecting nutrient dynamics included nitrogen fixation, light limitation due to resuspended sediments, and intense grazing on algae by cultured fish. As a result of these complex interactions, simple empirical models developed to predict in-lake responses of total phosphorus and algal biomass to external nutrient loads must be used with caution. While published models may provide 'good' results, in terms of model output matching actual data, this may not be due to accurate representation of lake processes in the models. The variable nutrient dynamics that we observed among the three study lakes appears to be typical for shallow lake systems. This indicates that a greater reliance on lake-specific research may be required for effective management, and a lesser role of inter-lake generalization than is possible for deeper, dimictic lake systems. Furthermore, accurate predictions of management impacts in shallow eutrophic lakes may require the use of relatively complex deterministic modeling tools. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Shallow lakes; Nutrient cycling; Phosphorus; Eutrophication models

1. Introduction

Shallow, polymictic lakes display a number of features that set them apart from the more often-studied deeper, dimictic systems: (1) a lack of stable long-term thermal stratification (Beaver et al., 1981; Muraoka and Fukushima, 1981); (2) frequent mixing of the entire water column and resuspension of unconsolidated sediments (Ishikawa and Tanaka, 1993); and (3) substantial internal loading of nutrients from the sediments to water column (Goda and Matsuoka, 1986; Sondergaard et al., 1992). In lakes that have such features, water quality conditions [total phosphorus (P) concentrations, turbidity, chlorophyll *a*, and algal blooms] may have complex relationships with external nutrient loads and in-lake processing (Sas, 1989). Such lakes also may be relatively unresponsive to watershed nutrient management programs (Sas, 1989; Welch and Cooke, 1995).

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In recent years, there has been considerable research that provides a better understanding of shallow lake nutrient dynamics. This work has been driven by a need to develop successful approaches (both in-lake and in the watershed) for protecting or enhancing water quality (e.g. Van Liere and Gulati, 1992). Studies have included long-term observations (Aizaki and Otsuki, 1987; James et al., 1995a,b), experimental manipulations (Moss et al., 1996), detailed studies of the processes involved in nutrient cycling and trophic dynamics (Fukushima et al., 1987; Olila and Reddy, 1993), and the application of dynamic models (Goda and Matsuoka, 1986; Matsuoka et al., 1986; James et al., 1997).

One approach that is useful for identifying general properties of shallow lakes is the comparison of research results from different ecosystems, as has been done with some lakes in Europe (Sas, 1989) and the USA (Havens et al., 1999). This is the objective of this paper, which is a product of a shallow lake workshop held in Tsukuba, Japan, in October 1993, at the National Institute for Environmental Studies (NIES). Discussions at the workshop focused on limnological features, human impacts, and resource management issues dealing with three shallow lakes (Fig. 1): Lake Kasumigaura (Japan), Lake Donghu (PR China), and Lake Okeechobee (USA). The three lakes all are shallow and eutrophic, and they are heavily influenced by human actions. However, they differ in terms of key limnological attributes, relationships among attributes, and the nature of human influences. Taken together, the case studies presented here provide good insight into the major issues of eutrophication management in shallow lake ecosystems.

The objectives of the paper include the presentation and comparison of: (1) general properties of the lakes and their watersheds; (2) nutrient budgets and trophic state classifications; (3) major processes affecting in-lake P concentrations; and (4) the utility of empirical models for predicting shallow lake responses to external nutrient load reductions. In the last item, we consider simple correlative models relating nutrients to algal biomass within the lake, and Vollenweider-type input–output models relating in-lake nutrient concentrations to loads. These simple tools are still widely used by lake managers, and by these case studies, we demonstrate where they may have serious shortcomings.

2. Lake characteristics

Lake Kasumigaura (Table 1) is a moderate-size shallow lake located in the Ibaraki Prefecture, approximately 50 km northeast of Tokyo, Japan. The lake originally was a brackish-water lagoon, with indirect connections to the Pacific Ocean via the Hitachigawa and Tone Rivers. In 1963, a gate was constructed near the confluence of these rivers, disconnecting the lake from its sources of ocean water. Since that time, salinities have declined, and today the lake contains fresh water. Water depths average 4.0 m, with little seasonal or year-to-year variation. Due to a construction project completed in the mid-1970s, the shoreline of the lake consists largely of a concrete dike. As a result, the pelagic region dominates this ecosystem. Major land uses in the watershed are rice paddy fields, plowed fields for other row crops, and fruit orchards. Taken together, they account for 51% of the watershed area. Natural, undeveloped lands account for 30% of the watershed, and 12% of the land has urban, industrial, and residential uses. The 620,000 humans who live in the watershed are concentrated near the lake, primarily in the city of Tsuchiura. In urban areas, centralized sewage systems capture water and waste, and divert most of it to treatment plants outside the watershed. In rural areas, most human habitations have septic systems.

Lake Donghu is a small shallow lake located in Wuhan City, in the Hubei Province of the People's Republic of China. The lake was formed in the early

Locations of the Three Shallow Lakes

Fig. 1. Global map showing the location of three lakes considered in this study. 1, Lake Okeechobee; 2, Lake Kasumigaura; 3, Lake Donghu.

Table 1
General features of the three lakes and watersheds

Attribute	Lake Kasumigaura	Lake Donghu	Lake Okeechobee
Origin recession	Lagoon	Lateral	Ocean
Latitude	36.02 N	0.33 N	26.58 N
Longitude	140.23 E	114.23 E	80.50 W
Elevation (m)	0.16	0.00	0.00
Lake area (km²)	168	28	1740
Mean depth (m)	4.0	2.2	2.7
Maximal depth (m)	7.0	4.8	5.5
Lake volume (km³)	0.65	0.06	4.73
Residence time (τ_w, years)	0.57	0.43	3.8
Watershed area (km²)	1429	97	22,500
Natural shoreline (%)	0	0	0
Human population	620,000	200,000	50,000
Population density (km⁻²)	434	2062	2

Holocene as a 'lateral lake' attached to the right bank of the Chang Jiang River. The lake has been developed and modified for water storage and flood control purposes, and today there is no natural shoreline. A number of roadway dikes have been constructed across the lake, dividing it into several distinct basins. Inter-basin water exchange occurs only through bridge under-passes and culverts beneath the roadways. Water depths average 2.2 m, and display little seasonal or year-to-year variation. This stability is maintained by pumping water into the lake from a nearby river during the dry season to ensure a continuous water supply (4 million liters day^{-1}) for a large steel mill. Agriculture accounts for 72% of land use in the watershed, and the remaining 28% is urban, industrial, and residential. The human population located within the watershed is 200,000, although Wuhan City contains over 4 million people. At present, untreated waste from portions of the city is discharged into the lake.

Lake Okeechobee is located approximately 100 km to the northwest of the city of Miami, in Florida, USA. It is one of the largest lakes in North America, but has a shallow depth that averages 2.7 m. The natural lake originated 6000 years ago during oceanic recession, and it occurs in a region that once was a depressed area of the ocean floor. In the mid-1900s, a flood control dike was constructed around the lake, and today, water inputs and outputs are controlled by locks and gates. Water depths vary considerably from year-to-year and between the summer wet and winter dry seasons (Aumen, 1995; Havens, 1997); surface elevations as high as 5.5 m above mean sea level (m.s.l.) may occur during the summer rainy season (May–October), and minima as low as 3.5 m above mean sea level (m.s.l.) have occurred during the winter dry season (November–March). Variations in lake water levels may exert substantial ecological effects, especially in the large littoral zone, which occupies 25% of this lake's total surface area. In the Lake Okeechobee watershed, the major land use is animal agriculture, especially beef cattle pastures, which account for 32% of the land (Flaig and Havens, 1995). Nearly 40% of the land is undeveloped, and 18 and 10% are used for crop plants, and urban/residential purposes, respectively. The human population is quite small (approximately 30,000, or 2 persons km^{-2}), and located in small towns adjacent to the perimeter dike. There are no human habitations directly on the lake shore. Urban areas use centralized sewage treatment systems, while rural areas utilize septic systems for treatment of domestic waste.

3. Materials and methods

Our objective, formulated at the workshop, was to compare and contrast the three lakes using data that included a sufficient period of record to account for

natural year-to-year variations in limnological conditions. For Lake Kasumigaura and Lake Okeechobee, which have benefited from long-term comprehensive research and monitoring programs, we evaluated data collected during approximately the last decade. It was not possible to use this approach for Lake Donghu, because there has not been a regular program to quantify nutrient loads coincident with measurements of in-lake conditions. Such data existed only for the year 1997–98, when complete P and nitrogen (N) mass balances were determined along with routine water quality sampling. However, according to researchers studying the lake, this year is representative of conditions during the last decade. Furthermore, 1997–98 was not an atypical year in terms of rainfall or other weather conditions in the region.

A nutrient budget for Lake Kasumigaura was based on the average of 10 years of data. Surface inputs and outputs of P and N were estimated using data on water measured at 14 river gauging stations, and empirical relationships between the inputs and outputs with nutrient concentrations (Ebise, 1981; Muraoka, 1981). Bulk (wet + dry) atmospheric inputs of N and P were determined from concentration and amount collectors located in the watershed and maintained by the NIES. Total loads directly onto the lake surface were estimated from lake surface area and the measured areal loading rates. In-lake nutrient concentrations were determined from monthly samples collected by: (1) the NIES at 10 pelagic sites; (2) the Ibaraki Prefecture at six pelagic sites; and (3) the Ministry of Construction at eight pelagic sites. Total P, total N, and chlorophyll a concentrations were measured in the laboratory using standard methods, and the total mass of P and N in the lake at any given time was estimated as concentration times volume. The lake volumes were determined from daily estimates of water depth at a central lake station (Ministry of Construction and Fresh-water Fish Experimental Station, Ibaraki), and established volume versus depth relationships based on a morphometric map of the lake. Detailed studies of the sediments in Lake Kasumigaura have also been conducted, including measurements of P and N pool sizes and flux rates to and from the water column. Information regarding this internal P cycling may be found in Goda and Matsuoka (1986) and Otsubo and Muraoka (1987).

Hydrologic and nutrient loading data for Lake Donghu, from the year 1997–98, have not been previously published but are available by contacting the co-author, Dr. Xie. The data set includes estimates of tributary inputs and surface runoff, based on weekly estimates of flow and N and P concentrations (measured by standard methods); atmospheric loads (wet + dry), based on near-shore concentration and amount collectors; and industrial and domestic sources, based on weekly measurements of inflow volumes and N and P concentrations at discharge

culverts draining directly to the lake from developed regions of the watershed. There also are estimates of nutrient exports from the lake by commercial fish harvesting, public water supply, and surface outflows. In-lake concentration and mass data were based on lake volume estimates and measurements of total P and total N, determined on a monthly basis from samples collected at four in-lake stations. Chlorophyll *a* was measured at a single mid-lake station.

A nutrient budget for Lake Okeechobee was based on the average of 10 years of data. Nutrient inputs and outputs to the lake were determined by the South Florida Water Management District (SFWMD) at 32 sites where water enters or exits the lake via gates, pumps, or locks. Continuous or daily water flow rates were estimated from water depths at these structures using rating curves. Total N and P concentrations were measured in a variety of weekly, flow composite, and time-continuous samples using standard methods (USEPA, 1979, 1987), and loading rates were calculated as flow times concentration, with linear interpolation of data where necessary. Due to recurrent problems with contamination of bulk precipitation collectors by insects and bird excrement, atmospheric inputs were estimated as 35 mgP m^{-2} year^{-1} and 1809 mgN m^{-2} year^{-1}, based on peat accretion measurements made in the nearby Florida Everglades (Walker, 1993). In-lake total P and N concentrations were determined from biweekly (May–October) or monthly (November–April) near-surface samples collected by the SFWMD at eight pelagic sites. The total mass of P and N in the lake at any given time was determined as average concentration times volume. Lake volume estimates were derived from daily water levels measured at 19 stations within the lake, and a volume versus depth relationship derived from a lake morphometric map. Detailed information regarding nutrient load calculations, and the collection and analysis of samples for total P, total N, and chlorophyll *a* are described in James et al. (1995a, b). In addition, sediment P composition and dynamics have been studied, and the methods may be found in Olila and Reddy (1993), Kirby et al. (1994), and Olila et al. (1995).

4. Results and discussion

4.1. P budgets and trophic classifications

The concentration of total P in Lake Kasumigaura averaged 75 μg l^{-1} and the total mass of P in the water column was 49 metric tons (Table 2). The yearly P input to the lake was 220 t, the areal load (L_p) was 1.3 g m^{-2} year^{-1}, and the mass output was 78 t. The lake retained 65% of its P load on a yearly basis. The net P sedimentation coefficient (σ) of 2.9 year^{-1} indicates that the sediments were a strong sink for P (Vollenweider, 1975).

Table 2
Phosphorus (P) and nitrogen (N) budgets for the three lakes[a]

Attribute	Lake Kasumigaura	Lake Donghu	Lake Okeechobee
Phosphorus			
Lake concentration (μg TP l^{-1})	75	400	98
Lake mass (10^3 kg P)	49	24	464
Input (10^3 kg P year^{-1})	220	95	426
Output (10^3 kg P year^{-1})	78	10	148
Net sink (10^3 kg P year^{-1})	142 (65%)	85 (90%)	278 (65%)
σ (year^{-1})	2.9	3.5	0.6
Nitrogen			
Lake concentration (μg TN l^{-1})	1095	3083	1504
Lake mass (10^3 kg N)	712	185	7115
Input (10^3 kg N year^{-1})	3890	1480	5554
Output (10^3 kg N year^{-1})	1193	585	2986
Net sink (10^3 kg N year^{-1})	2697 (69%)	895 (60%)	2568 (46%)
σ (year^{-1})	3.8	4.8	0.3

[a] The net sedimentation coefficients (σ) were calculated as net sink/lake mass.

We evaluated the lake's trophic state using the simple input–output model of Vollenweider (1975), $[P] = L_p/(10 + q_s)$, where L_p is the areal P loading rate (g m^{-2} year^{-1}), q_s is the hydraulic loading rate $(= z/\tau_w$, m year^{-1}), and [P] is the lake water total P concentration (μg l^{-1}). In the equation for hydraulic loading, $z = $ mean depth of the lake (volume/area) and τ_w is water residence time in years. By substituting a concentration goal for [P] into the Vollenweider model, one can obtain a loading target for the watershed that can be used to guide management efforts. Here we consider the [P] goals of 20 and 10 μg l^{-1}, which Vollenweider (1975) defined as 'excessive' and 'permissible' isolines on a loading diagram (Fig. 2A) that delineate eutrophic, mesotrophic, and oligotrophic zones. With $q_s = 6.5$ m year^{-1} and $L_p = 1.3$ gP m^{-2} year^{-1} Lake Kasumigaura is classified as highly eutrophic.

The total P concentration in Lake Donghu was 400 μg l^{-1} and the total mass of P in the water column was 24 metric tons. The high total P concentration is consistent with the high yearly mass input (95 t) and the high areal loading rate (3.2 gP m^{-2} year^{-1}). The output of P from the lake was 10 t year^{-1} and the lake retained 80% of its P inputs. A sedimentation coefficient of 3.5 year^{-1} indicates an even stronger retention of P than in Lake Kasumigaura. Relatively large sedimentation loss terms have been reported for other urban lakes (e.g. Cullen et al., 1978), and may reflect the fact that much of the P in storm water runoff is associated with relatively large particles. With a hydraulic loading rate of 5.5 m year^{-1} and the high areal P load, Lake Donghu is classified as highly eutrophic according to the Vollenweider diagram.

The water column of Lake Okeechobee (100 μg l^{-1} total P) contained 460 t of P, and had inputs and outputs of 426 and 148 t year^{-1}, respectively. The lake

A Vollenweider Critical Phosphorus Loading Diagram

B Vollenweider Critical Nitrogen Loading Diagram
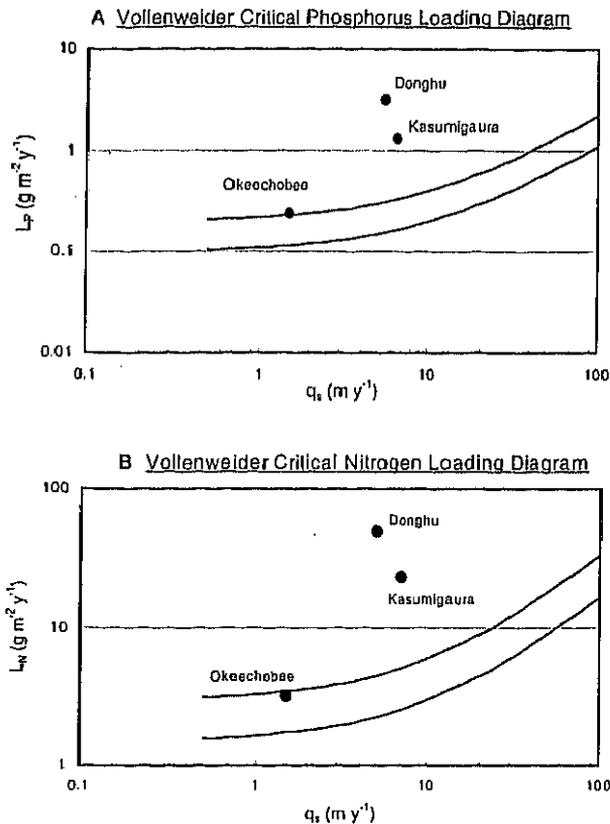
Fig. 2. Trophic classifications of the three lakes according to Vollenweider's (1975) (A) phosphorus loading diagram and (B) nitrogen loading diagram. In each panel, the two isolines separate regions of oligotrophic (bottom), mesotrophic (middle), and eutrophic (upper) lakes. Loading model terms are as defined in the text.

retained 65% of its P inputs, however σ was only 0.6 year^{-1}. With $q_s = 1.0$ m year^{-1} and $L_P = 0.24$ g m^{-2} year^{-1}, Lake Okeechobee is located just at the eutrophic to mesotrophic boundary in the Vollenweider diagram.

In the last two decades, the value of σ appears to have declined in Lake Okeechobee, from approximately 2.0 year^{-1} in the 1970s to near 0.2 year^{-1} in the mid-1990s (Havens and James, 1997). Our most recent calculations (1998–99) indicate that the lake now assimilates just 30% of the P inputs. This indicates that the ability to sequester P from the water has been reduced. Perhaps the sediments are becoming saturated with P, or for some other reason the rate of particle sedimentation has declined. A study conducted in 1988 indicated that the sediments had a large P storage capacity (Reddy et al., 1995); however, a re-analysis of lake sediments in 1999 (in progress) indicates that a greater percentage of sediment P now is in the soluble form. This is further evidence of a loss of P assimilative capacity in the lake. If it falls below 0 year^{-1} there will be net positive loading of P to the water column. Lakes with this condition generally are hypereutrophic, experience severe problems with algal blooms (Sas, 1989), and are very resistant to efforts to change their trophic state (Barica, 1995).

4.2. N budgets, trophic classifications and N:P ratios

The total mass of N in the water column of Lake Kasumigaura averaged 712 t (Table 2), with an average input of 3890 t year^{-1}, and an output of 1193 t year^{-1}. The total N concentration in lake water averaged 1095 μg l^{-1}. The N mass balance indicated a net deficit of 69% of inputs, and $\sigma = 3.8$ year^{-1}. These results indicate that either the sediment is a strong sink for N, or that there are large N losses from the system by other processes, such as denitrification.

Vollenweider (1975) indicated that critical areal loading rates for N also could be derived by multiplying the in-lake P goals by a 15:1 total N:P ratio, and then substituting the resulting total N values into the loading model given above. Taking this approach, we obtain a loading diagram (Fig. 2B) that classifies Lake Kasumigaura as highly eutrophic, with a 10-year average value of L_N (23.15 g m^{-2} year^{-1}) that greatly exceeds the excessive rate.

The total mass of N in Lake Donghu's water column was 185 t, and the lake water total N concentration averaged 3083 μg l^{-1}. The input of N to the lake was 3.890 t year^{-1}, while the output was only 585 t year^{-1}. This equates to a loss of 60% of the inputs, and again may reflect N transfers to sediments or the atmosphere. According to the Vollenweider diagram, areal N loading (49.33 g m^{-2} year^{-1}) was excessive.

The water column of Lake Okeechobee contained, on average, 7115 t of N, and the lake water total N concentration averaged 1504 μg l^{-1}. The N inputs and outputs averaged 5554 and 2986 t year^{-1}, respectively. The areal N loading rate was below the boundary for excessive loading, in the mesotrophic area of the Vollenweider diagram. There was a net loss of 46% of the N inputs to the system, with $\sigma = 0.3$ year^{-1}. These results suggest that Lake Okeechobee is not as strong a sink for N as the other two lakes. This is not intuitive, because the warm subtropical waters would be expected to favor rapid microbial processes such as denitrification in the Florida lake. What actually might be the case is that in Lake Okeechobee, a large source of N input is not accounted for in the budget, in particular the process of N$_2$ fixation. In a comprehensive study that measured N fixation rates at 18 pelagic locations during 1989 to 1992 (Phlips and Ihnat, 1995), it was observed that N$_2$ fixation could account for over 30% of the N inputs. Dominant taxa forming surface blooms in Lake Okeechobee include heterocystous species such as Anabaena circinalis and Aphanizomenon flosaquae (Havens et al., 1998). In contrast, the blooms of phytoplankton of Lake Kasumigaura primarily are dominated by Raphidiopsis, Oscillatoria, and Lyngbya (Takamura et al., 1998) taxa that are not N$_2$-fixers. Lake Donghu once displayed surface blooms that included Anabaena, but more recently, the dominant algae are diatoms, cryptophytes, and small

non-heterocystous cyanobacteria (Xie, 1996). The taxo-
nomic shift in Lake Donghu was attributed to intense
grazing on larger cyanobacteria by filter-feeding silver
carp. In summary, strong loss processes may exist for N
in all three lakes. This is not as evident from a tradi-
tional N mass balance in Lake Okeechobee, however,
because it does not include N_2 fixation, a process that
may be of great importance in that particular lake.

4.3. Sources and sinks for P

Detailed studies of P dynamics in Lake Kasumigaura
and Lake Okeechobee have indicated complex interac-
tions between the sediments and water column, and stu-
dies in all three lakes have documented the importance of
biological processes to the internal P cycling.

In Lake Kasumigaura, the total mass of P in the
upper, biologically active layer (0–5 cm) of sediments
exceeded the mass of P in the water column by 29 times
(Fig. 3A). It is estimated (Goda and Matsuoka, 1986)
that internal loading of P from sediments to water col-
umn is 396 t year^{-1}, which is 60% greater than the
external loading rate. The major process of internal
loading was biological resuspension. Diffusion accoun-
ted for a smaller portion of the internal P load, although
it may be a major source of P during mid-summer, when
the bottom waters of this lake periodically become
anoxic (Ishikawa and Tanaka, 1993). The major in-lake
loss process for P was sedimentation of particulate
material (Matsuoka et al., 1986). Other small loss terms
(but of the same magnitude as exports by surface out-
flows) included insect emergence and fish harvesting.

In the case of Lake Donghu (Fig. 3B), there were no
data for the internal P cycle, but there are good esti-
mates of P exports by commercial fish harvesting —
these averaged 9 t year^{-1}, and approximately equal the
amount of P exported in the lake ouflows. As indicated
above, 76 t year^{-1} of P was lost to the sediments in this
lake, perhaps as settling particulate material. However,
the rates of particular sediment–water transfer processes
have not been estimated.

The upper, biologically active layer (0–10 cm) of
sediments in Lake Okeechobee contained 24,700 t of P
(Fig. 3C), more than 53 times the amount in the water
column (Reddy et al., 1995). Wind resuspension is the
major process whereby sediment P is periodically
returned to the water column. The estimated rate, based
on laboratory studies and hydrodynamic modeling, is
744 t year^{-1}, which is 75% greater than the measured
external load. Diffusive fluxes, also estimated in the
laboratory (Moore and Reddy, 1994), are thought to be
an order of magnitude lower. However, this assumes that
anoxic conditions do not occur in the water column. We
recently have completed a 2-year study of redox condi-
tions at the sediment–water interface in Lake Okeecho-
bee. During summer, it is typical to observe diel changes
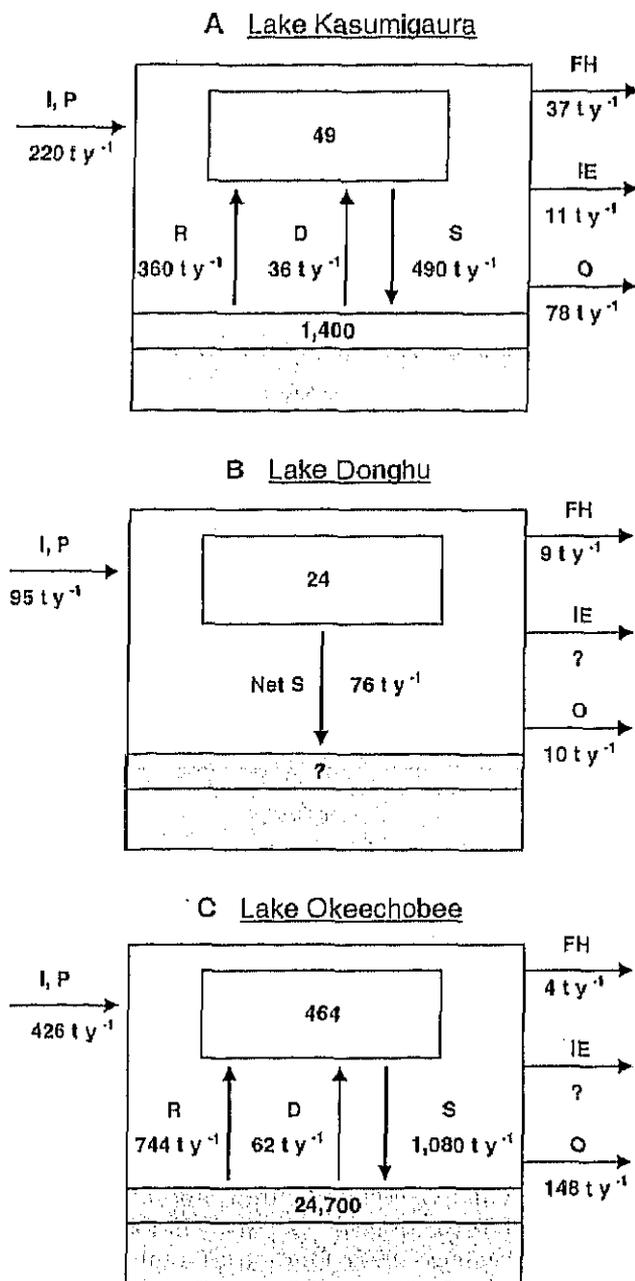
Fig. 3. Phosphorus (P) mass-balances for (A) Lake Kasumigaura, (B)
Lake Donghu, and (C) Lake Okeechobee, showing surface inputs
from tributaries and precipitation (I, P), sediment resuspension (R),
and diffusion (D), and losses by particle sedimentation (S), fish har-
vesting (FH), insect emergence (IE), and surface outflows (O). In each
panel, water column P mass is indicated in the open box, and surface
sediment mass is indicated by the shaded box.

in redox potential from +200 mV (when the water col-
umn is isothermal and wind velocities are relatively
high) to −300 mV (when there is a 2–3°C stratification
and calm winds). Laboratory studies have indicated that
P rapidly diffuses from the lake's mud sediments when
the overlying water is anoxic (Reddy et al., 1995), and
therefore, during summer, there may be high diffusive P
loading, as has been documented in Lake Kasumigaura.

The results of research on these two lakes suggests that a common view that shallow lakes are constantly mixed, isothermal, and well oxygenated is not valid.

The major loss term for the in-lake P cycle in Lake Okeechobee is sedimentation, which removes nearly 10 times more P from the water column than exits the lake via the outflows. A rough estimate of P export by fish harvesting, provided by the Florida Game and Fresh Water Fish Commission, is 4 t year^{-1} (Scovell, 1991), an insignificant amount relative to other pathways.

4.4. Nutrient loading models

Empirical models have been widely used to guide eutrophication management of lakes and reservoirs (e.g. Sas, 1989; Cooke et al., 1993; Hakanson and Peters, 1995). Log–log regression models relating phytoplankton chlorophyll a to lake water total P have been used in concert with nutrient loading models to predict algal responses to external P load reductions (e.g. Nicholls, 1997). There is evidence that shallow lakes may not be amenable to this approach, because their internal recycling processes (i.e. sediment–water interactions) affect in-lake conditions to a greater extent than in deeper, dimictic lakes for which most general models were derived. Thus, we considered how well a subset of published empirical models (Table 3) predicted in-lake P

and chlorophyll a in the three studied lakes. This comparison provides additional insights into similarities and differences among the ecosystems.

None of the published models considered gave consistent results among the three lakes. This reinforces the conclusion that there is considerable heterogeneity of nutrient dynamics and nutrient–algal interactions in shallow polymictic lakes, perhaps more so than among their deeper, dimictic counterparts.

A large number of empirical models have been presented in the literature relating lake water total P to external P loading. Nearly all of the models are based on Vollenweider's (1969) model: $[P] = L_P[z_m (\sigma + \rho)]$ where σ and L_P are as previously defined, z_m is mean depth (m) and ρ is flushing rate (year^{-1}). The published models generally differ only in regard to how σ, a term that is very difficult to measure, is empirically estimated or calculated. We considered three commonly used models, the Vollenweider (1975) equation, which approximates σ from an empirical relationship with mean depth, the Vollenweider (1976) equation, which considers both depth and water residence time in estimating σ, and the Dillon and Rigler (1974a) equation, which calculates a surrogate for σ (R, the net retention coefficient) from the P mass balance. The simplest model (Vollenweider, 1975) gave a relatively good estimate of [P] in Lake Kasumigaura, but substantially underestimated [P] in Lake

Table 3

Results of some standard models used in lake eutrophication management, in regard to predictions of in-lake concentrations of total phosphorus (TP) and chlorophyll a (CHLA) in the three shallow lakes[a]

Model	Reference	Lake	Predicted		Actual
$[TP] = L_P/(10 + q_s)$	Vollenweider (1975)	Kasumigaura	100	~	80
		Donghu	200	≪	400
		Okeechobee	20	≪	100
$[TP] = L_P/q_s(1 + \tau_w^{0.5})$	Vollenweider (1976)	Kasumigaura	120	>	80
		Donghu	350	~	400
		Okeechobee	60	<	100
$[TP] = \{L_P(1 - R)\}/zp$	Dillon and Rigler (1974a)	Kasumigaura	70	~	80
		Donghu	130	≪	400
		Okeechobee	160	>	100
Log [CHLA] = −0.390 + 0.874 log [TP]	Dillon and Rigler (1974b)	Kasumigaura	70	~	60
		Donghu	1000	≫	30
		Okeechobee	100	≫	20
Log [CHLA] = −2.49 + 1.06 log [TN/TP] + 1.33 [TP]	Canfield (1983)	Kasumigaura	20	≪	60
		Donghu	80	≫	30
		Okeechobee	30	>	20
Log [CHLA] = −0.28 + 1.06 log [TP]	Mazumder (1994) (SH-MIX)	Kasumigaura	50	~	60
		Donghu	295	≫	30
		Okeechobee	70	≫	20
Log [CHLA] = −0.06 + 0.64 log [TP]	Mazumder (1994) (LH-MIX)	Kasumigaura	10	≪	60
		Donghu	40	>	30
		Okeechobee	20	~	20

[a] L_P is the areal P loading rate (g m^{-2} year^{-1}) and q_s is the hydraulic loading rate (m year^{-1}). In the loading model of Dillon and Rigler (1974a), R is retention coefficient (1−{outflow P mass/inflow P mass}), ρ is lake flushing rate (year^{-1}), and z is mean depth (m). Other loading model terms are defined in Tables 1 and 2. In the models of Mazumder (1994), acronyms are SH-MIX = small herbivore mixed and LH-MIX = large herbivore mixed lakes. Symbols compare model predictions with data (~within 20%, > or < by more than 20%, ≫ or < < by more than 100%).

Donghu and Lake Okeechobee, where large sediment to water fluxes may contribute substantially to water column P. This situation is typical of shallow eutrophic lakes (Sas, 1989) and indicates that the position of the Lakes Donghu and Okeechobee on the loading diagram of Fig. 2 may be underestimated (i.e. the lakes are more eutrophic than indicated). It is surprising that the simple model, which does not consider internal processes, predicted [P] relatively well in Lake Kasmumigaura, since the sediments in this lake are known to be an important source of gross P loading. Perhaps the 'good' model result can be attributed to some major loss processes not considered, so that, by coincidence, the actual and predicted values were in agreement.

The Vollenweider (1976) equation is more complex, and also more widely used, because it gives explicit consideration of the effects of both hydraulic loading and residence time on [P]. Nevertheless, this model gave mixed results when applied to the three study lakes. It overestimated [P] in Lake Kasumigaura, provided a good estimate of [P] in Lake Donghu, and underestimated [P] in Lake Okeechobee. The strong improvement of results for Lake Donghu with the more complex model is intuitive because the lake has a moderately rapid flushing rate (> 2 year^{-1}), which can affect the extent to which P settles from the water column to the sediments. However, Lake Kasumigaura also has a moderately rapid flushing rate and its [P] was better predicted by the simple model.

The Dillon and Rigler (1974a) model gave the best result for Lake Kasumigaura, predicting a mean value for [P] that differed by only 13% from the measured value. However this model, which calculates all parameters from the lake's hydrologic and P budgets (rather than using empirical relationships), seriously underestimated [P] in Lake Donghu and overestimated [P] in Lake Okeechobee.

Although these results indicate that it may be possible to find a simple input–output type of model that can predict [P] in any given lake, questions will always arise as to whether the results are good by coincidence, or because the model is an appropriate one. Given the markedly different results that were obtained in any given lake using three models that have a very similar underlying structure, we conclude that consideration should be given to use of more complex models that explicitly consider internal P loading, when dealing with the management of shallow lakes.

4.5. Chlorophyll–P models

Since Dillon and Rigler (1974b) published a simple log–log model relating lake water chlorophyll a to total P, lake managers have been using empirical models of this sort to predict algal biomass responses to P reduction programs. However, studies during the last decade

have shown that quantitative nature of chlorophyll–P models can vary widely, depending on features of the lake, including grazing pressure on the algae, presence or absence of abiotic turbidity, lake flushing rate, and a number of other variables. We considered the performance of four published chlorophyll–P models, including models that give explicit consideration to N limitation and zooplankton size, two variables having the potential to markedly affect the relationships.

The Dillon and Rigler (1974b) model provided a very good estimate of chlorophyll a in Lake Kasumigaura (Table 3), with the predicted concentration differing by only 14% from that measured. This might indicate that phytoplankton in Lake Kasumigaura is primarily limited by P, which has been documented in experimental research (Takamura et al., 1992), or perhaps it just indicates that the algal cells in that lake are stoichiometrically similar to those found in the lakes studied by Dillon and Rigler. In striking contrast, the Dillon and Rigler model over-estimated chlorophyll a by > 30-fold in Lake Donghu and by > 5-fold in Lake Okeechobee. One interpretation of the results is that some factor other than P limits phytoplankton biomass in these lakes. This issue is discussed in greater detail below but, in general, it has been documented that in Lake Donghu, phytoplankton is heavily grazed by filter-feeding fish (Xie, 1996), and in Lake Okeechobee, phytoplankton often is limited by low irradiance due to wind resuspension of abiotic sediments (Havens, 1997; Phlips et al., 1997).

Canfield (1983) developed a more complex empirical model to predict chlorophyll a that considers both P and N. The model reflects the often-observed sigmoid relationship between chlorophyll a and P (e.g. Prairie et al., 1989; Mazumder, 1994; Mazumder and Havens, 1998), which Canfield explained as being due to N limitation in P-rich systems. This model gave a serious underestimate of chlorophyll a in Lake Kasumigaura, which as indicated above, appears to be P-limited. In contrast, it over-estimated chlorophyll a in Lake Donghu and Lake Okeechobee. N limitation does occur, primarily during the calm summer months, in Lake Okeechobee (Aldridge et al., 1995), and the somewhat improved performance of Canfield's model relative to the Dillon and Rigler model may indicate that some of that effect now has been accounted for. However, chlorophyll still is over-estimated by 50% (Table 3), indicating that an additional factor (presumably light availability) needs to be considered. Generally that level of complexity is found only in more complex deterministic models.

Lastly we considered empirical models that account for phytoplankton control by grazers, as well as differences in chlorophyll–P relationships among deep versus shallow lakes. Mazumder (1994) analyzed data from 367 lakes in North America and Europe, and found that

by sub-dividing the data set into four classes, much of the variation in the chlorophyll–P relationship could be statistically and mechanistically explained. The four classes represent a 2×2 matrix of two factors: (1) mixing regime — shallow mixed lakes display greater amounts of chlorophyll *a* per unit of P than deep stratified lakes; and (2) zooplankton size — lakes dominated by small zooplankton display greater amounts of chlorophyll *a* than those dominated by large (> 1.0 mm) *Daphnia*. We considered the two models developed for shallow lakes (Table 3) the SH-MIX (small herbivore, mixed) and LH-MIX (large herbivore, mixed) models.

In Lake Kasumigaura, the SH-MIX model of Mazumder (1994) predicted a mean concentration of chlorophyll *a* that differed by <20% from the measured value (Table 3). This lake is indeed a shallow mixed system with dominance by small-bodied zooplankton (Hanazato and Yasuno, 1987). Thus the results are 'good' not only in terms of model performance, but also from the standpoint of the behavior that is expected based on known mechanisms. The SH-MIX model seriously over-predicted chlorophyll *a* in Lake Donghu, where the dominant zooplankton are small, and there are other important herbivores, the silver carp (*Hypophthalmiochthys molitrix*) and bighead carp (*Aristichthys nobilis*). Xie (1996) documented with enclosure experiments that grazing by these fish accounted for substantial reductions in algal biovolume since the 1980s, as well as shifting the species dominance from large filamentous cyanobacteria to small unicellular forms. In Lake Okeechobee, the SH-MIX model also over-estimates chlorophyll *a*. Although this lake has small zooplankton, it also has strong control of phytoplankton by light limitation.

The LH-MIX model of Mazumder (1994) produced nearly the opposite results. It under-estimated chlorophyll *a* in Lake Kasumigaura, where zooplankton herbivores are not large-bodied, but it predicted mean chlorophyll *a* concentrations that were relatively close to measured values in Lake Donghu and Lake Okeechobee. This is interesting because these lakes do not contain large *Daphnia*. As with the case of nutrient loading models, this result indicates that lake managers should be wary of searching for models that provide the best fit to their chlorophyll *a* versus P data. Some models that provide 'good' results, in terms of agreement with actual data, may not reflect the actual mechanisms that are occurring in the lake. This could lead to erroneous management decisions. On the other hand, with a solid understanding of the ecological processes operating in a particular shallow lake (i.e. a solid basis of ecosystem research), one might find a very appropriate statistical model in the literature that can be used in lake management. The SH-MIX model of Mazumder (1994), for example, might be a good choice for lakes with features like those found in Lake Kasumigaura.

5. Conclusions

Shallow eutrophic lakes, such as those considered here, can display complex nutrient dynamics, with processes such as sediment–water exchanges playing a much greater role than in deep, dimictic lakes. Shallow eutrophic lakes often have associated with them other features, such as intense N-fixation and light limitation, and human influences such as fish harvesting, that add further complexities to the relationships between nutrient inputs, in-lake nutrient concentrations, and the biomass of algae in the water column. Simple empirical models, developed from research on deeper lakes, may be useful under certain conditions in shallow eutrophic lakes, but their application should be approached with great caution. In particular, scientists and resource managers should be careful that model predictions are consistent with ecological processes occurring in the lakes. A high degree of heterogeneity among shallow lake systems may necessitate a greater reliance on lake-specific research results, and less inter-lake generalization than is possible for deeper systems. In particular, there appears to be a need for models that consider the impacts of fish grazing activities on nutrient–chlorophyll relationships in lakes.

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〈論　文—Original Paper〉

水域の生物活性鉛直分布の測定

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Measurement of Vertical Distribution of Biological Activity in Aquatic Systems

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Abstract

At the center of Lake Kasumigaura, water temperature, DO, pH, and chlorophyll a were measured at 6 different depths at 24-minute intervals for four 1-week periods. Using the models for vertical mixing and air-water exchange, the vertical distribution of biological changes in the lake water was estimated quasi-continuously, although the estimation was difficult when the decay of stratification occurred. Simultaneous measurements of DO and pH demonstrated the accuracy of the estimated biological activities. This system shows potential for field measurements of biological activities, e. g., primary productivity and respiration in the columns of aquatic systems.

Key words : vertical distribution of biological activity, continuous measurement, DO, pH

1. はじめに

様々な環境改変，地球温暖化，毒性物質などが水界生態系に及ぼす影響については，社会的に大きく注目されているにもかかわらず，いまだ不明な点が多い。こうした影響や対策の効果を定量的に評価する技術として，生態系の活性を簡易に，定量的に測定することができる手法の確立が望まれている。

従来，水域での生物生産，消費の大きさは，水域にボトルを吊し，期間前後での溶存酸素（DO）や無機態炭素濃度（DIC）の変化を測定することから推測されてきた（ボトル法）[1]。しかし，この方法では，1）時間的にも空間的にも短期の，離散的な観測値しか得られない（時間的に，空間的に密に，長期の測定を行おうとすると極めて膨大な労力が必要となる），2）ボトル効果によりアーティファクトが生じる（ボトル壁の影響，混合の差，など）といった問題点を有していて，水域での生物活性を時間的，空間的に連続に測定することは出来ない。一方，水中に吊した DO, pH などのセンサー出力結果から生物活性を時間的に連続測定する方法があり，フリーウォー

ター法と呼ばれているが，大気との交換，鉛直拡散を正確に見積もる必要がある。このため，水質の鉛直差が発生しないような系[2~5]やそうした差を無視して生物活性の連続測定[6]が行われてきた。なお，ボトル法とフリーウォーター法を組み合わせて，一片20cm の明箱，暗箱中の水を定期的に交換し，箱中の水の DO, pH を連続測定する方法もあるが[7]，やはり鉛直特性の評価は行えない。

本研究は，水中に吊した DO, pH, 水温などのセンサーを定期的に上げ下げし，多くの水深での DO や DIC（アルカリ度と pH から計算）の経時変化を疑似的に連続測定する装置を開発し，湖沼のような水域で利用可能かどうかを調べることを目的とした。すなわち，1）上下させる装置の安定性，ならびに固定型システムとの精度比較，2）流れが変動する場合の大気交換，鉛直拡散の補正方法，3）生物活性の評価方法，を報告し，議論する。

2. 方　　法

2.1 測定システム

水質測定にはゾンデ YSI-Model6600を用いた。水温（サーミスター；分解能0.01°C），深度（圧力式；1 mm），

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DO（クラーク型ポーラログラフ電極；0.01mg・l^{-1}），pH
（ガラス複合電極；0.01），クロロフィル a（蛍光式；0.1
μg・l^{-1}），電気伝導度のセンサー（温度補正回路組み込み
式電極；1 μS・cm^{-1}）を有し，また測定データを内部の
データロガーに内蔵できるものである。そのゾンデの昇
降装置は糸の巻き上げ装置と糸，ゾンデ回転防止用のガ
イド（4 m の 2 本のチューブを平行に測定区間に設置
し，それらをゾンデの腹に固定した 2 つのパイプの中に
それぞれ通すことでゾンデの回転をなくし，また流され
ないようにしたもの），ならびに昇降を制御するコン
ピュータ，電源で構成されている。なお，糸の巻き上げ，
巻き下ろしのカウント数を数えるシリアルリンクボック
スをパソコンが制御することで，指定の時間に，指定の
位置にゾンデを上下させることが可能なシステムであ
る。本観測では，最浅水深を60cm 前後，最深水深を 4 m
前後とし，その間を等間隔に分割するよう，全 6 水深で
測定を行うようプログラムを設定した。なお，測定の時
間間隔，繰り返しに関しては3.1に示すような検討を行
い，決定した。

測定前にセンサーの校正を行った。また，測定前後に
数水深で採水した水の分析を行って，測定値のキャリブ
レーションをするとともに，アルカリ度を測定した。水
の分析方法は既報[3,5,7]と同じである。また，無機炭素
（DIC）濃度は pH とアルカリ度から算出した[2]。また，気
温，風向・風速，日射量，水位，大気圧は，2.2に示す湖
心観測所と同じく霞ヶ浦湖心域にある国立環境研究所の
湖上モニターの測定値[8]を用いた。

なお，3.1と3.2では測定方式の検討，固定型システム
との比較を行うが，個別の実験，観測方法はそれぞれの
節で示す。

2.2　測定場所と期間

霞ヶ浦の湖心にある国土交通省霞ヶ浦工事事務所霞ヶ
浦湖心観測所に，上述のシステムを設置して測定を行っ
た。2001年 8 月（8 月27日—9 月 3 日），9 月（9 月18日
—25日），10月（10月26日—11月 7 日），2002年 1 月（1
月11日—21日）に，それぞれで約 1 週間にわたり連続測
定を行った。以降，それぞれ 8，9，11，1 月調査と呼
ぶ。電源には自動車用12V バッテリーを10個程度用い
た。しかし，電源の供給，ゾンデ昇降用の糸の切断など
問題によりゾンデが上下しなくなる事態も発生したの
で，本論文では正常に上下した期間のデータの解析結果
のみを示す（8 月：6 日間，9 月：2 日間，11月：4 日
間，1 月 1 日間）。

3．結果と考察

3.1　測定の安定性から見た測定方式の検討
(1)　水深

どの測定期間中とも水位変化は小さかったが（8 月の
観測で最大 3 cm の変化），水深観測結果には約10cm の
変化が見られる場合があった。そこで大気圧の補正を
行った結果，補正水深の変化は 1 cm 程度となり，ゾンデ
の昇降装置が指定通りに稼動したことが確認された。こ
のため，以下の解析では一定水位，固定水深での観測結
果として取り扱う。

(2)　測定間隔

ゾンデが移動することから，センサーの反応の遅れや
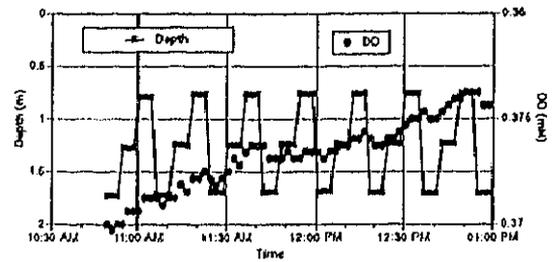
Fig. 1　Change in depth and DO, (1) during mixing condition (moderately strong wind).
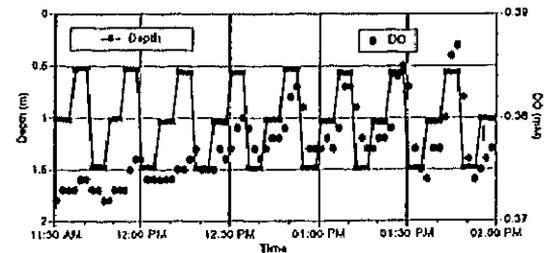
Fig. 1　(2) during calm condition (negligible wind).

水界の攪拌による誤差が懸念される。予備実験として，
国立環境研究所屋外実験池において，3 水深でそれぞれ
2 分間隔，各 3 回の測定を行った。すなわち，各水深に
6 分留まり，その間，1，3，5 分に値を読み，データ
ロガーに記録し，次の水深に移動するように設定した。

Fig. 1には，風が比較的に強く（5 m・s^{-1}前後）水界
がよく混合している期間と，風が弱く（1 m・s^{-1}以下）鉛
直分布が観察される期間の測定結果を示す。前者の場合
（Fig. 1(1)），もともと水質の水深差は少なく，水質は時
間的に変化しているので，ゾンデの測定結果はほぼ滑ら
かに推移している。これに対して後者では（Fig. 1(2)），
移動後の 1 分目と 3，5 分目ではかなり値が異なること
がわかる。時間的な推移からみても，1 分目の測定値は
その前の測定値の影響を受けているようである。この原
因はセンサーの反応の遅れ，ゾンデの移動に伴う水界の
移動，あるいは混合ではないかと考えられる。このため
本実験は，6 水深で各水深にそれぞれ 4 分留まり，その
1，3 分目に測定を行い，その内 3 分目のデータを解析
に供することとした。

3.2　固定型システムとの比較

3.1に示したような測定の安定性の観点では，各水深に
ゾンデを固定するシステムの方が優位である。しかし，
以下に示すようなゾンデセンサーの長期安定性の問題が
あるので，そうした観点を加味して移動型と固定型のシ
ステムを比較する必要がある。

ゾンデセンサーの安定性を調べるために，容器に純水
（Milli-Q. TOC）を入れ，エアバブリングしながら暗恒温
室に置き，10分間隔で約 1 週間にわたりセンサー出力を
計測した。すなわち，水温，DO，pH 等を一定に保った
ときのセンサーの安定性を調べた。センサーには 1 時間
以内の短期変動，1 日程度の中期変動，1 週間程度の長
期変動，すなわちトレンドが存在した（Fig. 2）。それぞ
れ，センサーの短，中，長期的な安定性と関係している
と考えられるが，中期変動に関しては恒温室内でも外界
の 1 日変動を消しきれず，その影響が出た可能性もある
（すなわち，その場合は濃度変化が実際に存在したことに
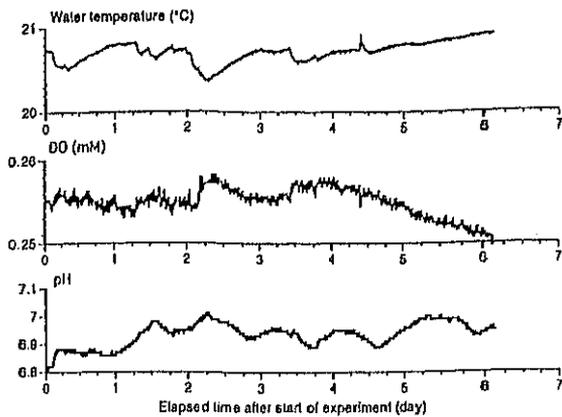
Fig. 2 Variations in water temperature, DO and pH when the sonde was put in air-saturated Milli-Q water placed in a dark and thermostatic chamber.

Table 1(1) Main causes of the errors.

	One-sonde system	Plural-sonde system
Diurnal difference	M	M
Vertical difference	S	L

S: Variation in a short-term time scale, M: Variation in a middle-term time scale, L: Variation in a long-term time scale

Table 1(2) Estimated error magnitudes for DO and pH by one-sonde system and plural-sonde system.

		one sonde	plural sondes
DO	Diurnal	±0.557	±0.557
(μM)	Vertical	±0.296	±5.0
pH	Diurnal	±20.4	±20.4
(10⁻³)	Vertical	±2.63	±200
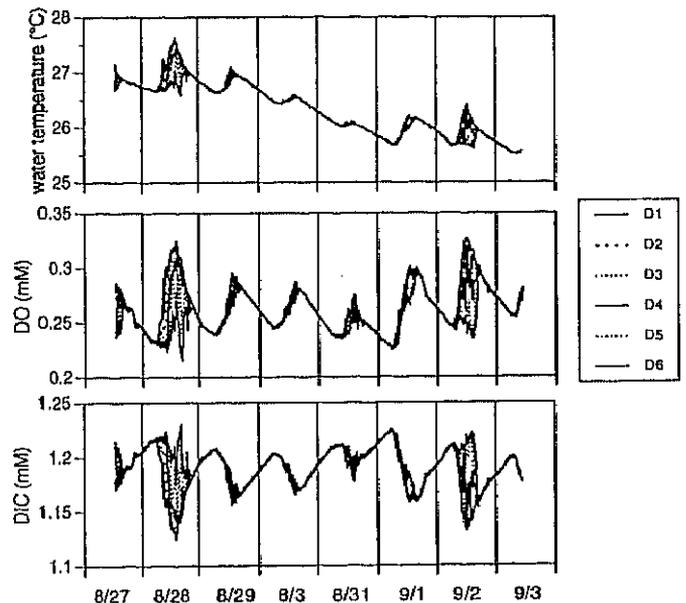
Fig. 3 Changes in water temperature, DO and DIC at 6 depths at the center of Lake Kasumigaura during the period from Aug. 27 to Sept. 3, 2001. D1: 0.64m, D2: 1.30m, D3: 1.96m, D4: 2.62m, D5: 3.28m, D6: 3.94m.

なり，以下の中期変動の大きさは過大評価となっている）。それぞれの大きさは，短期変動は3個の測定値の移動平均値と測定値との差の標準偏差として，中期変動は1日の移動平均値と測定値との差の標準偏差として，長期変動は測定期間中での初期値からの最大のずれとして求めた。後述するように，長期，中期，短期の順に，特に長期で大きいことがわかる。

ここでは，生物活性を測定することを目的としているので，一日の濃度変化の大きさや，物理的な混合の大きさを補正するため鉛直方向の濃度差（詳細は次節）の測定精度が重要である。そうした観点から，1台のゾンデを昇降させるシステムと複数のゾンデを固定するシステムでは測定誤差に関わる要因をTable 1(1)のように整理できる。すなわち，1日の濃度変化の精度はともに中期変動の大きさで推測できるが，鉛直方向の濃度差に関しては1台システムでは短期変動であるのに対して，複数台システムでは値のキャリブレーションの関係で長期変動の大きさとなる。1台システムでは鉛直濃度差を精度よく測定出来るのが大きな利点である。この結果，Table 1(2)に示すように測定精度が推定されるが，鉛直濃度差の精度は，1台システムでは複数台システムと比べDOで17倍，pHで76倍もよいことがわかる。なお，pHではセンサーの初期変動が大きいので，その部分を除いて長期変動の大きさを推定すると（3日目以降の最大値と最小値の差）0.12と若干小さくなるが，やはり短期変動の46倍であり，1台システムの優位性が示される。

3.3 観測結果，大気交換，鉛直拡散の補正方法

(1) 観測結果

水温，DO，pHともに昼間高く，夜低いパターンを繰り返している（Fig. 3と後述のFig. 6）。風の強い日には全水深で水質差は小さいが，風の弱い日では水深間の水質差が大きい。

(2) 大気交換，鉛直拡散の補正

水平方向の濃度差が無視できるとすると，DOやDICの濃度変化は下記のような生成・消失項のある鉛直拡散方程式で記述される。

$$\partial C/\partial t = \partial(K_z \partial C/\partial z)/\partial Z + F_{biot} \tag{1}$$

ここにCは水質濃度，tは時間，zは鉛直下向きの座標軸，K_zは鉛直拡散係数，F_{biot}は光合成や呼吸といった生物現象よる濃度変化，である。

式(1)をある水深範囲で積分すれば，その範囲での生物活動によるDO，DIC変化の大きさが推定できる。ここでは，ゾンデの留まる水深間の中間の位置の範囲（層と呼ぶ。上から順に1から6層）で積分を行い，層内ではCが一定とする。なお，1層は水表面までを考えるが，6層は2－5層と同じ厚さとする（例えば8月の測定では1層は0～97cm，2層は97～163cm，3層は163～229cm，4層は229～295cm，5層は295～361cm，6層は361～427cm）。さらにこの時，濃度勾配，K_z，ならびに水表面，底面でのフラックスを与えられなければならない。まず，濃度勾配は濃度差を水深差で割って求める。水表面のフラックスは福島ら[2]で用いたのと同じように，飽和濃度と水中濃度の差にガス拡散係数を乗じたものとし，ガス拡散係数は風速の関数とする。DICではChemical Enhancement効果を補正したものを用いる。また，底面でのフラックスはゼロと近似する。

最後に，鉛直拡散係数は以下のように与えた。すなわち，鉛直成層場での鉛直拡散係数K_zはリチャードソン数Riを用いて次のようにモデル化される[9,10]。

$$K_z = K_{z0} \cdot f(Ri) \tag{2}$$

Table 2 Percentage of inappropriate MQ (%).

	Raw data			elimination within -0.001 to 0.001		elimination within -0.002 to 0.002	
	MQ<0.5	MQ>2.0	total	eliminated	MQ<0.5 or MQ>2.0	eliminated	MQ<0.5 or MQ>2.0
D1	7.0	4.8	11.9	12.1	4.8	28.1	1.9
D2	2.4	4.8	7.3	9.9	1.9	28.8	0.2
D3	3.9	3.6	7.5	11.6	2.9	28.8	1.7
D4	4.6	5.6	10.2	15.7	2.2	33.9	0.7
D5	4.6	5.6	10.2	16.5	2.9	35.8	1.5
D6	7.3	7.0	14.3	17.4	3.4	38.5	1.2

再現しているのではないかと考えられる。なお，モデル4を8月のデータに当てはめたが，成層破壊時にはすべての層で生物現象による変化が負となるような結果となった。この時，成層は4mよりも深く形成されていて，この期間すなわち，成層破壊が4m以下の層にも及ぶ期間では，今回の計測の最下層4mより上の層すべてでDOが減少し，DICが増加する結果となった。すなわち，混合により濃度変化が急激に起こっている層の観測を行っていないので，そうした期間の生物現象による変化を推測するのは難しい。9，11，1月では成層が表層部にのみ生じたので，4mまでの観測でも生物現象の推定が可能であったものと考えられる。以上から，観測システムの設置にあたっては，生物現象の影響の深さに加えて，成層の深さに注意すべきことがわかる。

3.4 生物活性の評価

(1) MQ

MQは生物現象によるDIC変化に対するDO変化の比である[2,3,5]。光合成の際の窒素源，生成有機物，分解の際の生成物，酸素条件が影響していると考えられている。ここでは，その比が1から大きく隔たらないことを利用してモニタリングへの活用法を考える。

3.3のモデルを用いて推定された生物現象によるDO，DIC変化量をもとにMQを計算すると，0.5以下や2以上と一般的な状態では予想されない値が得られる場合があり，全観測値の10%程度を占めた（Table 2)。これは，現実にそのような比の反応が生じているという可能性があるものの，両者の値が小さいことによるばらつきや鉛直混合の評価誤差などにより生じた可能性が大きい。そこで，生物現象によるDOとDICの変化(絶対値)のいずれかがある値より小さい場合にはMQの計算を行わないとして，MQが0.5以上，2以上となる割合を計算した(Table 2)。閾値を0.001mM・h⁻¹，0.002mM・h⁻¹とすると，それぞれ10〜17%，28〜38%が削除されることになるが，MQが0.5〜2の範囲外となるのはそれぞれ2〜5%，0〜2%と極めて少なくなる。また，MQの平均値は既往の報告値[11,12]に近い1.06〜1.15の範囲に入る（Table 3)。その時間変化もかなり滑らかとなるので(閾値0.001，0.002mM・h⁻¹の例を示す；Fig. 8)，このような配慮をしながらMQの算定を行うことから，モニタリング結果ならびに解析の適切さを評価できるものと考えられる。なお，生物現象ではDOとDIC変化はカップリングしていて，その比であるMQの短時間での急激な変化は起こり得ないので，MQの滑らかな変化を期待した。

(2) 水界全体での光合成量，呼吸量

得られた生物現象によるDO，DIC変化と物理量との関係を調べた。光合成量は以下のように表現されることが多いので[13]，

Table 3 MQ. Mean±standard deviation (number of data for calculation, number of data excluded for MQ<0.5 or MQ>2). elimination limit=0.001mM h⁻¹.

	Daytime	Nighttime
D1	1.145 ± 0.142 (92, 4)	1.115 ± 0.141 (108, 0)
D2	1.066 ± 0.207 (92, 3)	1.106 ± 0.153 (109, 0)
D3	1.113 ± 0.240 (88, 3)	1.105 ± 0.154 (109, 0)
D4	1.037 ± 0.240 (85, 1)	1.118 ± 0.179 (109, 0)
D5	1.192 ± 0.301 (70, 6)	1.104 ± 0.179 (110, 0)
D6	1.160 ± 0.278 (66, 7)	1.103 ± 0.160 (106, 0)
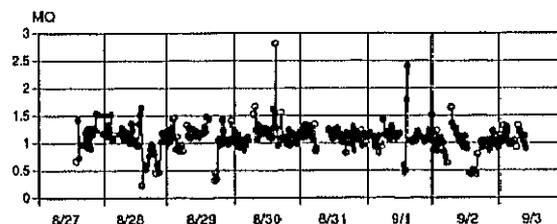
Fig. 8 Change in MQ of the data shown in Fig. 3 at D1. open circle: elimination limit=0.001mM h⁻¹, solid circle: elimination limit=0.002mM h⁻¹. The four negative data (open circle) were removed.
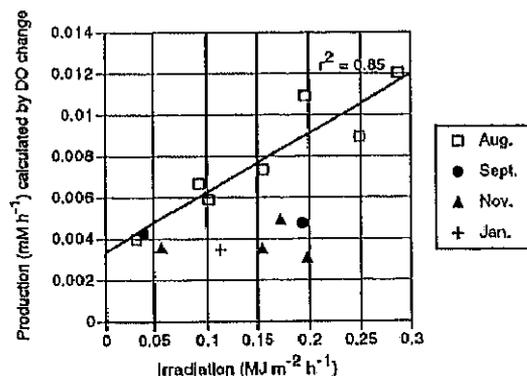
Fig. 9 Irradiation vs. production of the whole depth. Each plot corresponds to each morning (from dawn to noon).

$$P = P_0 \cdot f(I) \cdot Chla \qquad (8)$$

$$f(I) = I(z, t)/I_0 \qquad (9)$$

$$I(z, t) = I(t)\exp(-\varepsilon z) \qquad (10)$$

$$\varepsilon = 0.2 \times Chla + 1.1 \qquad (11)$$

水深ごとの光とクロロフィルa濃度の積の全水深積分値と光合成量の全水深積分値との関係を見た（Fig. 9)。

$$\int_{t_1}^{t_2} \int_0^{z_{max}} P dz dt$$
$$= (P_0/I_0) \int_{t_1}^{t_2} \int_0^h Chla \cdot I(t)\exp(-\varepsilon z) dz dt \qquad (12)$$

ここに，Pは光合成速度，P_0はクロロフィルa当たり，

光量が I_0 での光合成速度，$I(z, t)$ は水深 z，時間 t での光量，$I(t)$ は水面での光量，I_0 は基準光量，ε は光消散係数（式(11)での単位は $Chla$: $\mu g \cdot l^{-1}$, ε : m^{-1}），$Chla$ はクロロフィル a 濃度，t_1 と t_2 は測定開始と終了時間である。

生物現象による変化は光合成速度に呼吸速度が加味されているので，光合成量は水深ごとに生物現象変化に前夜の呼吸速度（後述）を足し，全水深で積分した。また，前節に示したように，午後になると成層の効果による誤差が入る可能性があるので，ここでは午前中の平均値を求めた。Fig. 9 から，8月には光量と光合成量の間に有意な相関があること，すなわち，式(12)の関係が大まかに成立しているので，光合成が光律速になっていると推測される。これに対して，その他の期間では同じ光量でも光合成量が少なく，(P_0/I_0) の部分が季節的に変化している。また，11月の測定期間中では両者に正の相関が見られないことから，光合成が光以外の要因で変化しているのではないかと推測される。

次に，夜間（18時〜4時）における生物現象による DO 減少速度から呼吸速度を推測し，それをクロロフィル a 濃度で除したものと水温との関係を見たのが Fig. 10 である。両者はかなり高い相関係数を有することがわかる。また，多くの文献で示されるように[13]，10℃ の上昇で 1.5〜2 倍の増加となっている。以上から，本論文で提案した手法を用いれば，湖内での全水深にわたる生物活動を定量化しうるといえる。

4．おわりに

浅い，富栄養化した水域において，水質測定センサーとその記憶装置を昇降装置に取り付けることから，以下のことを明らかにした。

1）水質の鉛直分布，時間変化を連続的に，精度よく観測可能である。

2）1）の結果に鉛直混合，大気拡散を表現するモデルを組み合わせて，水中の生物現象による変化を空間，時間的に連続して定量化することが可能である。

3）観測システムの設置にあたっては，生物現象の影響する深さに加えて，成層の深さにも注意しなければならない。

4）DO，DIC 両方の変化を同時に測定することからモニタリングの正確性を検証しうる。

5）光合成，呼吸などのモデル化に必要な資料を現場で測定可能である。

なお，今回の霞ヶ浦での観測では，昇降装置に問題が発生し，当初予定していた期間すべてでの測定が8月を除いて行えなかった。これは，今回作成した昇降システムの問題であり，その部分の改良を図れば，固定型システムと比べより精度が高く，情報量に富むデータの取得が可能と考えている。

謝　辞

システムを設置させて頂いた国土交通省霞ヶ浦工事事
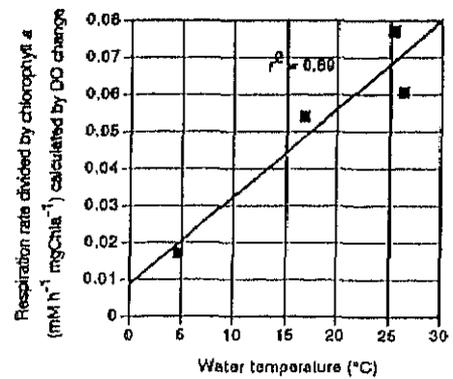
Fig. 10　Water temperature vs. respiration rate divided by chlorophyll a measured during night.

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水域における生物活性鉛直分布の測定システムの開発

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1．目的

地球温暖化、湖や池の富栄養化などの環境問題は、水域の生態系に重大な影響を及ぼすと考えられている。水域の生態系への影響を知るための一つの手段として、生物活性(呼吸量・光合成量)という指標がある。本研究では水質測定器(ゾンデ)を昇降させる装置を開発し、それを利用して実際の水域の生物活性を水深ごとに評価することを目的とする。

2．方法

初めに、DO、pH、水深、水温、クロロフィルaの測定セン
サーを有するゾンデ(YSI6600)を実験池の水深0.5mに固
定した連続測定を行った。次に同じ実験池において10分を1
サイクルとしてゾンデを昇降させて連続測定を行った(図1
上図参照)。最後に、霞ヶ浦において18分を1サイクルとし
た連続測定を行った(図1下図参照)。

図1　ゾンデの動きと測定時刻

この測定によって得られた水質の連続測定値から生物活性
を求めるためには次の式を用いた。

$$\left(\frac{dC}{dt}\right)_{biol} = \frac{dC}{dt} - \Delta E_X - \Delta Q \quad \cdots (1)$$

ここで、$(dC/dt)_{biol}$ は生物現象による変化(生物活性)、dC/dt は水域でのDO、DICの濃度変化、ΔE_X は大気との交換量、ΔQ は水の流入・流出に伴う変化量である。dC/dt は連続測定による濃度変化の差分から求まる。大気との交換量は次の方法によって計算した。

① ガス交換係数 k_L(cm/h)を求める。 $k_L = a\, EF\, Rv(Dm_{20})^{0.5}(U_{10})^{1.5}$ ・・・(2) ここでaは定数、Rvは20℃純水と現地水の動粘性係数の比、Dm_{20} はガスの20℃での分子拡散係数(cm^2/s)、U_{10} は地上10mでの風速(m/s)である。EFはガス交換量の増加倍率を表す。

② 大気との交換フラックス F($mmol \cdot cm \cdot l^{-1} \cdot h^{-1}$)を求める。 $F = k_L(C_{sat} - C_w)$ ・・・(3) ここで k_L はガス交換係数(cm/h)、C_{sat} は大気と平衡状態にある水中濃度(mmol/l)、C_w は水中濃度(mmol/l)である。

③ 各水深における大気との交換量 ΔE_X($mmol \cdot l^{-1} \cdot h^{-1}$)を決める。例えば水塊が鉛直方向に十分に混合していて、大気との交換の影響が全水深均一であるとすると、ΔE_X は次のように表現できる。

$\Delta E_X = F/h$ ・・・(4) ここでFは大気との交換フラックス($mmol \cdot cm \cdot l^{-1} \cdot h^{-1}$)、hは池の水深(cm)である。

3．結果

ゾンデを昇降させたときの実
験池と霞ヶ浦でのDOの測定結
果を示す(図2、3)。これらか
ら水深ごとに生物活性の評価を
行った(図4)。この際、大気と
の交換に関して、①全層均一に
交換する、②上層のみ交換する、
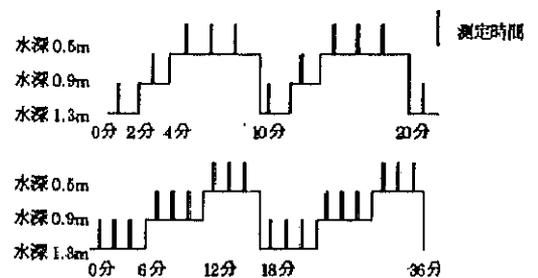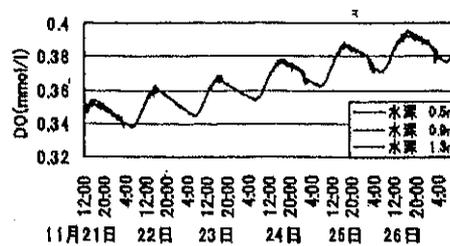
図2　実験池での連続測定結果
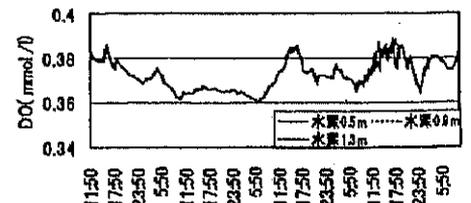
図3　霞ヶ浦での連続測定結果

という２つの仮定を考えた。次に、それぞれの仮定ごとに生物活性を求め、日射量と得られた光合成量との関係を比較した(図5、6)。なお、仮定②は池の水が混ざっていないという仮定であるため、鉛直方向の日射量の消散を考慮した。
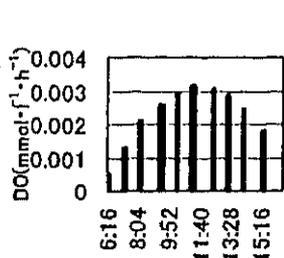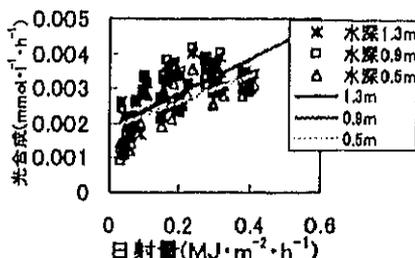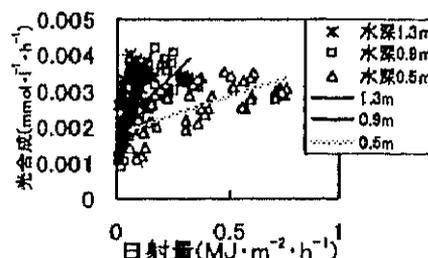
図4　霞ヶ浦1月9日の　　図5　全層均一交換を仮定した　　図6　上層のみ交換を仮定した
生物活性　水深0.5m　　　　　日射量と光合成量の関係　　　　　日射量と光合成量の関係

図5、6から全水深における日射量と光合成量の関係がほぼ同じ直線上に乗っているという理由で、全層均一に大気交換を行っているとする仮定を利用した。

４．システムに関する考察

　本研究は1台のゾンデを昇降させて測定を行うものであるが、複数のゾンデを多水深に固定させるというシステムも考えることができる。そこで、両システムの問題点について考察を行い、どちらが良いか検討した。

　1台を昇降させる場合は水の攪拌を考慮しなければならない。図7より測定値はゾンデが移動した直後のみ低く、その後はほぼ一定であることが分かる。すなわち、ゾンデ1台を昇降させる場合は、移動後2、3回目の測定値を使用すれば問題ないことが分かる。しかし、目的は差分を取ることであるので昇降後1回目の測定値を使用しても結果は変わらない。
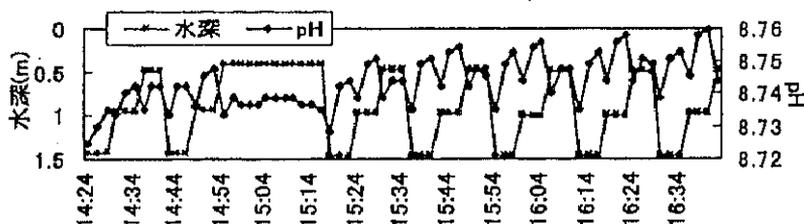
図7　ゾンデの測定水深とpHの関係

表1　測定パターンごとの誤差の大きさ

		1台のゾンデ	複数のゾンデ
DO	日変化	±0.557	±0.557
(μmol/l)	鉛直差	±0.296	5.0
pH	日変化	±0.0204	±0.0204
	鉛直差	±0.00263	0.2
クロロフィル	日変化	±0.305	±0.305
(μg/l)	鉛直差	±0.242	1.2

　複数のゾンデを固定させる場合には、鉛直方向の差分を取るときにゾンデの長期安定性が問題となる。そこで、ゾンデを同じ状態の水に長期間放置し、測定値にどれだけのずれが生じるか調べる実験を行い、ゾンデ1台を昇降させる場合と複数台を固定させる場合にどれだけ誤差が生じるか計算を行った。表1よりゾンデ1台を昇降させた方が正確に測定できることが分かる。これらの結果から鉛直方向を考慮した生物活性の評価を行うときは1台のゾンデを昇降させる測定の方が良いと考えられる。

５．結論

(1)実験池と霞ヶ浦でゾンデを昇降させた測定を行った結果、測定水深ごとに生物活性の評価を行うことができた。しかし、純粋な生物活性の評価をするには、ゾンデによる測定のみでは不十分であるため、別の測定方法との併用が必要である。

(2)鉛直方向の差分を求める場合には、1台のゾンデを昇降させて測定を行った時は、複数のゾンデを固定させて測定を行ったときに比べ、1/5から1/76ほど誤差が少なくすることができることを確認した。

湖沼における生物活性の測定と評価

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1. 研究の背景と目的

地球温暖化や湖沼における富栄養化が水域生物へ及ぼす影響を知ることは重要な課題である。そこで本研究では、湖沼の水質を測定し、水域の生物活性の評価を行うことを目的とした。

2. 水質測定方法

水深、水温、DO 濃度、pH、クロロフィルa 濃度、電気伝導度の測定センサーを有するゾンデ（YSI6600）を、霞ヶ浦湖心において鉛直方向に移動させ、約1週間の連続測定を4回行った。ゾンデを昇降装置に取り付けることで鉛直方向の移動を可能とした。測定水深は 3.94m、3.28m、2.62m、1.96m、1.30m、0.64m（順番に水深6、5、…、1）の6水深で、昇降は4分おきに行い各水深において2回ずつ測定（2分間隔）を行った。

3. 測定結果及び生物活動による濃度変化速度の算定

風速や日射量等の気象条件により、全層で水質がほぼ均一である結果（図1）と各水深によって水質の異なる結果（図2成層の形成）とが得られた。成層形成時には、水深の深い部分において日中でも DO 濃度が減少する結果（図2）も得られた。しかし、測定期間中においてはほとんどの場合気温低下時に全層が均一に混合した。

得られた測定結果から、生物活動のみによるDO 濃度及びDIC濃度変化速度をモデルにより算定した。従来は浅い水深（約 1.3m）までの測定しか行っていなかったため、水質が常に全層均一という仮定のもとで大気交換の影響を考慮してきた。しかし、本研究においては各水深によって水質が異なる結果も得られたため、拡散も考慮に入れた算定方法の考案が必要となった。そこで、移流拡散方程式（水平方向の濃度は一定等の仮定を考慮）を用いて、拡散の影響を算定した（式 (1)）。

$$\frac{\partial C}{\partial t} = \frac{\partial}{\partial z}\left(K_z \frac{\partial C}{\partial z}\right) + F_{biol} \qquad \cdots (1)$$

ここで、($\partial C/\partial t$) は測定濃度変化速度、K_zは鉛直拡散係数(水深間の密度差及び風速等から算定)、($\partial C/\partial z$) は測定鉛直濃度差、F_{biol}は生物活動に
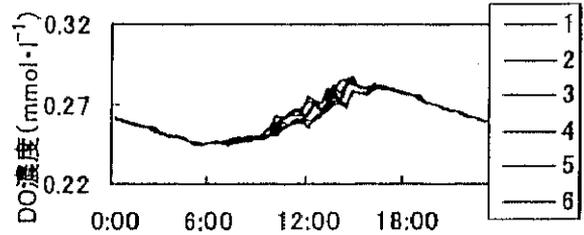
図1　水深別 DO 濃度変化（8/30 風速大、日射弱）
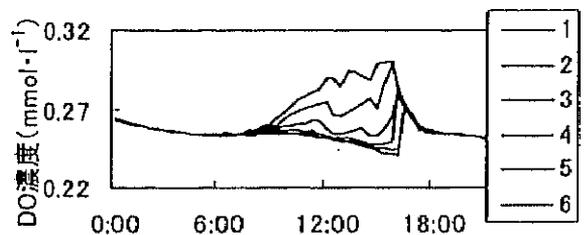
図2　水深別 DO 濃度変化（11/4 風速小、日射強）
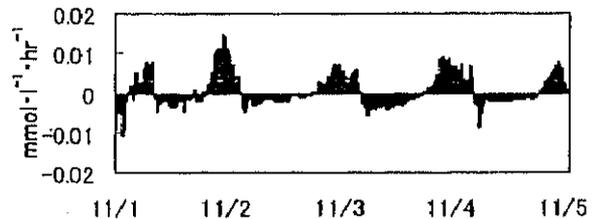
図3　水深1の生物活動による DO 濃度変化速度
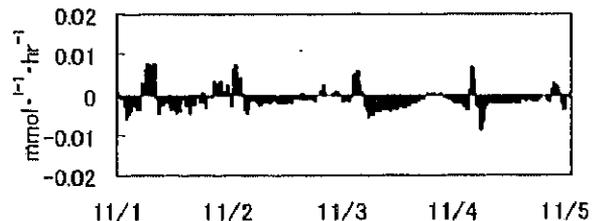
図4　水深6の生物活動による DO 濃度変化速度

よる濃度変化速度である。また、水質が全層で均一と仮定した場合（大気交換のみ考慮）の生物活動による濃度変化速度を算定する式を以下に示す。

$$\frac{\partial C}{\partial t} = \Delta E_x + F_{biol} \qquad \cdots (2)$$

ここで、ΔE_xは大気との交換速度である。生物活動による濃度変化速度の算定の際、式 (1) を用いる方法をモデル1、式 (2) を用いる方法をモデル2とした。本研究では、成層形成時にはモデル1を、全層均一時にはモデル2を用いる算定方法

をモデル3として提案し生物活動による濃度変化速度を算定した。モデルを用いて算定した生物活動による濃度変化速度を図3、4に示す（11月の水深1と水深6）。日中におけるDO濃度変化速度は水深6と比較し、水深1の方が大きく水深の浅い方が光合成活動が活発である。

4．考察

4-1．呼吸速度及び光合成速度

生物活動によるDO濃度変化速度より呼吸速度及び光合成速度を求めた。水温と呼吸速度には強い相関があることが示された（図5）。また、8月においては日射量と光合成速度に強い相関がみられたが、その他の時期では日射量に関わらず光合成速度はほぼ一定となった（図6）。
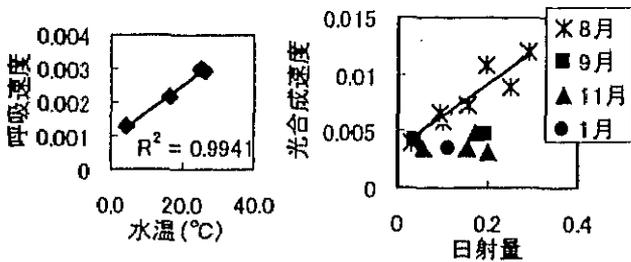
図5 水温と呼吸速度　　　図6 日射量（MJ・m^{-2}・hr^{-1}）と
（mmol・l^{-1}・hr^{-1}）　　　光合成速度（mmol・l^{-1}・hr^{-1}）

4-2．MQ

生物活動による濃度変化速度よりMQ（DO濃度変化とDIC濃度変化の比）を求めた。多少の差はあるものの全ての測定においてMQは昼夜共に約1であり、霞ヶ浦における光合成の窒素源が主にNH$_4$-Nであったこと、夜間の呼吸・分解時においては好気性の割合が高かったことが分かった。さらに、本研究における水質測定の精度及び、生物活動による濃度変化速度の算定方法の信頼性の高さが示されたと考えている。

4-3．霞ヶ浦の現状及び予想される危険性

求めた呼吸速度及び光合成速度より、水域のDO濃度変化の予測を行える。n日後のDO濃度は以下の式で計算できる。

DO(n)＝DO(0)＋(P×S－R×24)×n×32・・・(3)
ここに、DO(n)はn日後のDO濃度（mg・l^{-1}）、Pは光合成速度、Rは呼吸速度（共にmmol・l^{-1}・hr^{-1}）、Sは日照時間（hr）である。

水域におけるDO濃度は4mg・l^{-1}程度まで減少すると水域生物に生理的な異常が表れると言われている。呼吸速度、光合成速度の結果及び日照時間から求めた各測定における1日のDO濃度の平均増減を表1に示す。表1より、DO濃度の平均増減は時期によって大きく異なることが分かる。このことや鉛直測定の結果より、霞ヶ浦は現在の生物活性状態を維持できればDO濃度の減少による水域生物への影響はないと考えられる。しかし、これは夜間に必ず全層で水質が均一になるためであり、もし、成層状態が夜間も続けば貧酸素水塊の発生が予想される。

表1 各測定時における1日のDO濃度の平均増減

	8月	9月	11月	1月
平均光合成速度(mmol・l^{-1}・hr^{-1})	0.0079	0.0045	0.0038	0.0035
平均呼吸速度(mmol・l^{-1}・hr^{-1})	0.0030	0.0030	0.0022	0.0013
平均日照時間(hr)	13	13	11	11
DO濃度の平均増減(mmol・l^{-1}・day^{-1})	0.0324	-0.0134	-0.0105	0.0073
DO濃度の平均増減(mg・l^{-1}・day^{-1})	1.04	-0.43	-0.34	0.23

そこで、混合のない日が数日間続いた場合、霞ヶ浦下層のDO濃度がどのように変化するかシミュレートした。式（3）に、夏の飽和DO濃度である8（mg・l^{-1}）と8月の呼吸速度と8月の平均日照時間13（hr）を代入した結果のDO濃度変化を図7に示す。2日後には4（mg・l^{-1}）を下回り、さらに貧酸素水塊が発生すると予想される。
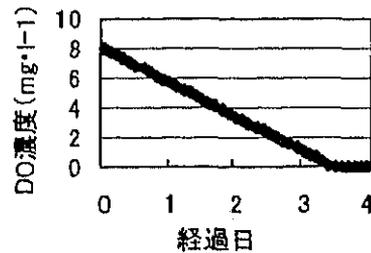
図7 混合のない日が続いた場合の霞ヶ浦下層におけるDO濃度変化

5．結論

①霞ヶ浦の多水深における連続的な水質変化を知ることができた。

②モデルを用いて生物活動による濃度変化速度の算定がほぼ行えた。

③水温と呼吸速度の間に強い相関が示された。

④霞ヶ浦において混合のない日が続くと、数日後にも下層で貧酸素水塊が発生する危険性があることを示した。

B. 箱方式による水域生物活性連続測定システムの試作と運転

B. 箱方式による水域生物活性連続測定システムの試作と運転

1. 箱方式の開発の目的

　海域，観潮域など水の入れ替わりに激しい水域においては，フリーウォーター法ではその地点での生物活性以外に水の移動に伴う変化もあわせて計測してしまう．このため，生物活性の測定という観点では誤差が大きい．そこで，プラスチック製の箱中に水質センサーを取り付け，定期的に中の水が入れ替わる仕組みを作り，また底面にスターラーを配置しセンサーをゆるやかに撹拌しうるシステムを試作した．その設計図面を示す．

2. 屋外実験池での試運転

　このシステムを独立行政法人国立環境研究所臨湖実験施設の屋外実験池に設置して（写真参照），その動作確認を行うとともに，約1週間にわたり生物活性を連続測定した．得られた結果をまとめると以下のようである．

(1) 10分に1回，箱の開口部が開き，外部の水を引き込み，またその水塊のDO, pH等を2分に1回測定する方式で運転した．システムは指定通りの動作を行った．また，プラスチック壁に付着性藻類が付くような現象は生じなかった．実験結果の一部を図で示すが，システム内でのDOは外部のDOとほぼ同じように変化しているものの，詳しく見るとその変化率は池内での変化率（取り込んだ水のDO変化で推測される変化率）と異なる．すなわち，システムに取り入れた水塊のDO変化率を測定可能である．

(2) 期間中，停電でスターラーが停止した期間が存在したが，その場合には乱れた変化を示した．センサーの特性などから，システム内での撹拌が重要であることがわかった．

(3) DOが12 mg/lを超える場合は過飽和のDOがバブル化する場合があり，測定値の振動が激しくなる．すなわち，このような過飽和の状態ではこのシステムの使用が適切ではないといえる．

光合成測定装置　ウインチ部計画

700(ウインチワイヤー中)

650

571

360

150(角形状範囲)

120

5

105

15

sensor ares

スターラー

スターラーはケースから
取り出して使用を想定

吊り下げ用
バンド

エアーシリンダー まて300

バラスト

300

600(丸形状範囲)

860

120
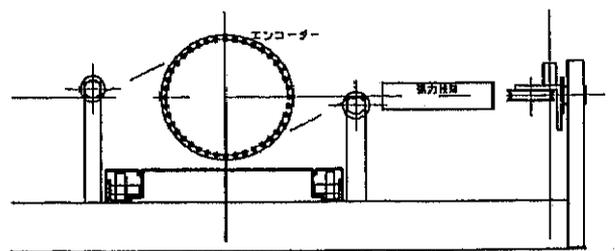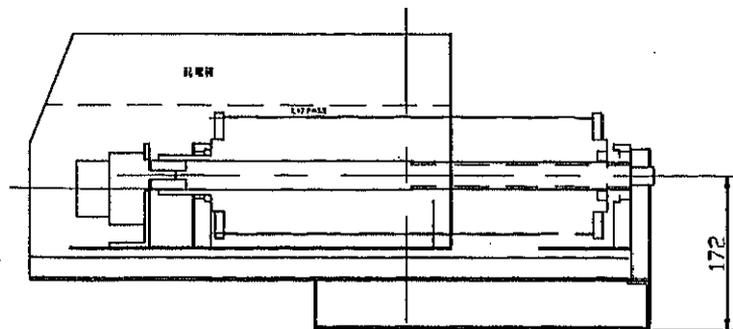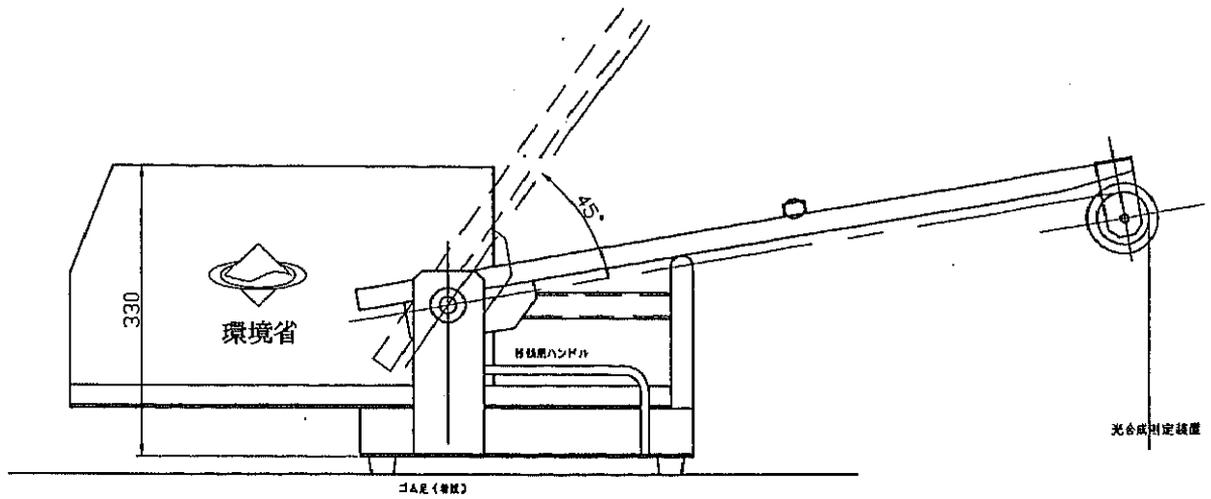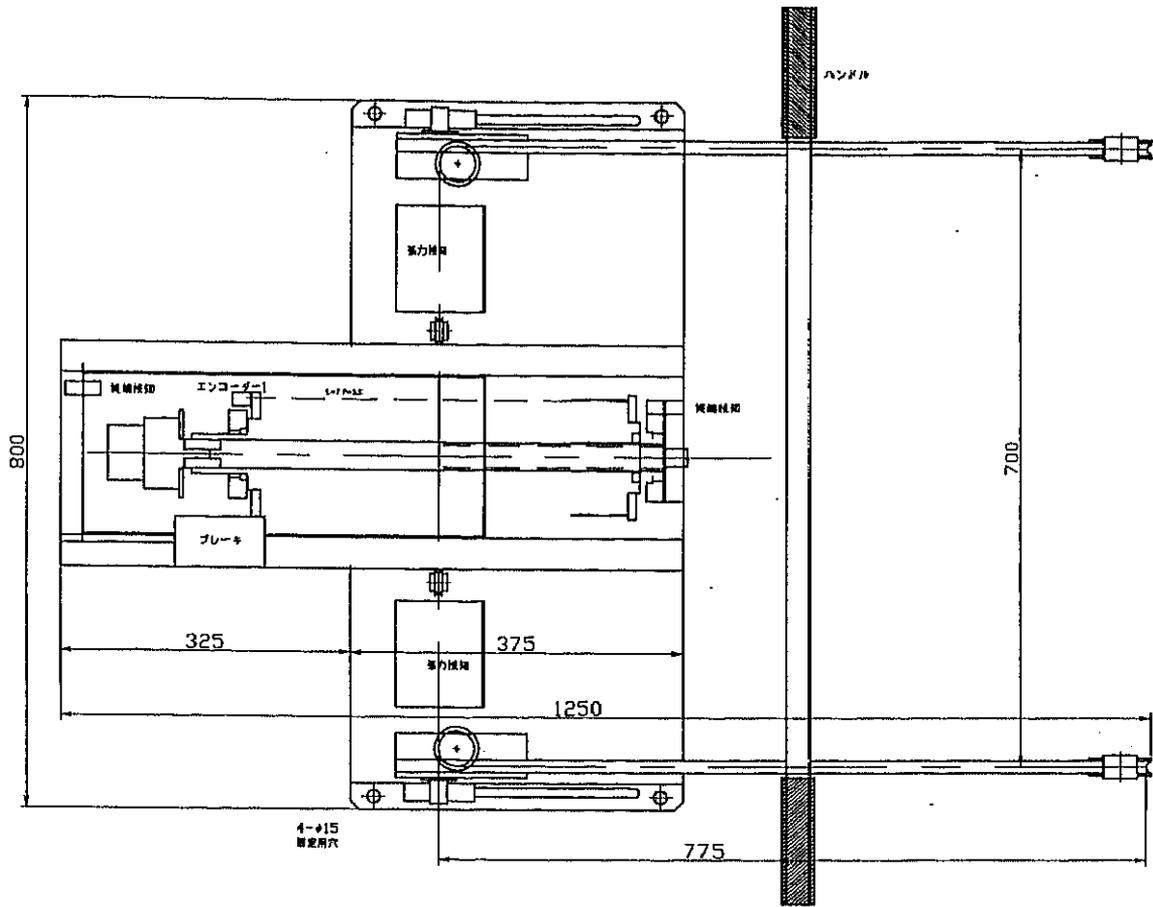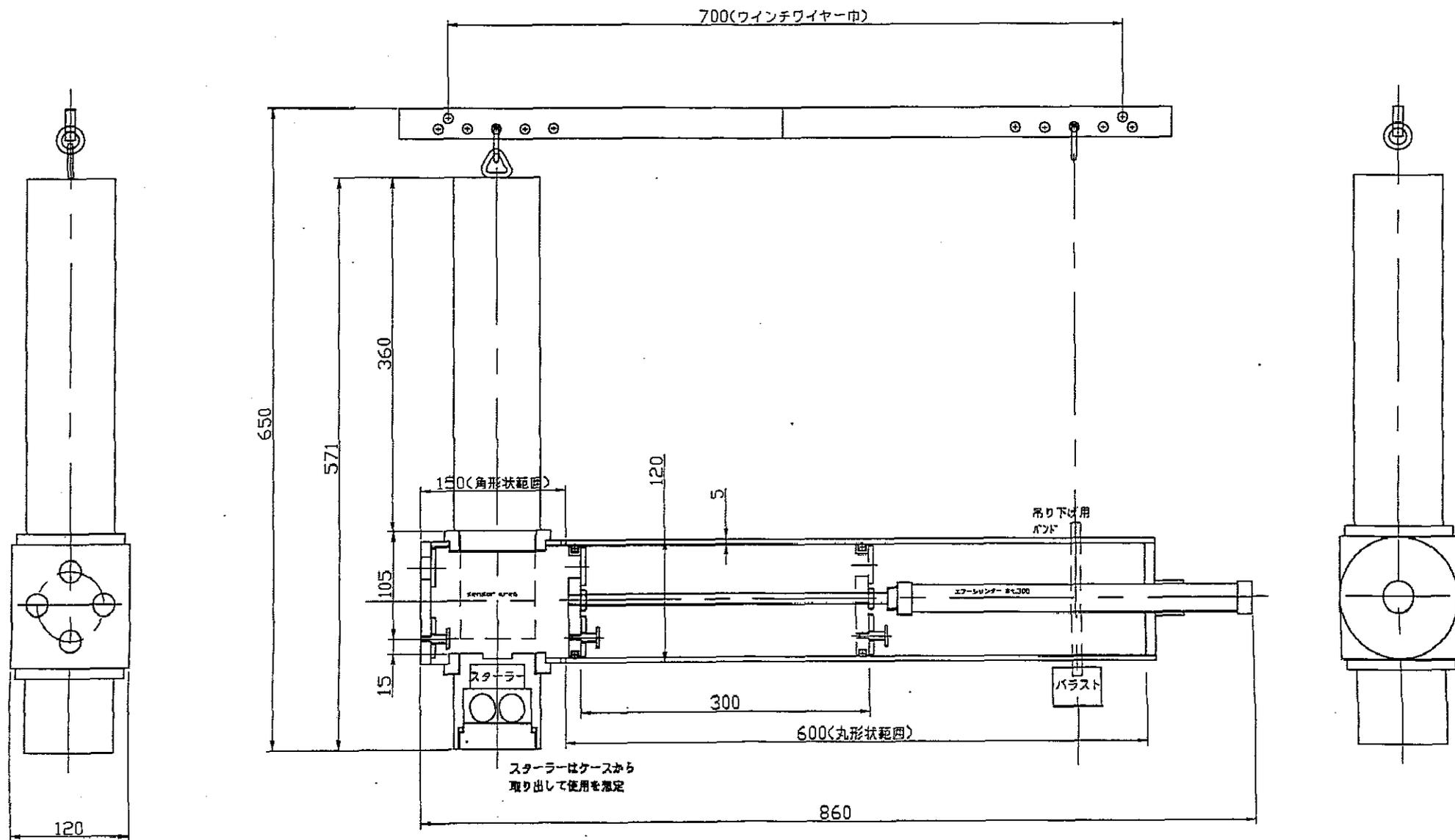
光合成測定装置　測定部計画

写真 B-1. 箱方式の生物活性連続測定装置
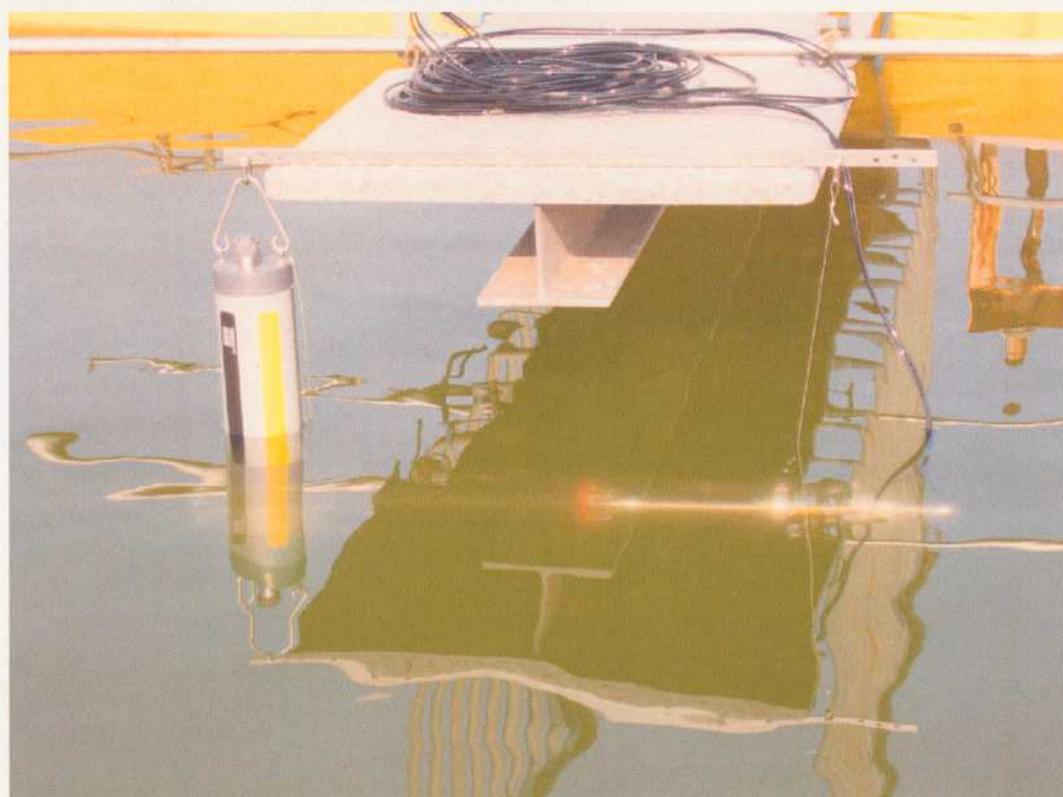
写真 B-2. 屋外実験池に箱方式の生物活性連続測定装置を取り付けた様子

屋外実験池におけるDO変化の様子
2003.3.8-9：10分ごとに水を入れ替え，2分ごとに測定
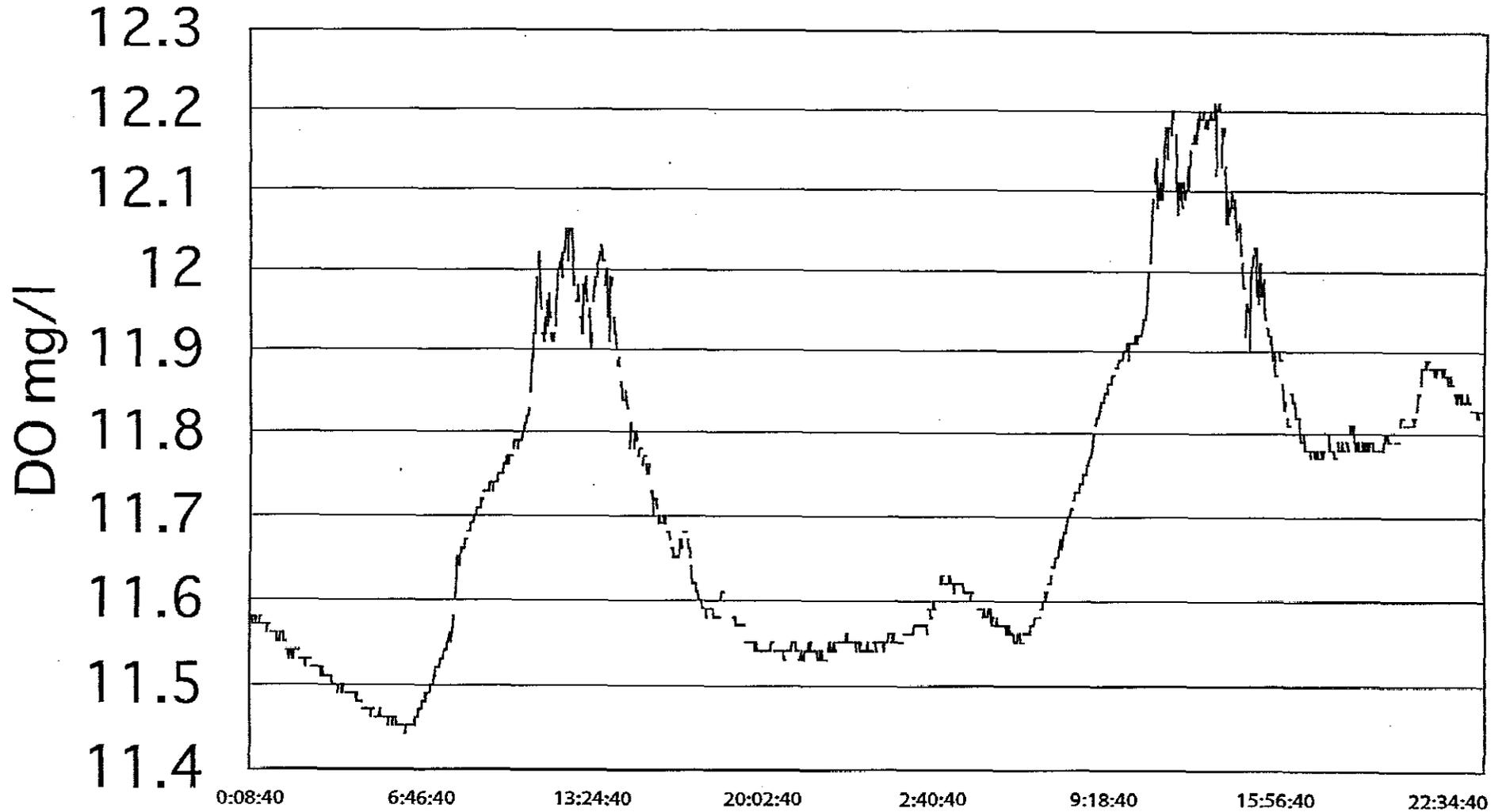
C. ダム湖における水質連続観測データの解析

C. 島地川ダムでの連続測定
1. ダム湖の概要
　　島地川ダム（山口県南陽市）は佐波川水系上流に位置する多目的ダム（洪水調節，都市用水供給，河川環境保全）である．その諸元は下記に示すとおりである．なお，このダムは 1981 年 3 月に完成したが，1990 年代に入り夏期に植物プランクトンが異常発生するようになった．特に，1999 年以降，アオコが発生し，水質悪化が問題となっている．

堤高	89 m
集水面積	32.0 km²
湛水面積	0.80 km²
総貯水量	20.6 x 106 m³
有効貯水量	19.6 x 106 m³
常時満水位	EL. 286.5 m

2. 観測方法
2.1 観測期間
第 1 回 ; 2002. 6.11 16:00 – 6.20 14:00
第 2 回 ; 2002. 8.10 12:00 – 8.19 9:00
第 3 回 ; 2002.10.25 9:00 – 11. 7 9:00
第 4 回 ; 2003. 1.31 18:00 – 2.12 12:00

2.2 観測場所と層数，層間の移動
ダム堤体わき．貯水池水深 1m ピッチと 0.5m の 21 層．
　（なお，毎 9 時には，上記に加えて最下層（約 42m）まで 1m ピッチで測定）
なお，各層では 2 分止まり，計測後，次の水深に移動．

2.3 観測回数
0, 2, 4, 6, 8, 9, 12, 14, 16, 18, 20, 22 時の 12 回／日とした．

2.4 観測項目と測定方式，単位

水温：白金測温抵抗方式，℃

濁度：積分球式，mg/l

電気伝導度：電磁誘導式，mS/m

DO：隔膜電極法，mg/l

pH：ガラス電極法

クロロフィルa：蛍光光度法，μg/l

2.5 ダム諸量

(1) 放流水深

第1回；水深 2.5 – 4 m

第2回；水深 2.5 – 4 m

第3回；水深 2 – 3.5 m

第4回；水深 2 – 3.5 m

(2) 降水量

第1回；(6/11: 13.0 mm), 6/14: 1 mm, (6/20: 25 mm)

第2回；(8/10: 8.0 mm), 8/11: 14.0 mm, 8/12: 11.5 mm, 8/14: 1.0 mm,

第3回；10/26: 4.5 mm, 10/28: 0.5 mm, 10/31: 6.5 mm, 11/1: 9.0 mm, 11/3: 2.0 mm

第4回；2/5: 5.0 mm, 2/8: 28.0 mm, 2/11: 1 mm

2.6 測定結果

図(1-1-1)～(1-4-6)：4回の調査での水温，濁度，電気伝導度，DO，pH，クロロフィルaの時間，鉛直分布図

図(2-1-1)～(2-4-4)：4回の調査での水温，DO，pH，クロロフィルaの（18:00の値）マイナス（6:00の値）

図(3)：DO，pHの（18:00の値）マイナス（6:00の値）の関係

図(4-1)～(4-2)：第1，2回測定時の表層 0-4m 層平均の DO，pH の時間変化

2.7 得られた結果のまとめ

1) 鉛直成層が時間的に変化している様子がはっきりと観察された（図(1)）．特に時間経過とともにかなり一定速度で変化するのが EC であり，増加（第 1, 3 回），あるいは減少（第 4 回）するケースがあった．

2) 水温，DO，pH ではかなりはっきりとした日周変化がみられる．図(4-1), (4-2)に示されるように，DO，pH では 18-24 時あたりにピークを有している．18 時のピークは光合成活動の影響と考えられるが，24 時のピークはより生物活動が活発な上流域での水質変化がダム放流水に乗ってダム堤体近くのこの場所にやってきたものと考えられる．

3) 図(2)から明らかなように，水温，DO，pH といった水質項目では，日間変動が大きいのは表層の約 5m 水深までである．一般的には 6:00 – 18:00 の期間でそれらは増加するが，減少する日も存在した．そうした日では水温も減少していることも多く，天気が悪かったことが原因しているのではないかと考えている．

4) 6:00 – 18:00 差の鉛直積分値を DO と pH で比較したのが図(3)であるが，強くはないが正の相関関係がみられる．しかし，期間によって，その勾配は異なっている．これはアルカリ度があまり変化していないのに，表層の pH が大きく変化しているので（第 1 回：7 前後，第 2 回：9 前後，第 3, 4 回：6.5 前後），pH 当たりの DIC（溶存無機炭素）変化量がそれぞれの回で大きく異なることが原因している．

5) このため，アルカリ度を用いて DIC 濃度を予測し，6:00 – 18:00 差をとったが，下層の pH が低く，その微妙な差により生じる DIC 濃度差が大きく計算された．すなわち，こうした水域では pH 変化をもとに生物活性を推測するのが難しいといえる．

写真 C-1. 島地川ダム湖

写真 C-2. ダムの概要

写真 C-3. 観測機器取り付け用ウィンチ

写真 C-4. ウィンチ巻き取り装置

(1-1-1) 2002. 6 Water temperature
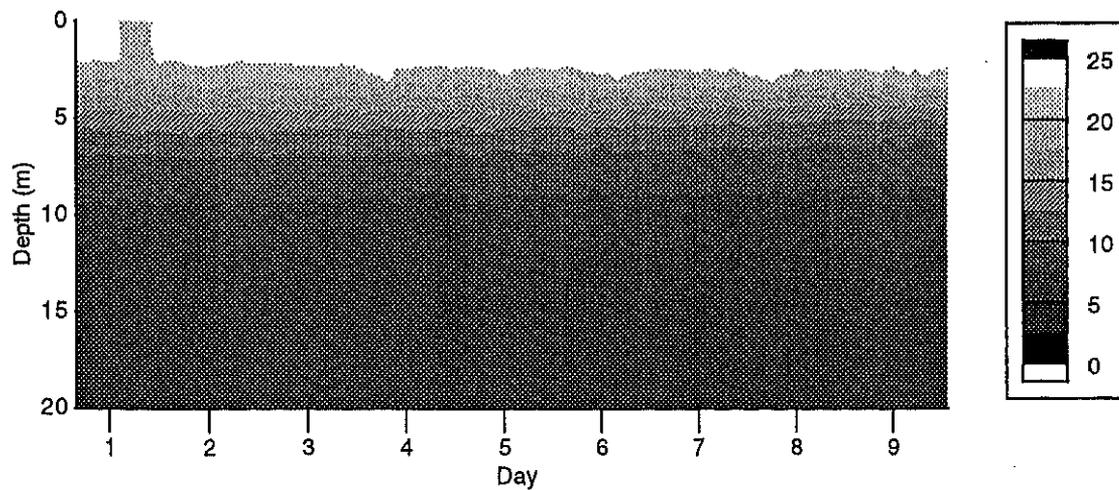
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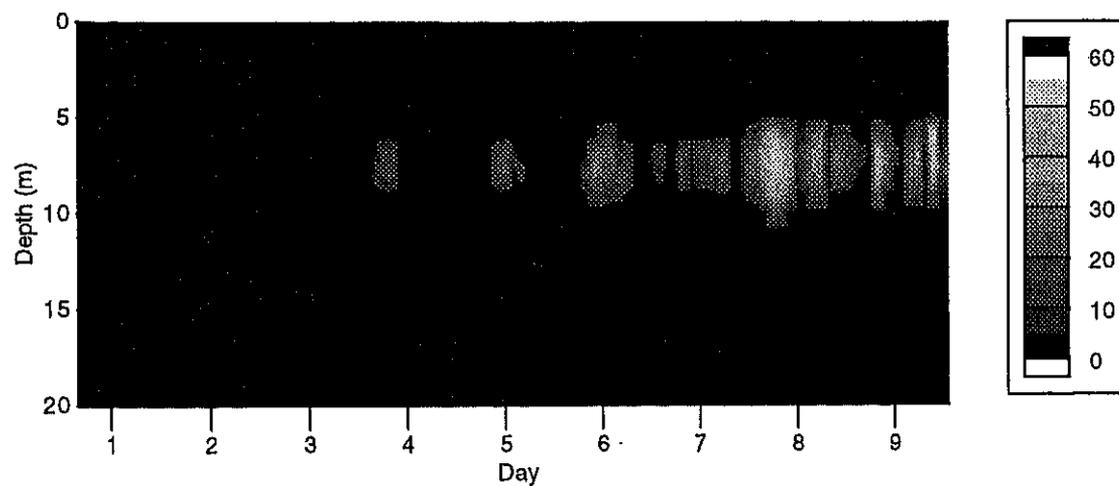
(1-1-3) 2002. 6 EC
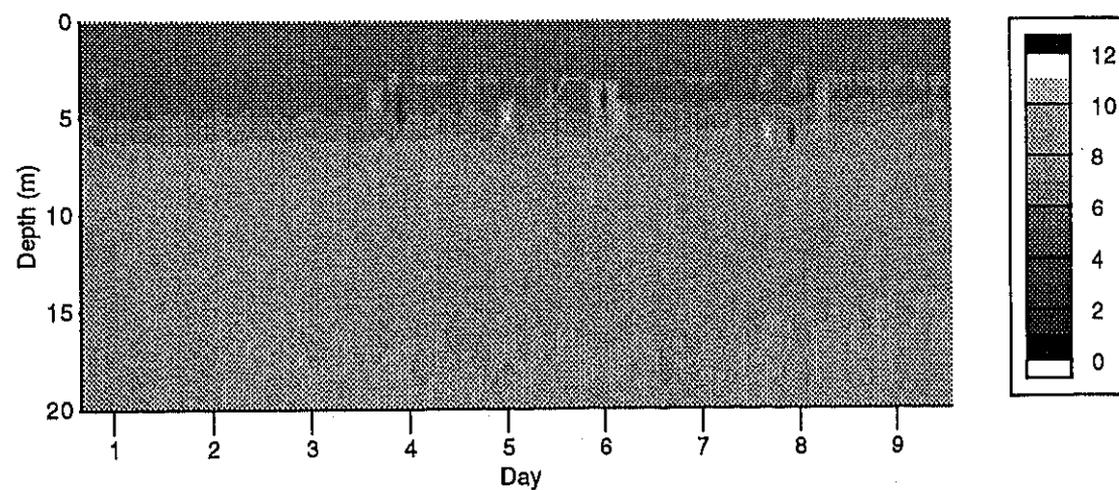
(1-1-4) 2002. 6 DO
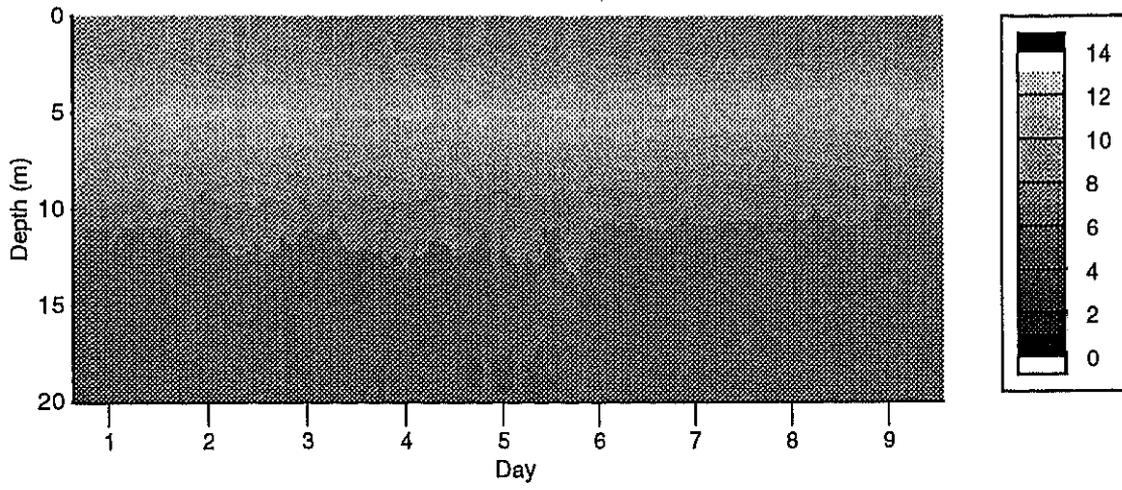
(1-1-5) 2002. 6 pH
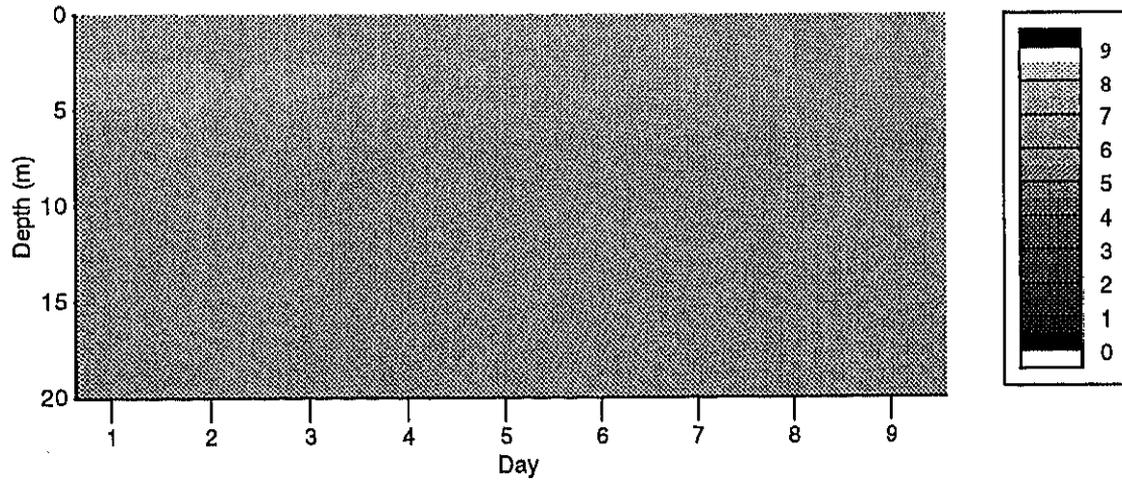
(1-1-6) 2002. 6 Chlorophyll-a
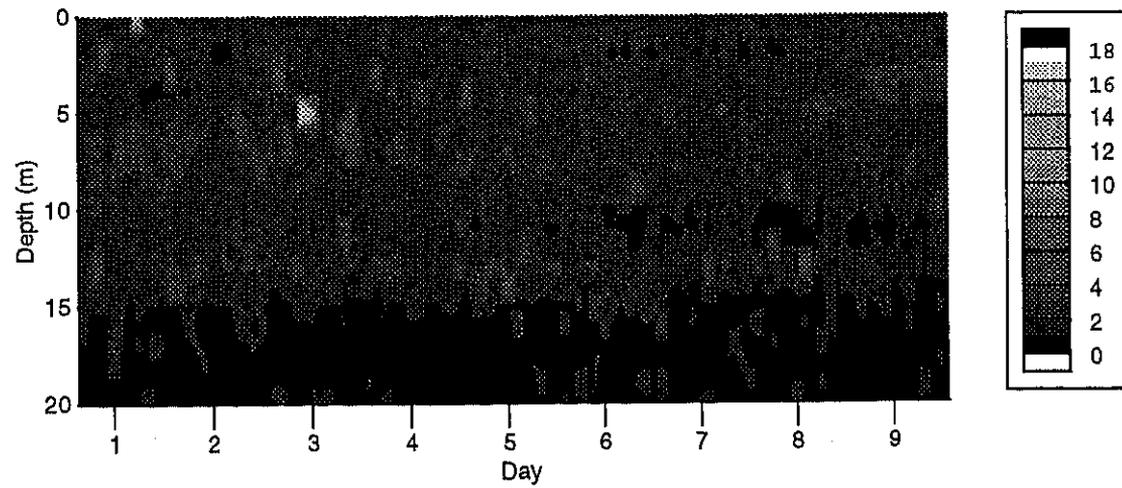
(1-2-1) 2002. 8 Water temperature
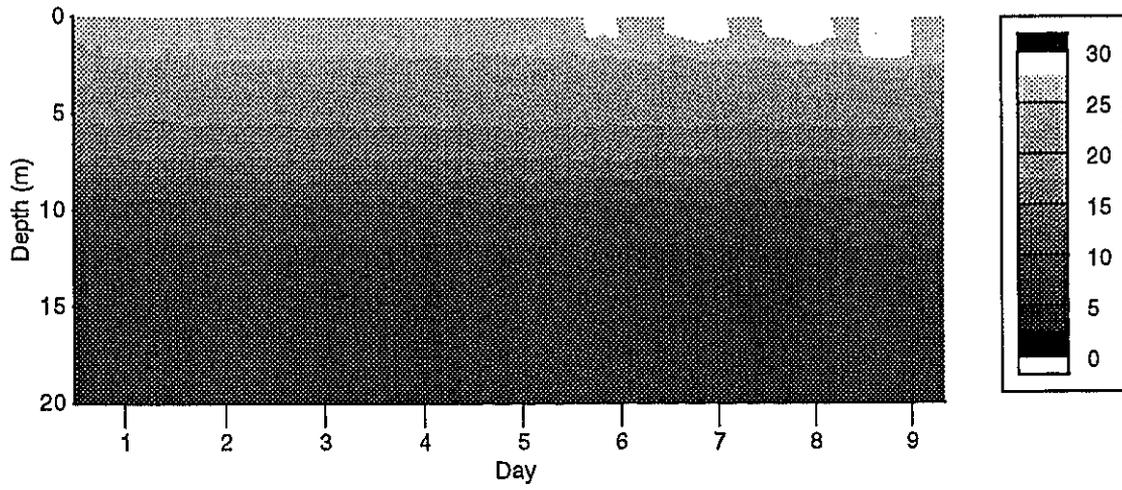
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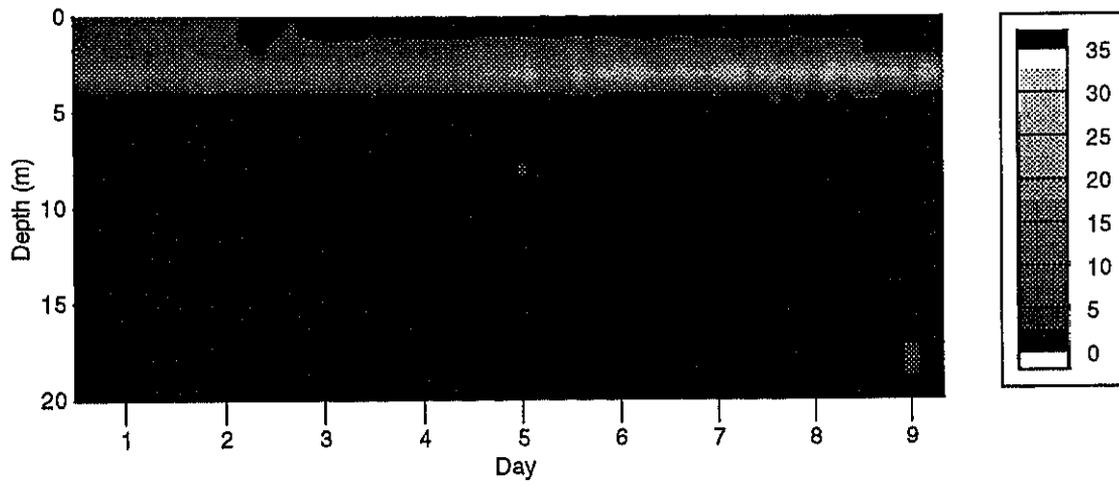
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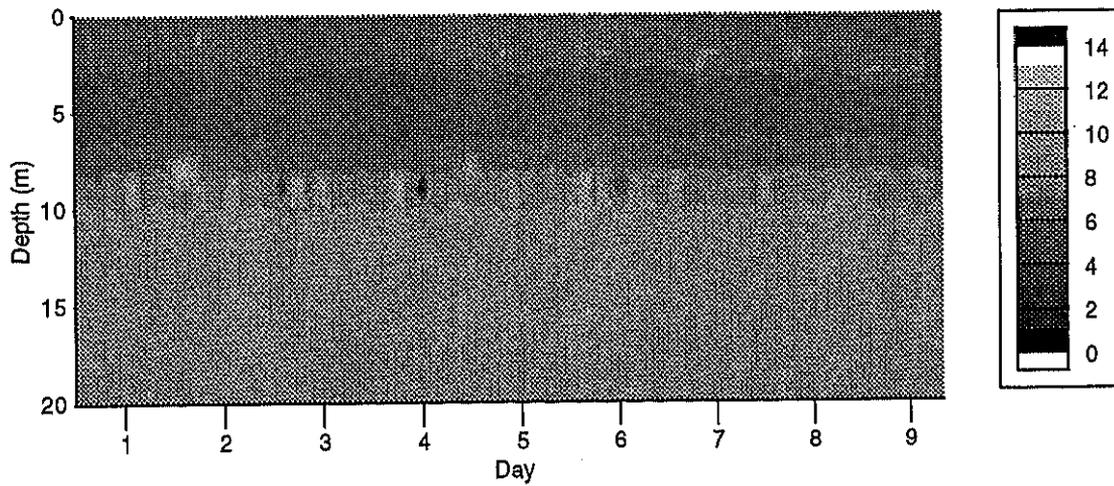
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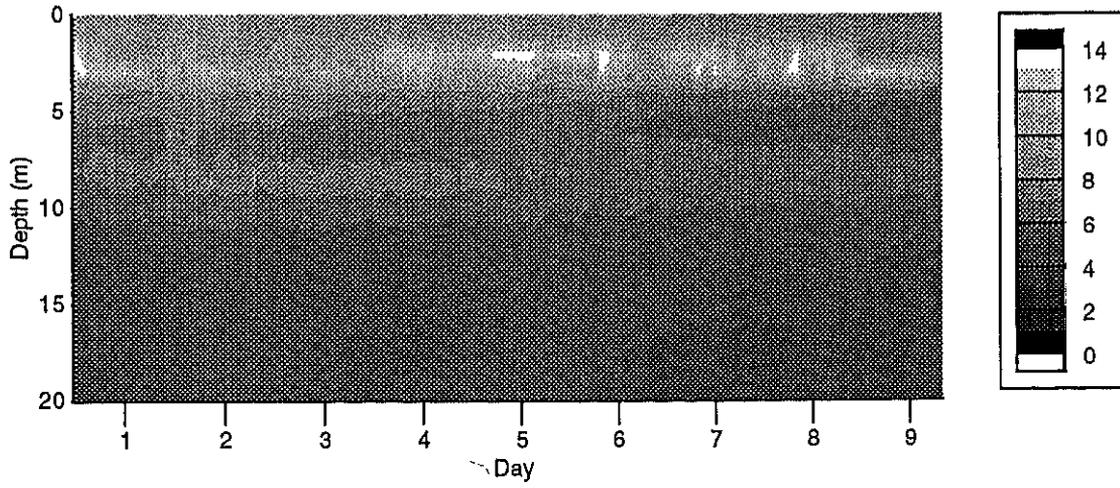
(1-2-5) 2002. 8 pH
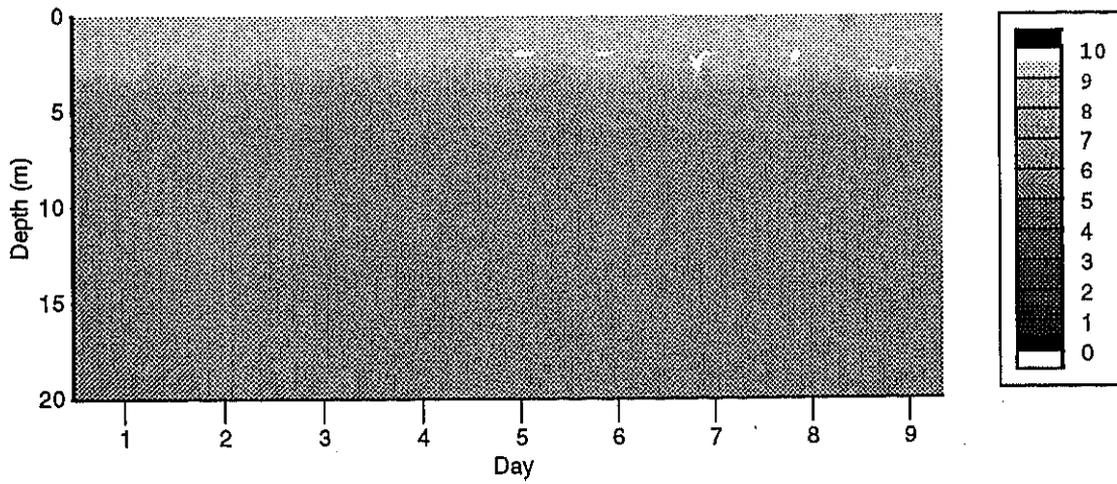
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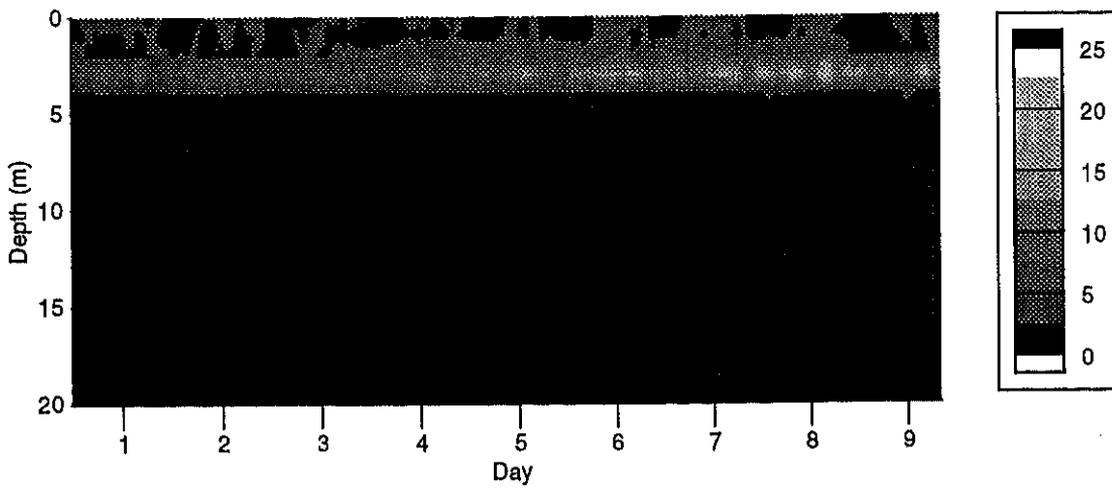
(1-3-1) 2002.10-11 Water temperature
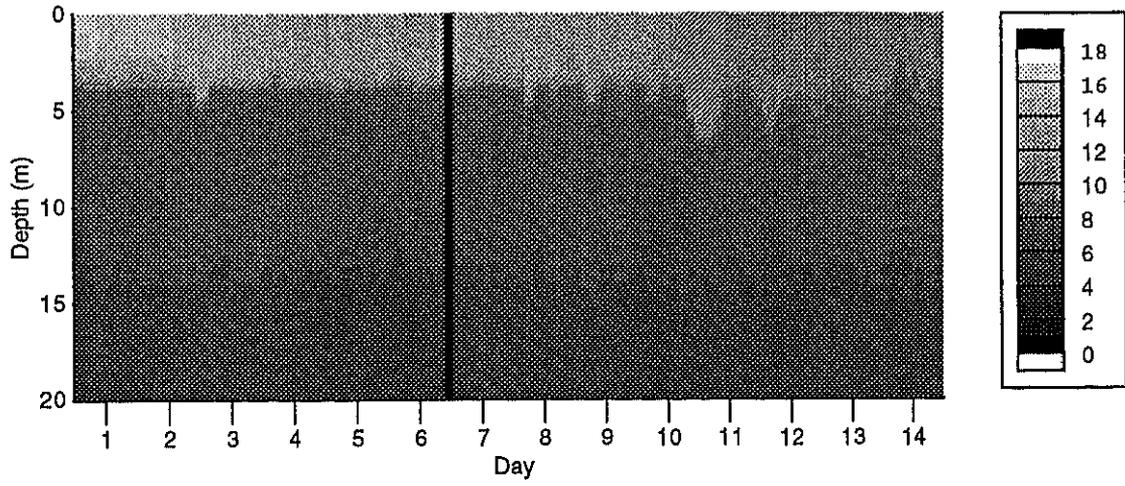
(1-3-2) 2002.10-11 Turbidity
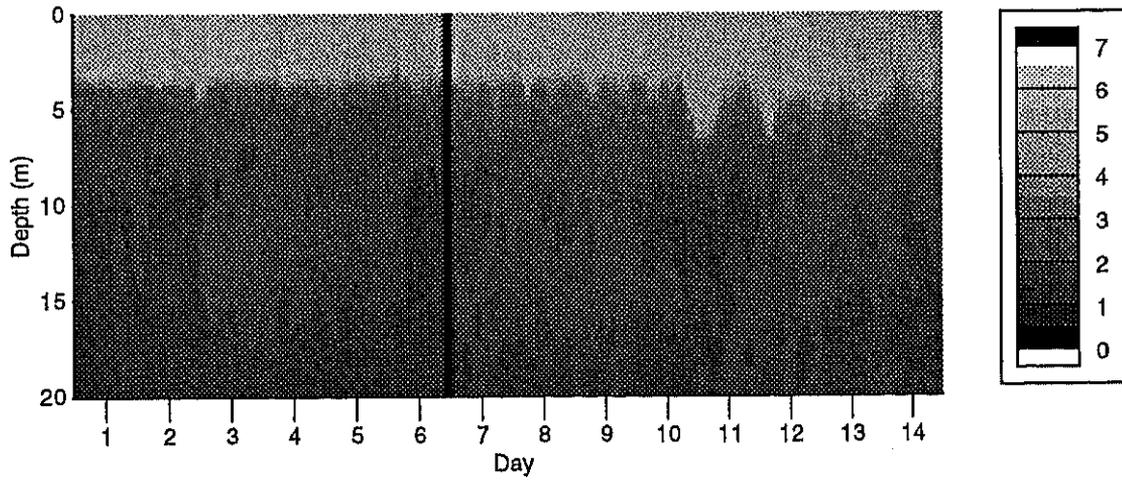
(1-3-3) 2002.10-11 EC
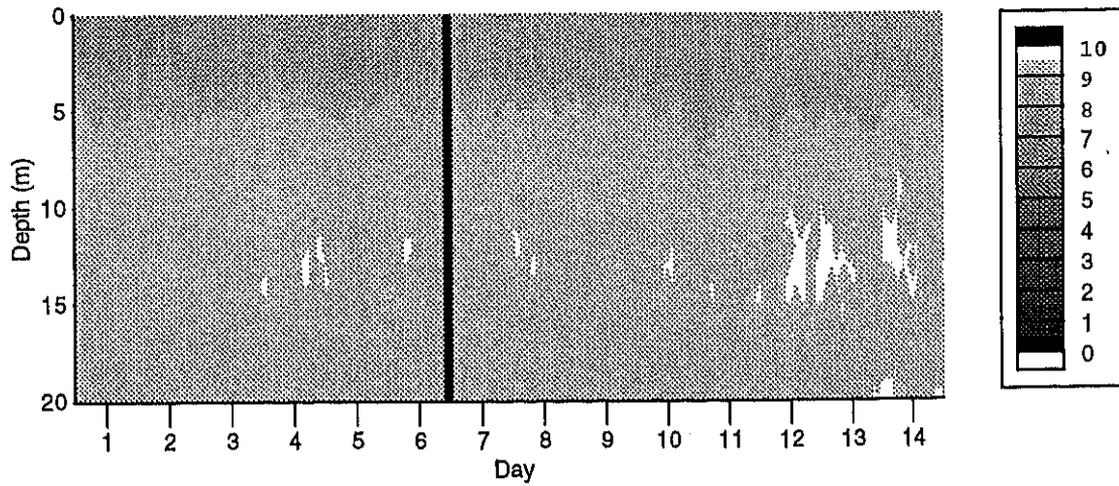
(1-3-4) 2002.10-11 DO
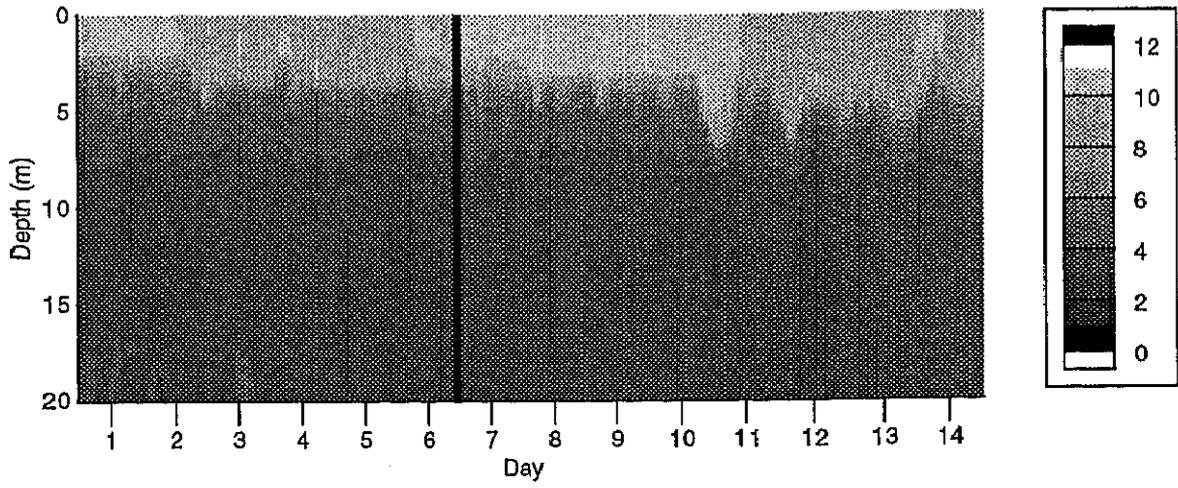
(1-3-5) 2002.10-11 pH
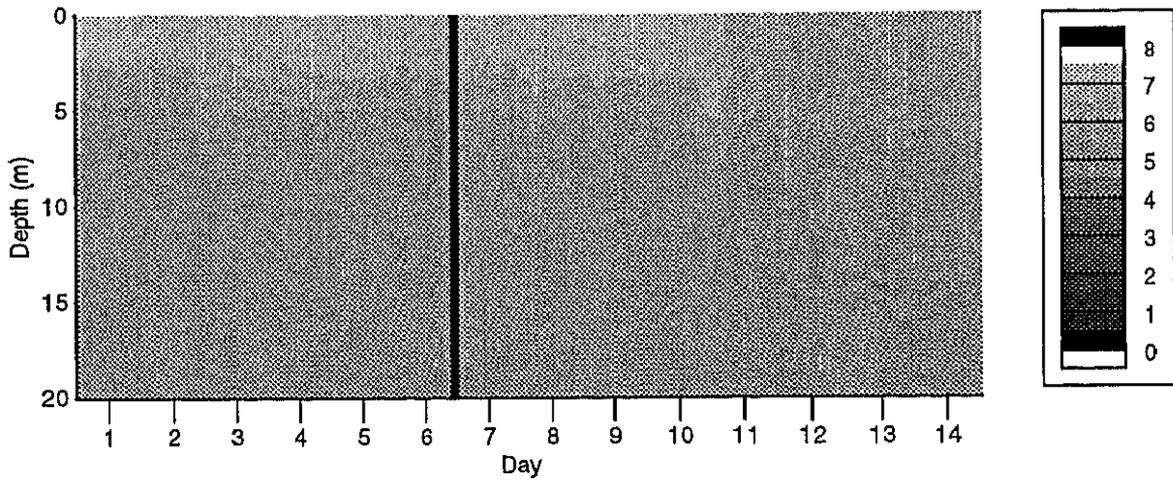
(1-3-6) 2002.10-11 Chlorophyll-a
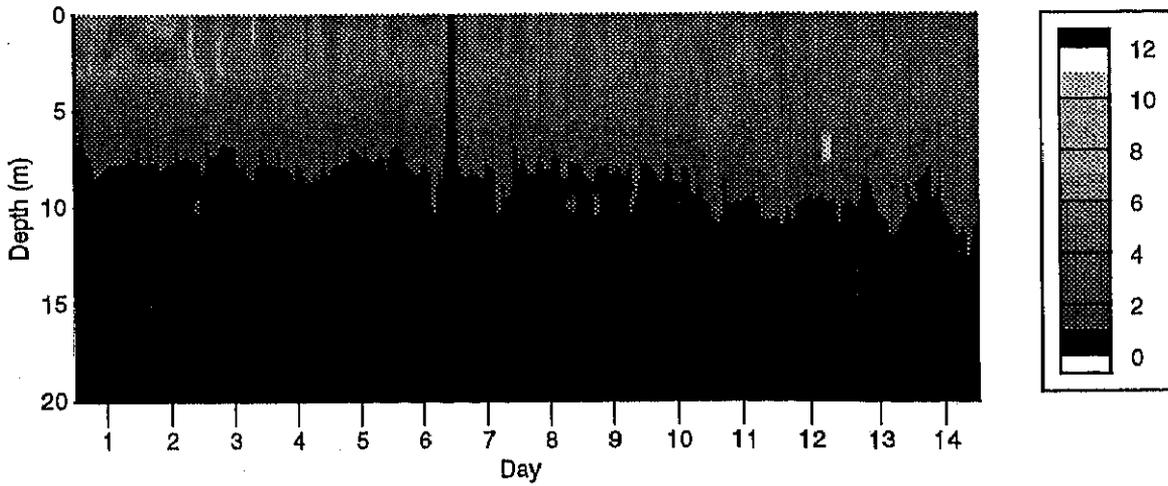
(1-4-1) 2003.1-2 Water temperature
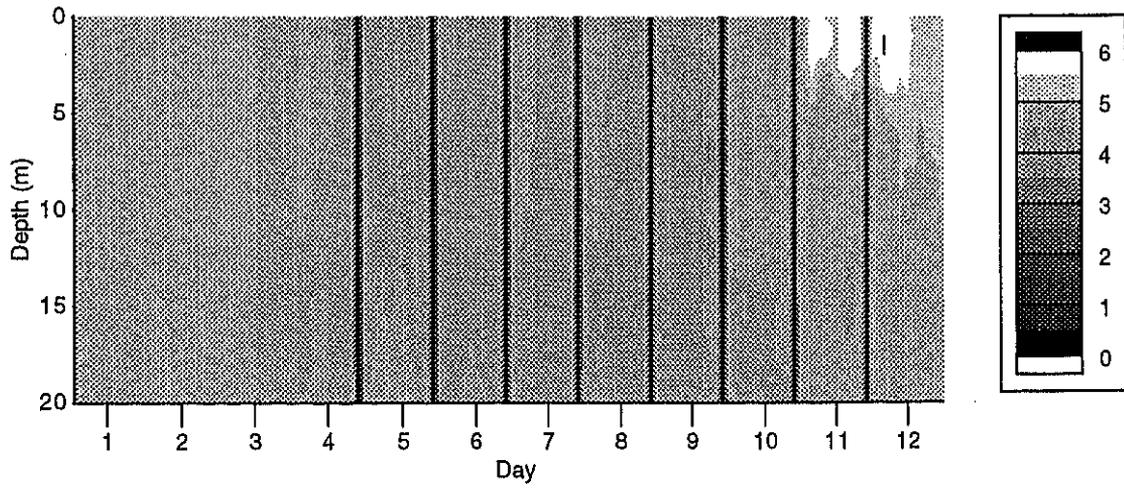
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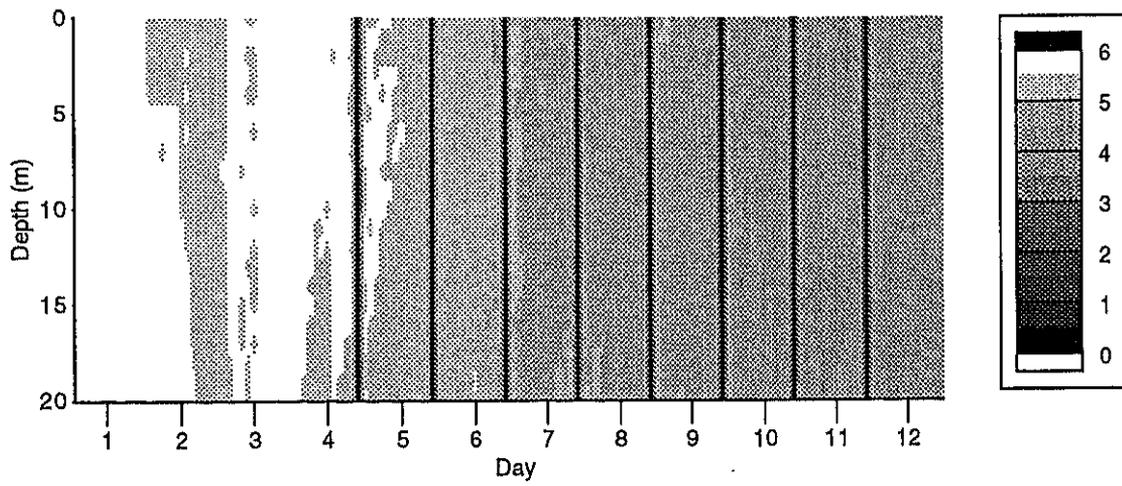
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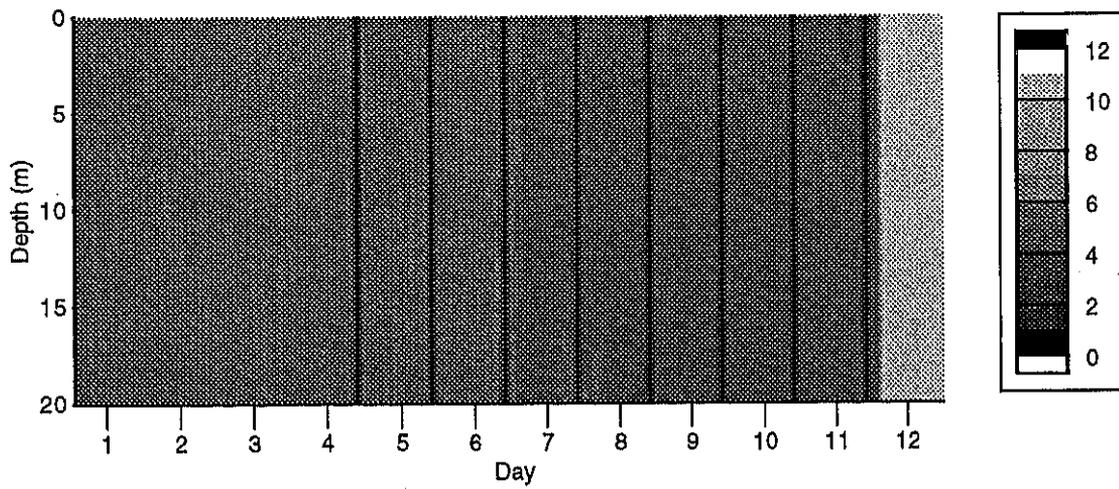
(1-4-4) 2003.1-2 DO
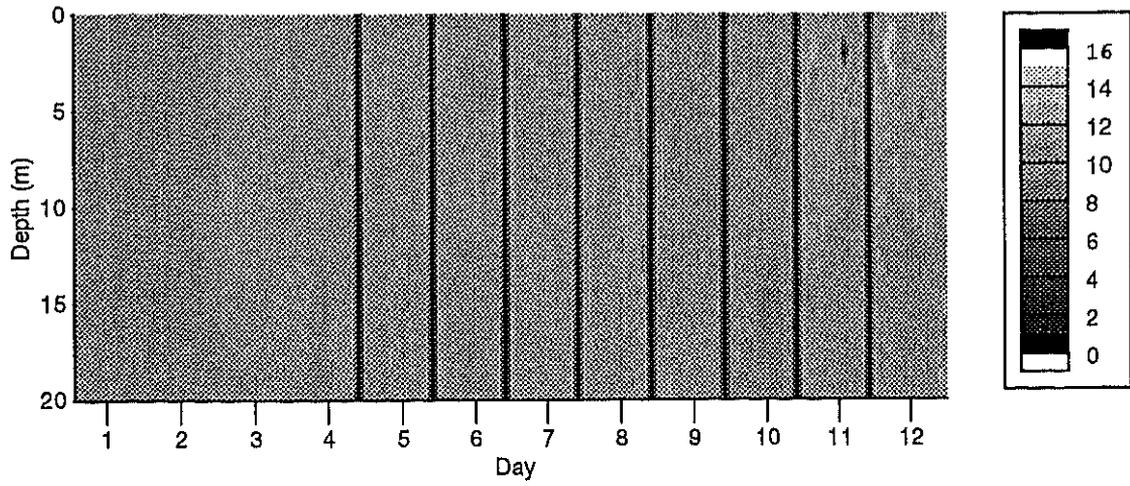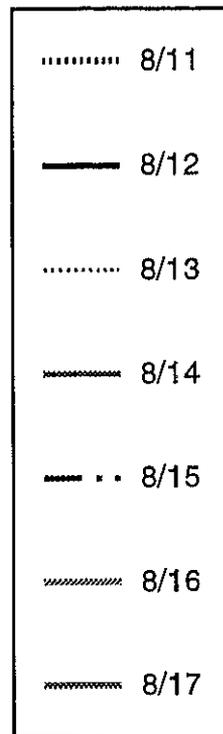

(1-4-5) 2003.1-2 pH
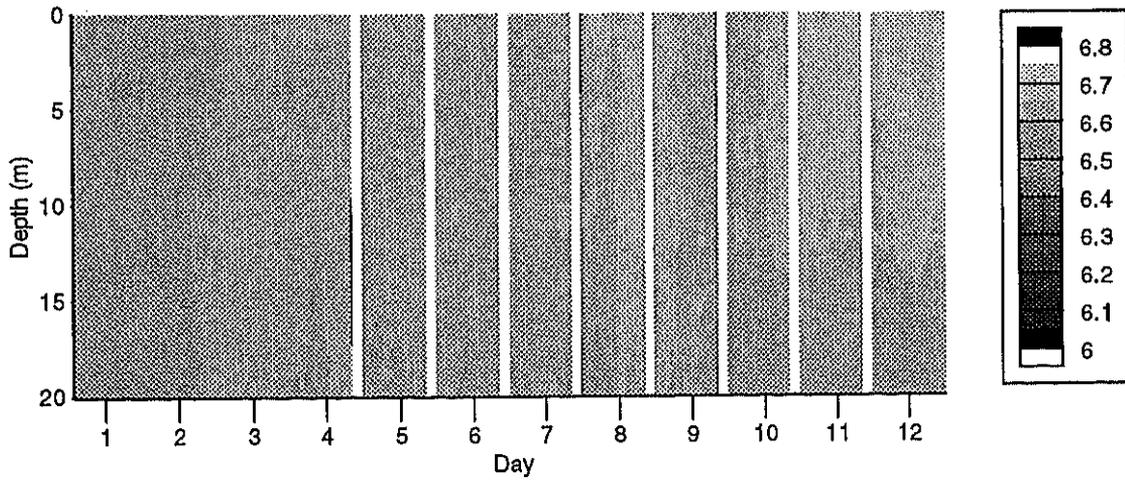
(1-4-6) 2003.1-2 Chlorophyll-a
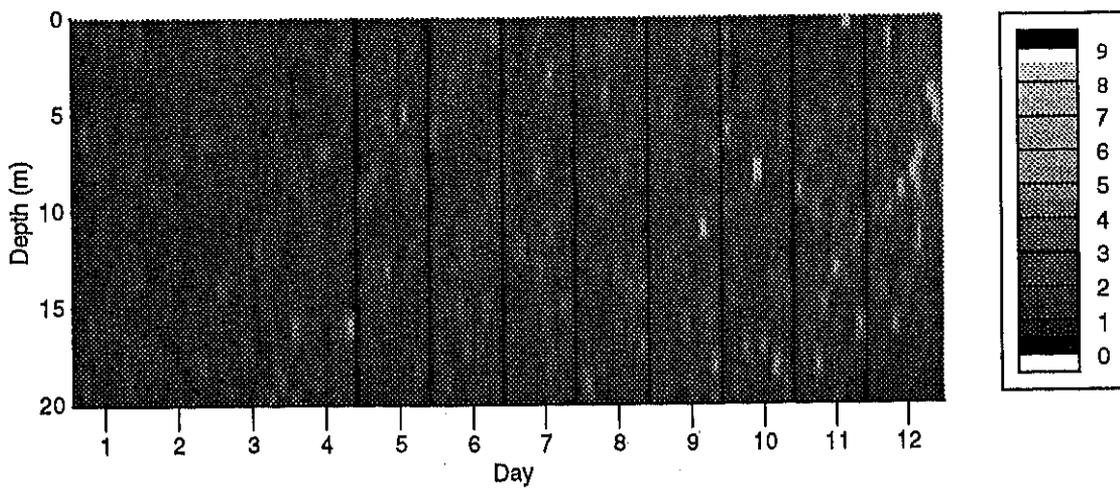
(2-1-1) 2002. 6 Water temperature difference between 18:00 and 06:00 (moving averaged)

Legend: 6/12, 6/13, 6/14, 6/15, 6/16, 6/17, 6/18, 6/19
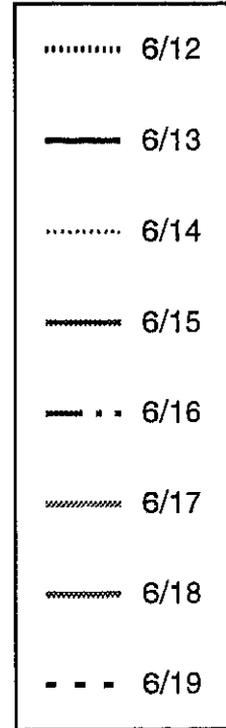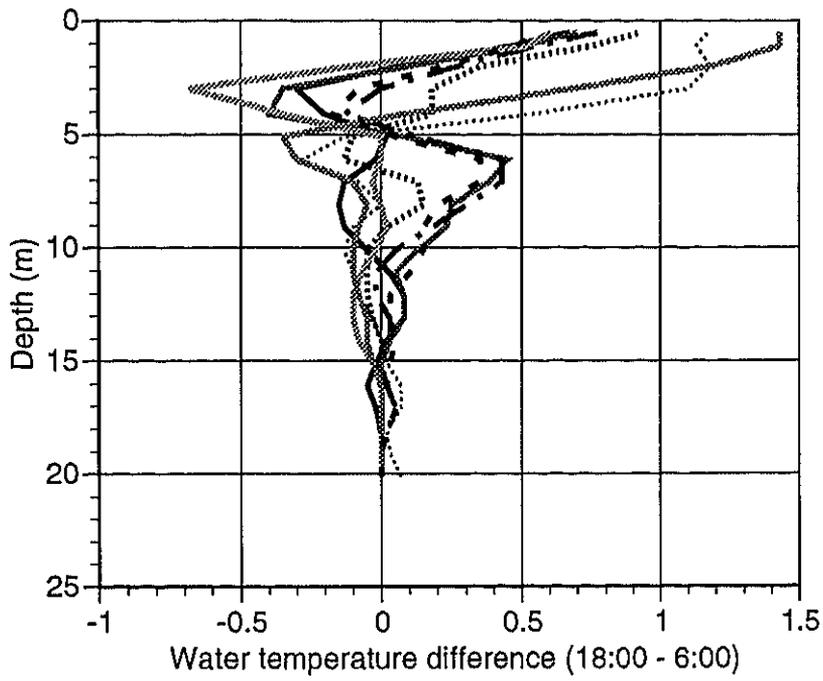
(2-1-2) 2002. 6 DO difference between 18:00 and 06:00 (moving averaged)

Legend: 6/12, 6/13, 6/14, 6/15, 6/16, 6/17, 6/18, 6/19
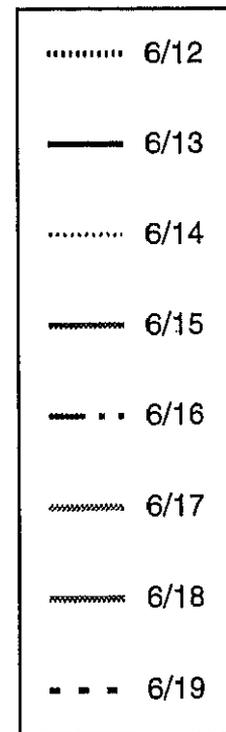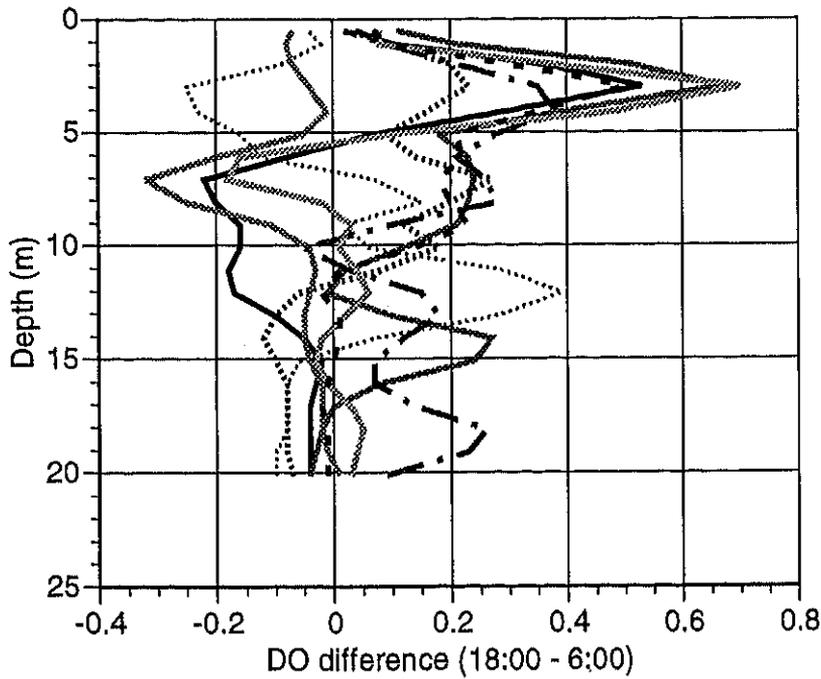
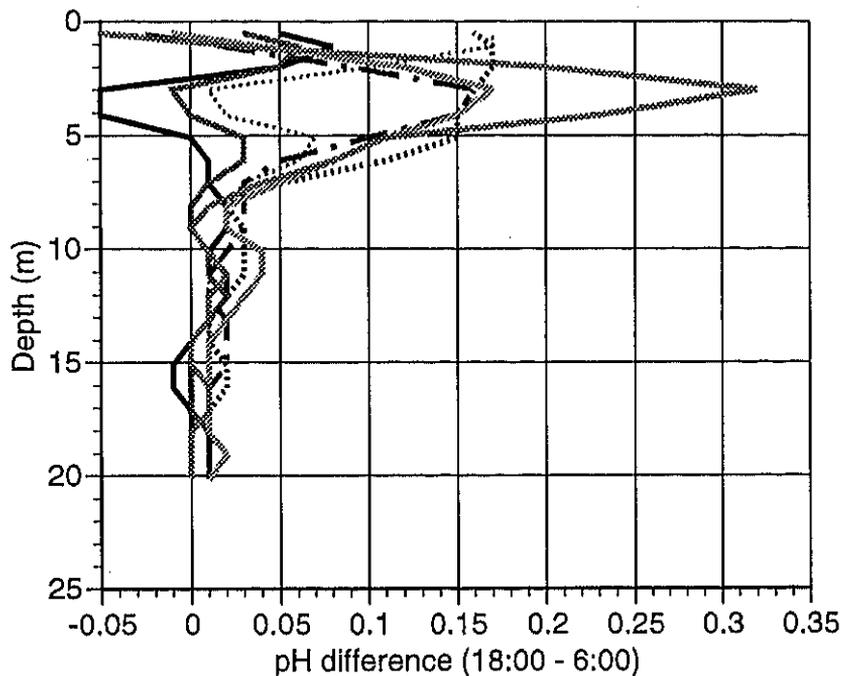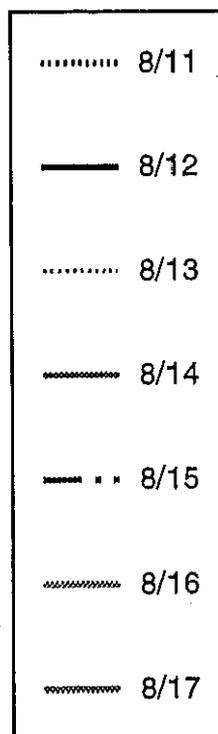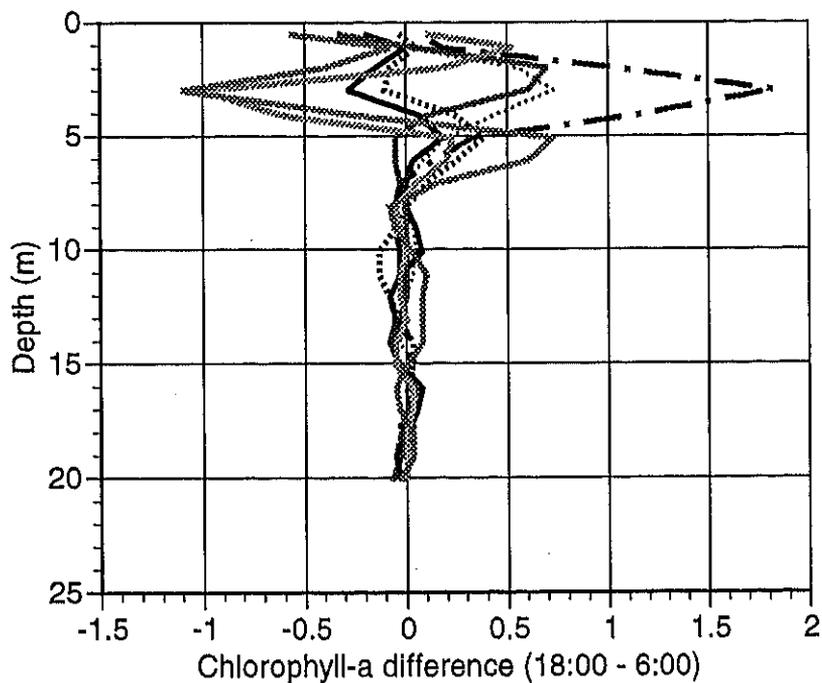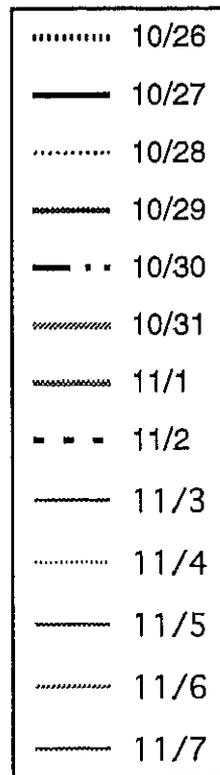(2-1-3) 2002. 6 pH difference between 18:00 and
06:00 (moving averaged)

···········	6/12
⸻	6/13
··········	6/14
⸻	6/15
— · ·	6/16
⸻	6/17
⸻	6/18
- - -	6/19

Depth (m)

pH difference (18:00 - 6:00)
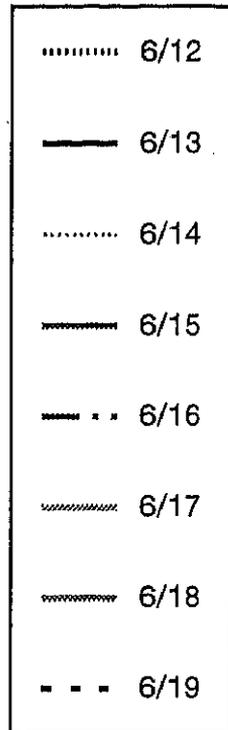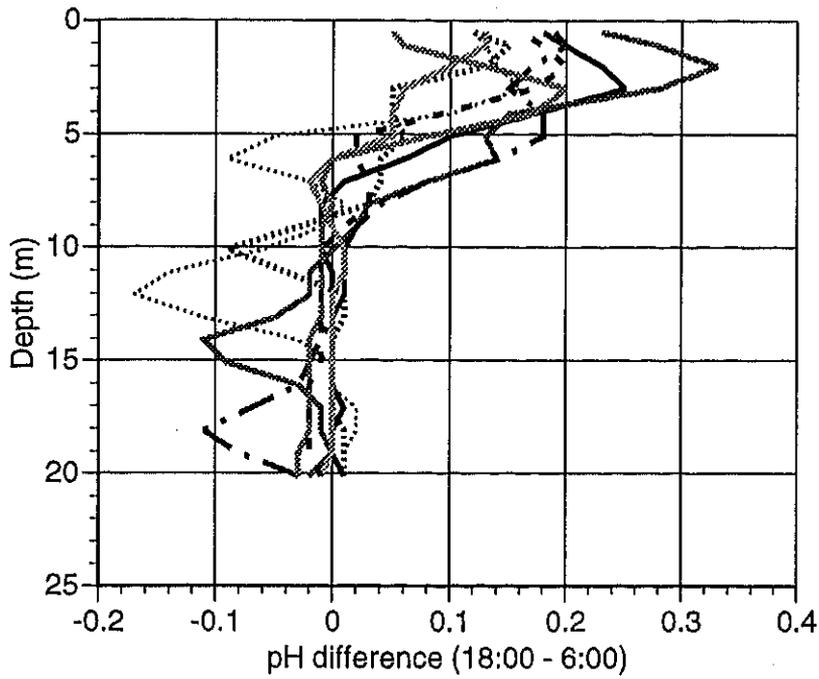
(2-1-4) 2002. 6 Chlorophyll-a difference between
18:00 and 06:00 (moving averaged)
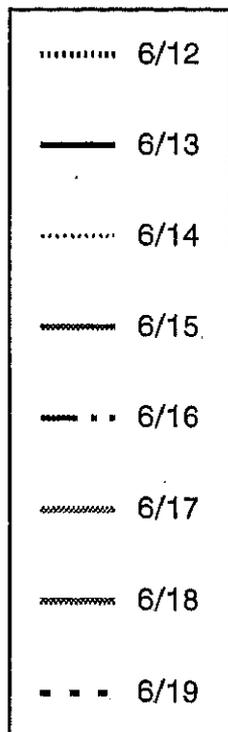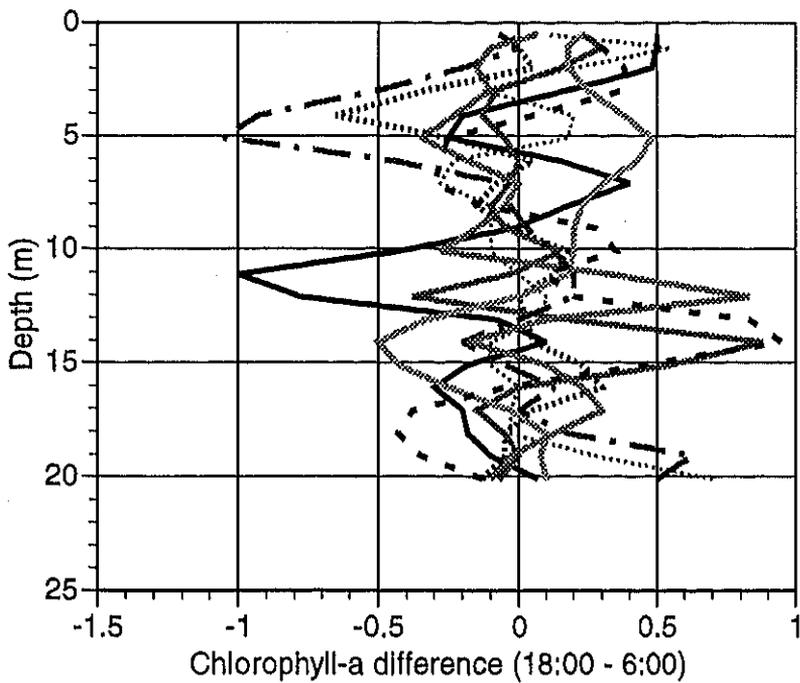
···········	6/12
⸻	6/13
··········	6/14
⸻	6/15
— · ·	6/16
⸻	6/17
⸻	6/18
- - -	6/19

Depth (m)

Chlorophyll-a difference (18:00 - 6:00)

(2-2-1) 2002. 8 Water temperature difference
between 18:00 and 06:00 (moving averaged)

Water temperature difference (18:00 - 6:00)

8/11
8/12
8/13
8/14
8/15
8/16
8/17
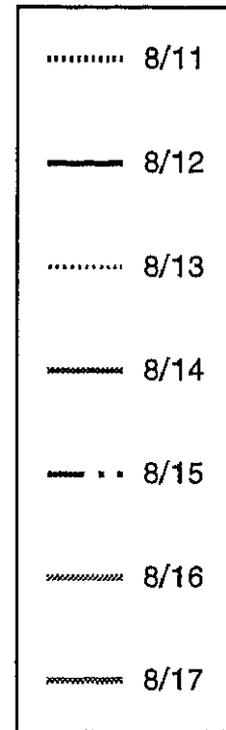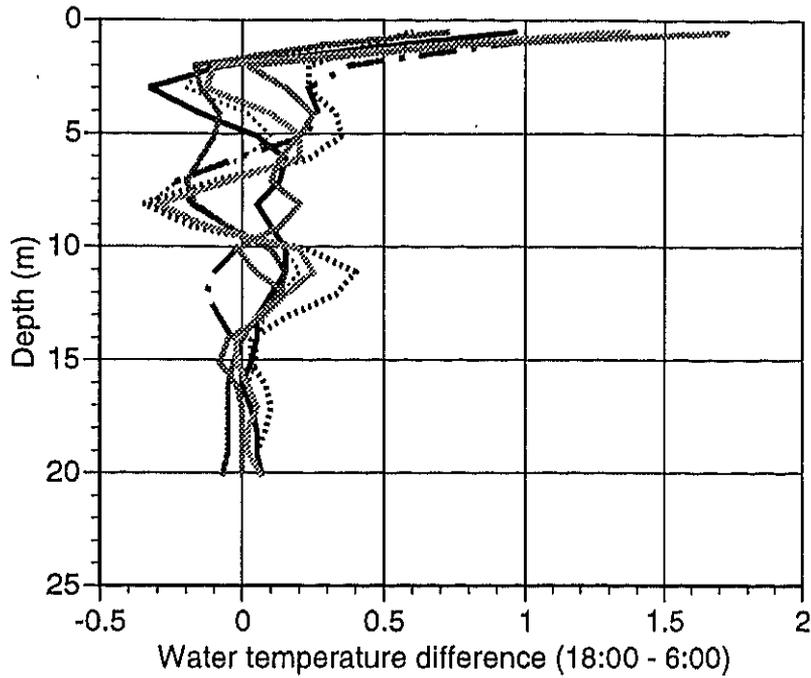
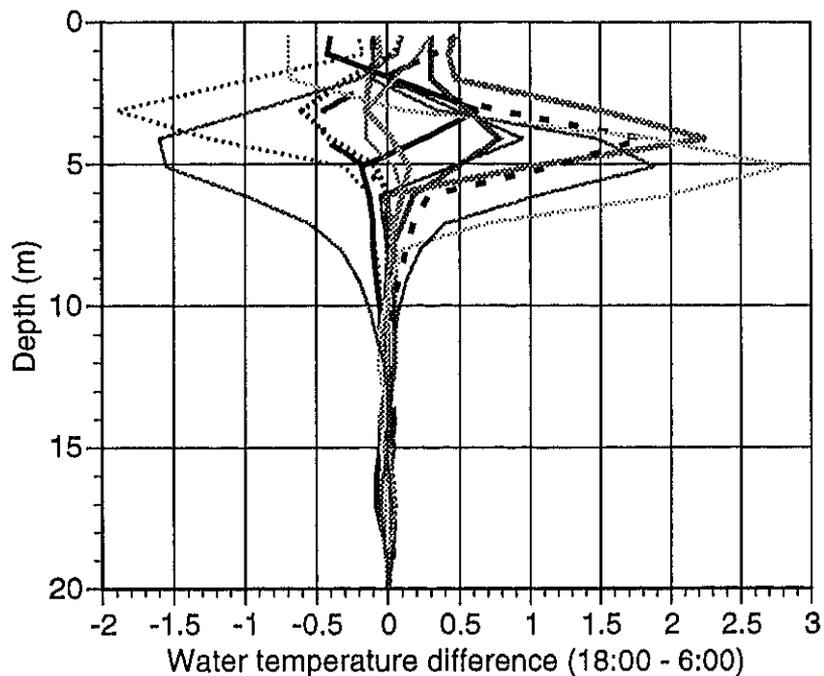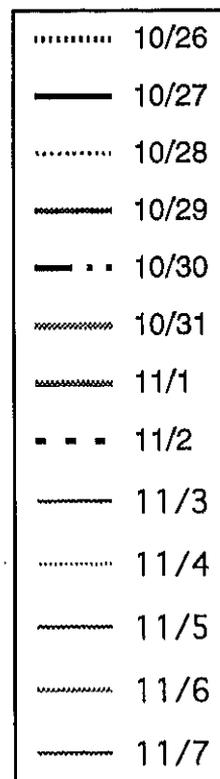(2-2-2) 2002. 8 DO difference between 18:00 and
06:00 (moving averaged)

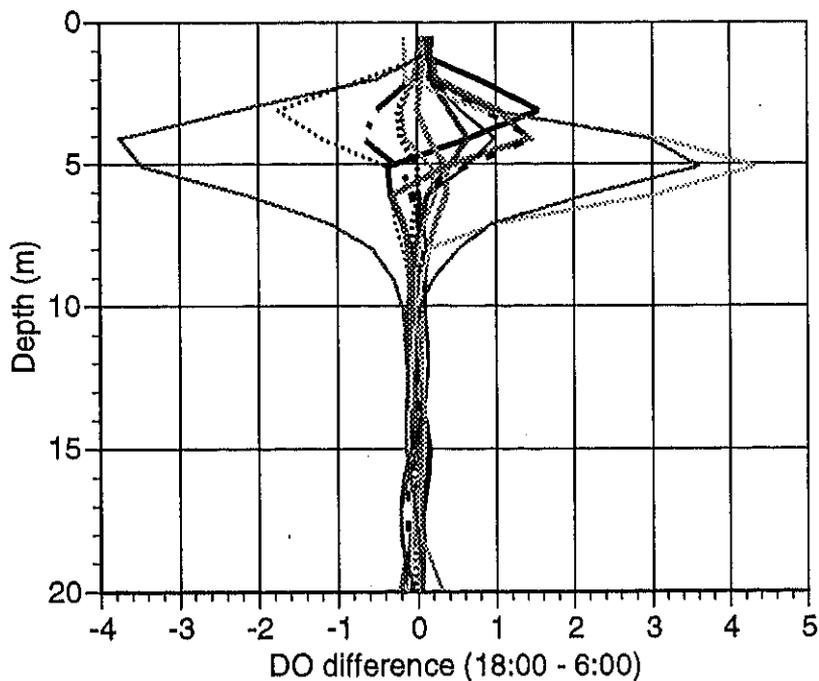DO difference (18:00 - 6:00)

8/11
8/12
8/13
8/14
8/15
8/16
8/17
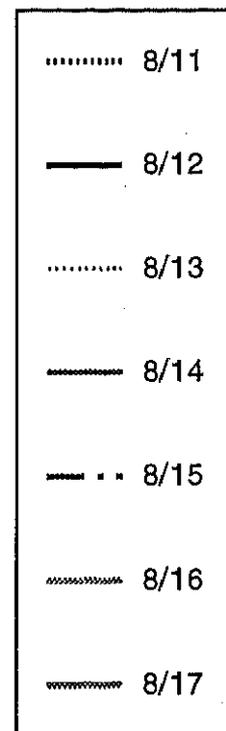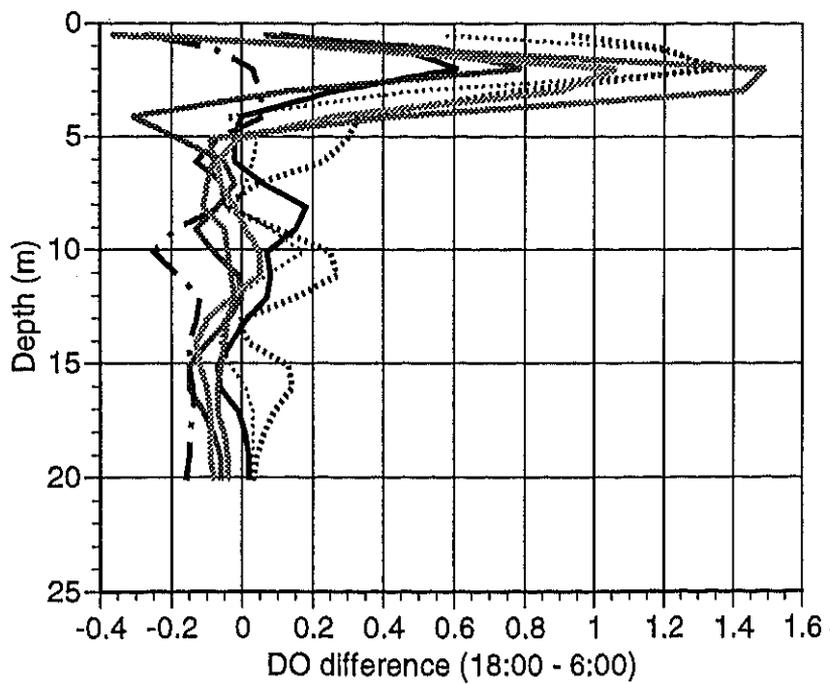
(2-2-3) 2002. 8 pH difference between 18:00 and
06:00 (moving averaged)

··········	8/11
——	8/12
·········	8/13
~~	8/14
—— ··	8/15
~~	8/16
~~	8/17

(2-2-4) 2002. 8 Chlorophyll-a difference between
18:00 and 06:00 (moving averaged)

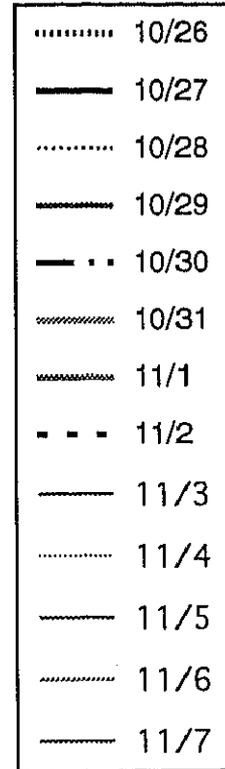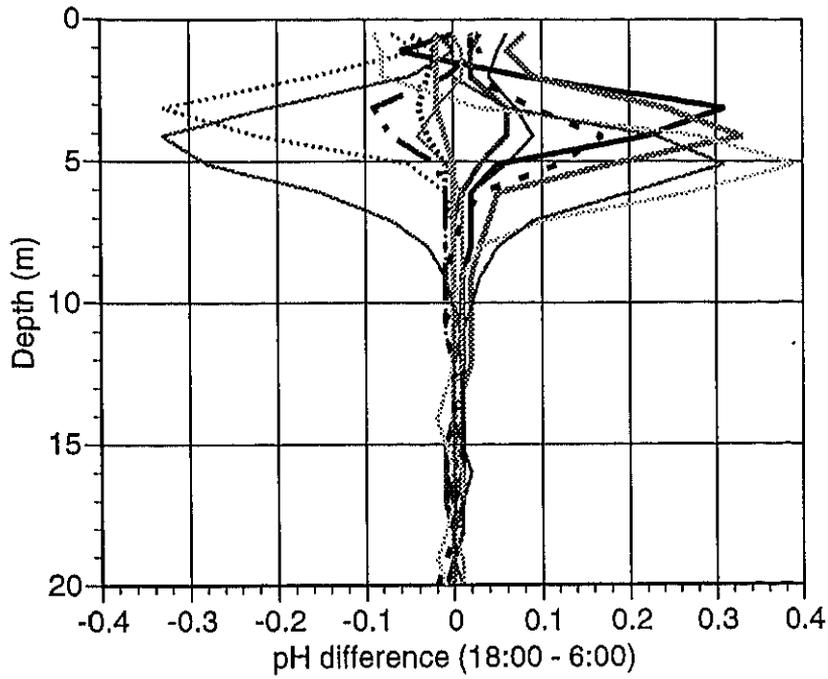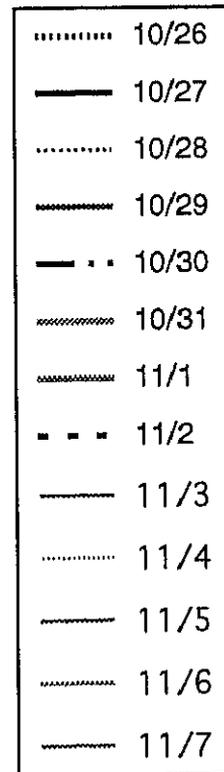|	
··········	8/11
——	8/12
·········	8/13
~~	8/14
—— ··	8/15
~~	8/16
~~	8/17

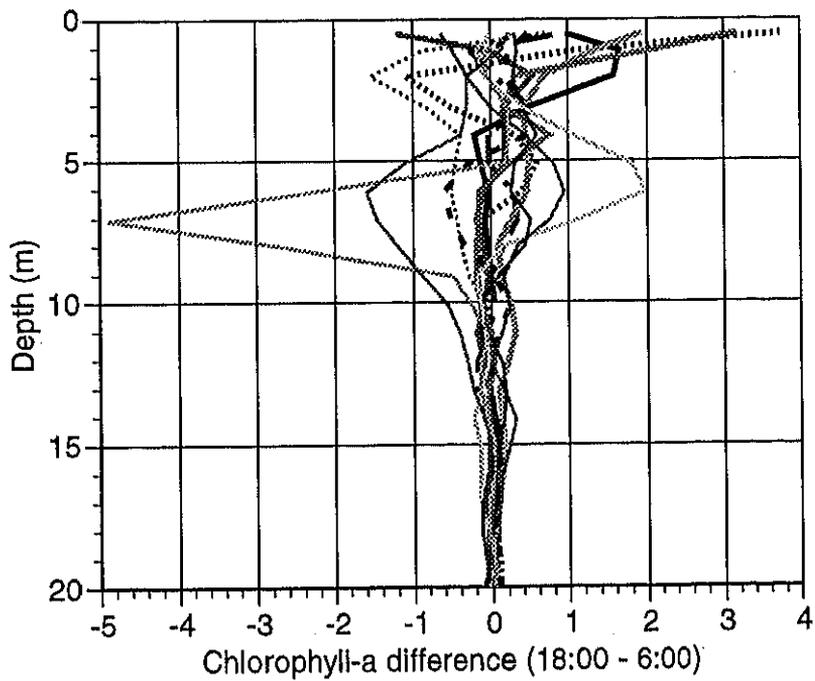## (2-3-1) 2002. 10-11 Water temperature difference between 18:00 and 06:00 (moving averaged)

Water temperature difference (18:00 - 6:00)

··········	10/26
——	10/27
·········	10/28
————	10/29
— ··	10/30
~~	10/31
~~	11/1
- - -	11/2
————	11/3
············	11/4
————	11/5
~~	11/6
————	11/7

(2-3-2) 2002. 10-11 DO difference between 18:00 and 06:00 (moving averaged)

DO difference (18:00 - 6:00)

··········	10/26
——	10/27
·········	10/28
————	10/29
— ··	10/30
~~	10/31
~~	11/1
- - -	11/2
————	11/3
············	11/4
————	11/5
~~	11/6
————	11/7

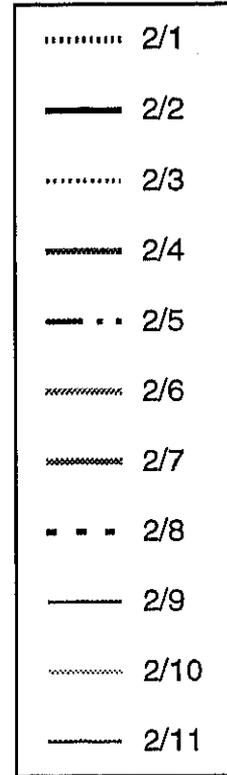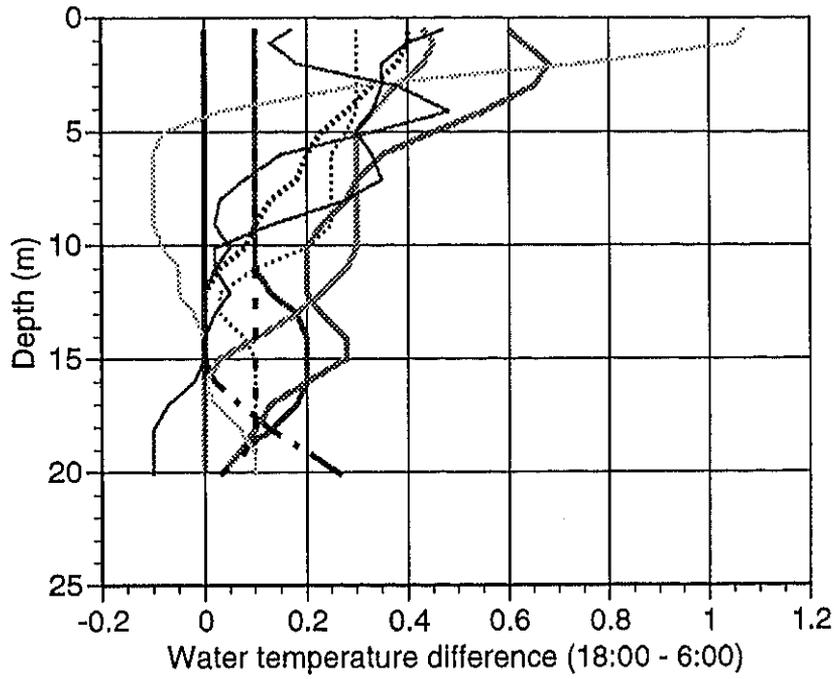# (2-3-3) 2002. 10-11 pH difference between 18:00 and 06:00 (moving averaged)

Legend:
- 10/26
- 10/27
- 10/28
- 10/29
- 10/30
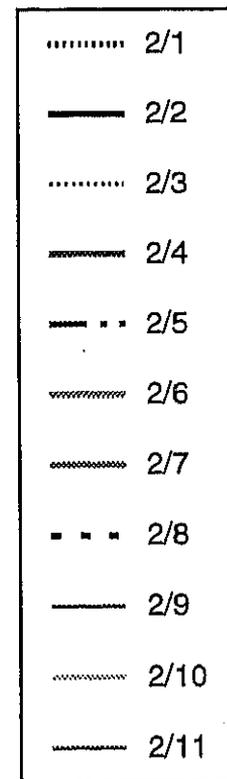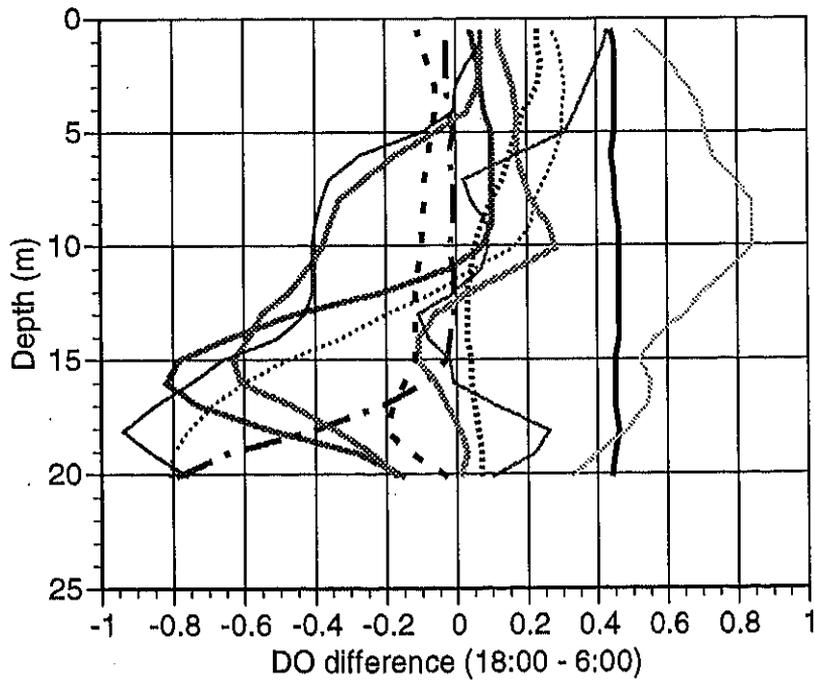- 10/31
- 11/1
- 11/2
- 11/3
- 11/4
- 11/5
- 11/6
- 11/7

(2-3-4) 2002. 10-11 Chlorophyll-a difference between 18:00 and 06:00 (moving averaged)

Legend:
- 10/26
- 10/27
- 10/28
- 10/29
- 10/30
- 10/31
- 11/1
- 11/2
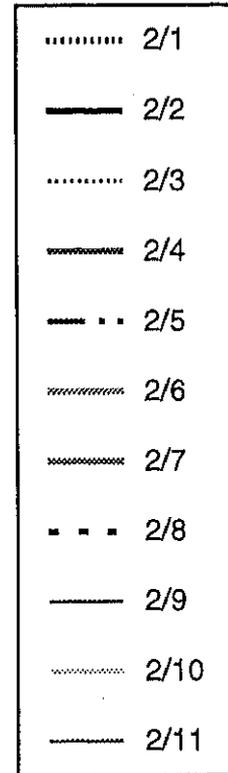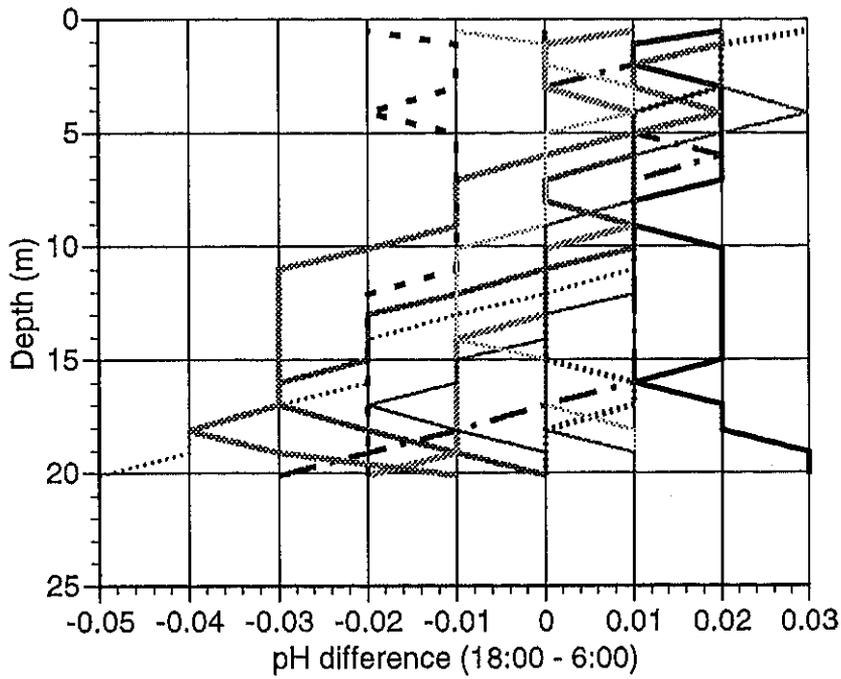- 11/3
- 11/4
- 11/5
- 11/6
- 11/7

(2-4-1) 2002.1-2 Water temperature difference between 18:00 and 06:00 (moving averaged)

Depth (m)

Water temperature difference (18:00 - 6:00)

|	
⋯⋯⋯⋯	2/1
——	2/2
⋯⋯⋯⋯	2/3
～～～～	2/4
—— · ·	2/5
～～～～～	2/6
∞∞∞∞∞	2/7
▪ ▪ ▪	2/8
——	2/9
⋯⋯⋯⋯	2/10
——	2/11

(2-4-2) 2002.1-2 DO difference between 18:00 and 06:00 (moving averaged)

Depth (m)

DO difference (18:00 - 6:00)

⋯⋯⋯⋯	2/1
——	2/2
⋯⋯⋯⋯	2/3
～～～～	2/4
—— · ·	2/5
～～～～～	2/6
∞∞∞∞∞	2/7
▪ ▪ ▪	2/8
——	2/9
⋯⋯⋯⋯	2/10
——	2/11

(2-4-3) 2002.1-2 pH difference between 18:00 and
06:00 (moving averaged)

pH difference (18:00 - 6:00)

Legend: 2/1, 2/2, 2/3, 2/4, 2/5, 2/6, 2/7, 2/8, 2/9, 2/10, 2/11

(2-4-4) 2002.1-2 Chlorophyll-a difference between
18:00 and 06:00 (moving averaged)

Chlorophyll-a difference (18:00 - 6:00)

Legend: 2/1, 2/2, 2/3, 2/4, 2/5, 2/6, 2/7, 2/8, 2/9, 2/10, 2/11
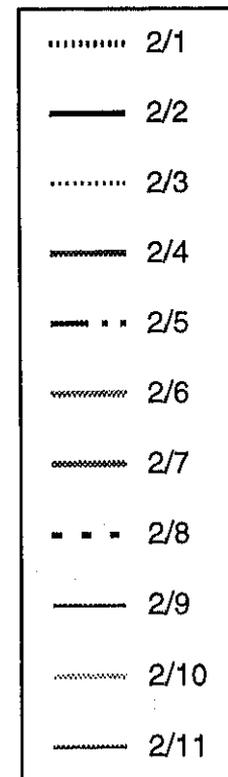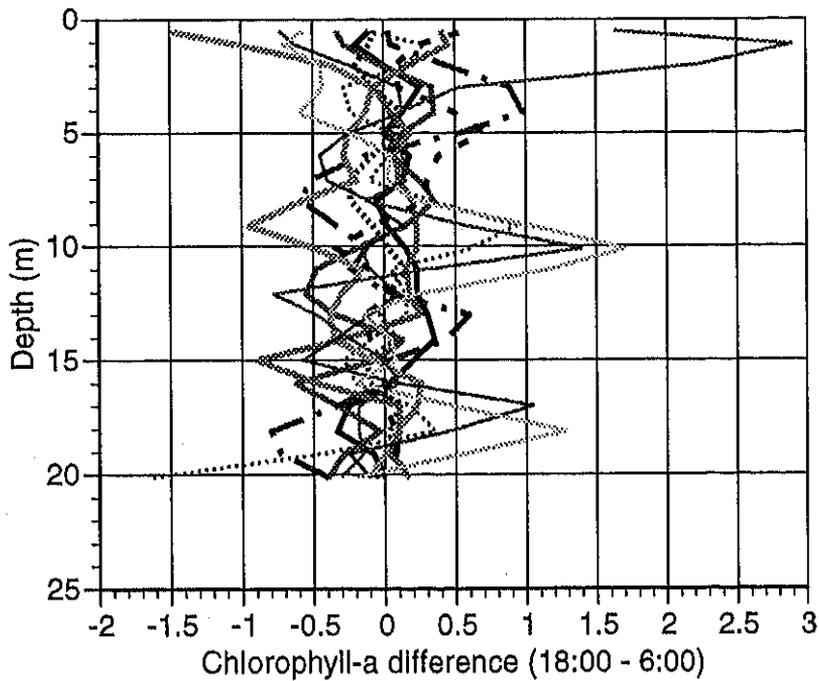
(3) DO difference between 18:00 and 6:00
vs. pH difference between 18:00 and 6:00
r^2=0.22, 0.15, 0.75, 0.26, respectively.

Legend:
□ 2002.6
○ 2002.8
▲ 2002.10-11
◆ 2003.1-2

Axes: pH (18:00 - 6:00) vs DO (18:00 - 6:00)
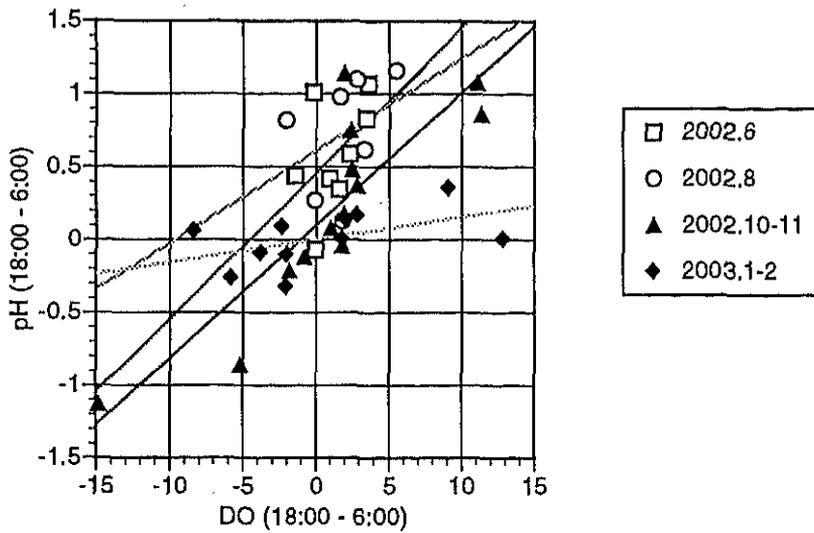
(4-1) Temporal change in DO and pH averaged 0 - 4 m during 2002.6

(4-2) Temporal change in DO and pH averaged 0 - 4 m during 2002.8