Reply

Net production and heterotrophy in Lake Apopka: a reply to BACHMANN et al.*

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With 1 figure

We want to thank the authors for their comment on the continuing debate as to whether Lake Apopka is net heterotrophic or net autotrophic. The heterotrophy hypothesis formulated by BACHMANN et al. (2000) is based on the assumption that high rates of community respiration (CR) are characteristic of the water column during daily photic and aphytic periods. Our contention has been that this assumption is not correct and that the authors have overestimated CR by extrapolating rates measured in short-term experiments in the photic zone to 24 hr over the water column (SCHELSKE et al. 2003). SCHELSKE et al. (1992) state that measured CR “is obviously an overestimate of phytoplankton respiration” (Chapter 2–27) and that “our data provide no good means of estimating phytoplankton respiration” on a 24-hr basis (Chapter 2–28). BACHMANN et al. (2000), however, used these data to support their case for internal heterotrophy, i.e. heterotrophy dependent on organic matter in historic sediments as a carbon source. SCHELSKE et al. (2003) presented analyses of primary production and dissolved oxygen (DO) that were inconsistent with hypothesized internal heterotrophy and concluded again that extrapolated CR overestimates daily CR in the water column. SCHELSKE et al. (2003), therefore, provide evidence that it may not be appropriate as suggested by BACHMANN et al. (2005, 2006) to apply “standard techniques” routinely in making reliable estimates of phytoplankton community respiration in lakes.

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paper by Schelske (2006) provides sediment evidence to reject the heterotrophy hypothesis. Here we present a number of independent lines of evidence to support the conclusion that the heterotrophy hypothesis is invalid and discuss shortcomings in our standard techniques.

The comment by Bachmann et al. (2006) and other papers (Bachmann et al. 2000, 2005) deal with one viewpoint about what happened in Lake Apopka after 1947 when primary producer community structure shifted abruptly from macrophyte dominance to phytoplankton dominance. Our conclusion is that nutrient enrichment, primarily from draining the lake’s floodplain marshes for agriculture in the 1940s, was the proximate cause for the shift (see Coveney et al. 2005, Schelske et al. 2005). Loosely consolidated sediments deposited after 1947 provide a clear signal of this shift in primary producer community structure (Schelske 2006, Schelske et al. 2005). We attribute the major sources of these highly organic sediments (65% organic matter) to byproducts of organic matter produced by phytoplankton primary production (Schelske et al. 2003). Bachmann et al. (2000, 2005) have proposed a different origin and contend that sediment liquefaction of sediments deposited before 1947 is the major source of this “fluid mud.” They conclude that the “fluid mud layer is less a direct consequence of eutrophication than a consequence of enhanced wave action on the lake bed” (Bachmann et al. 2005). However, Carrick et al. (1993) have shown that a near-bottom layer of readily suspended sediments contains high chlorophyll concentrations and viable meroplankton. This meroplanktonic community is an important component of the lake’s primary production during and after wind-resuspension events (Schelske et al. 1995). In contrast to Bachmann et al. (2000, 2005), total phosphorus and chlorophyll concentrations in the water column have decreased recently in response to decreased external phosphorus loading (Coveney et al. 2005).

Different terms have been used in the literature on the relationship between autotrophic production of DO and heterotrophic production of CO2. Early definitions for lakes dealt with the relationship between photosynthesis (P) and respiration (R) with P > R in autotrophic systems and P < R in heterotrophic systems. In the more recent literature, net autotrophy and net heterotrophy recognize that factors other than phytoplankton photosynthesis and respiration affect DO and CO2 dynamics. We, like Bachmann et al. (2006), will use definitions of net autotrophy and net heterotrophy given by Carignan et al. (2000): “Ecosystems where photosynthesis exceeds total planktonic respiration (P > R) are net autotrophic; they are net sinks for CO2 and net producers of O2 and organic matter. Conversely, ecosystems where respiration exceeds photosynthesis (P < R) are net heterotrophic; they are net sources of CO2 and net consumers of O2.” Of particular interest here is the source of organic matter in systems that are net heterotrophic. Allochthonous inputs are generally the source of organic matter for net heterotrophic lakes. Lake Apopka is unique in
that the proposed source of organic matter is from sediments deposited before the 1947 shift in primary producer community structure (BACHMANN et al. 2006). This process whereby heterotrophy is supported by organic matter in sediments was termed internal heterotrophy (BACHMANN et al. 2000). We use internal heterotrophy here because it is the proposed mechanism to support the heterotrophy hypothesis in Lake Apopka.

The magnitude of the proposed heterotrophy in Lake Apopka is large relative to literature values for net primary production in highly productive lakes. BACHMANN et al. (2006) report net heterotrophic production in Lake Apopka of $-4.49 \text{ g C m}^{-2} \text{ d}^{-1}$ for the pelagic region of the lake and $-4.75 \text{ g C m}^{-2} \text{ d}^{-1}$ when sediment respiration is included. The largest annual daily means for net production tabulated by WETZEL (2001) range from 1 to 2 g C m$^{-2}$ d$^{-1}$. Estimates of net production in Lake Apopka are within this range. Net production is 1.93 g C m$^{-2}$ d$^{-1}$ when calculated from a mean daily CR of $-6.68 \text{ g C m}^{-2} \text{ d}^{-1}$ (SCHELSKE et al. 2003) and estimated net heterotrophic production of $-4.75 \text{ g C m}^{-2} \text{ d}^{-1}$ (BACHMANN et al. 2006). SCHELSKE et al. (2003) used direct and indirect methods to conclude that net production ranged from 1 to 3 g C m$^{-2}$ d$^{-1}$. BIEDERMANN (1980) reported net production of 2.72 g C m$^{-2}$ d$^{-1}$ for Lake Apopka and 4.46 and 2.17 g C m$^{-2}$ d$^{-1}$ for Lake Beauclair and Lake Dora, respectively. These two lakes in the Harris Chain are immediately downstream from Lake Apopka.

We have argued previously that the proposed net heterotrophy based on 24-hr calculations of CR is also large relative to oxygen supplies in Lake Apopka (SCHELSKE et al. 2003). Estimated internal heterotrophy for seven of our 33 sampling dates was so large that the nighttime oxygen demand would have been greater than the DO supply in saturated lake water. It should be pointed out that the saturation DO concentration was relatively small during our study, ranging from 7.32 to 9.98 mg/L because water temperature ranged from 14.0 to 32.0°C in this polymeric lake (SCHELSKE et al. 1992, 2003).

BACHMANN et al. (2006) apparently do not understand how we measured areal net production (ANP). Community rates for photosynthesis and respiration were measured readily with the light- and dark-bottle oxygen method in short-term experiments (2 to 4 hr, n = 33) (SCHELSKE et al. 1992) using techniques in WETZEL & LIKENS (1991). Triplicate samples of lake water collected at 30 cm were incubated in situ at mid-day on a float designed to eliminate shading. Light bottles (tissue-culture flasks) were incubated at five light intensities using a series of neutral density filters to simulate known fractions of surface irradiation; triplicate dark bottles were used to measure CR. Depths for light intensities simulated during incubations were obtained from profiles of photosynthetically active radiation measured with a LiCor quantum meter on each sampling date. The concentration of DO was measured with high precision, the coefficient of variation (CV) of the mean averaged <2% for initial,
light, and dark bottles. Gross photosynthesis (GP), net photosynthesis (NP), and CR were calculated using standard techniques, including a respiration quotient of 1.0 and a photosynthetic coefficient of 1.2. Data for GP and NP were plotted vs. simulated depth and areas under the curves were used to estimate areal gross production (AGP) and ANP (WETZEL & LIKENS 1991). As suggested by WETZEL & LIKENS (1991), we introduced a diurnal factor whereby daily community photosynthesis is calculated based on the proportion of daily insolation received during the incubation period. Raw data for our experiments are available in appendices (SCHELSKE et al. 1992).

We agree with BACHMANN et al. (2000) that there are three components of system CR: CR in the photic zone and aphotic zone during the photosynthetic period and CR in the entire water mass during the remainder of the day (SCHELSKE et al. 2003). We disagree that these three components of CR can be estimated reliably using existing data. The controversy about the heterotrophy hypothesis then is whether it is valid to extrapolate short-term measurements of CR to daily (24-h) estimates (BACHMANN et al. 2006, SCHELSKE et al. 2003). According to WETZEL & LIKENS (1991), it is not valid to assume that daily respiration can be estimated from midday rates. Although we disagree strongly with the conclusion of BACHMANN et al. (2000, 2005) about hypothesized internal heterotrophy and its origin in Lake Apopka, this exchange of controversial views may provide insight about community metabolism in other lacustrine systems. Here we present data on lake-water pH and DO and additional data on CR and DO that are inconsistent with proposed internal heterotrophy and conclude that a number of independent lines of evidence are available to reject the heterotrophy hypothesis.

Line 1. We examined hypothesized rates of CR to determine whether they are commensurate with known supplies of DO in the water column. If CR averages -4.49 g C m$^{-2}$ d$^{-1}$ (Bachmann et al. 2006), then average DO consumption is 12.0 g O$_2$ m$^{-2}$ d$^{-1}$ or 0.31 mg L$^{-1}$ hr$^{-1}$ in a 1.62-m water column. Nighttime anoxia or hypoxia might be expected on some sampling dates because daily CR averaged 6.68 ± 3.45 g C m$^{-2}$ d$^{-1}$ (n = 33) (SCHELSKE et al. 2003, Table 4). This amounts to an average DO consumption of 0.46 mg L$^{-1}$ hr$^{-1}$ in a 1.62-m water column. On 7 of 33 sampling dates, calculated nighttime loss of DO for the water column exceeded the saturation DO concentration (SCHELSKE et al. 2003, Table 4). To restore DO to the average saturation concentration (8.21 mg/L) on these dates requires DO production equivalent to carbon fixation of 5.0 g C m$^{-2}$ over the fraction of a day prior to our mid-morning sampling, an unrealistic high rate of ANP. This estimate is conservative because DO saturation averaged 126% for our mid-morning samples. Thus, mid-day rates of CR appear to be grossly overestimated on some of our sampling dates.
Line 2. Hypothesized internal heterotrophy is not consistent with water-column DO in Lake Apopka. We examined DO saturation to determine whether it reflected the hypothesized magnitude of heterotrophy that would utilize large quantities of DO. Average percent saturation calculated from titration of triplicate water samples and measurements with an oxygen probe were 126 ± 19 % and 128 ± 19 % (n = 33), respectively, for mid-morning samples (Schelske et al. 1992). In 704 samples collected from 1985 to 1997, DO % saturation ranged from 0 to 180 % (Fig. 1); however, only 10 measurements were < 60 % saturation and 17 were > 160 % saturation (Fig. 1). Neither Bachmann et al. (2006) nor Biedermann (1980) reported diurnal ranges with minima < 60 % saturation. Neither set of observations provides evidence for nighttime DO consumption of 0.46 mg L⁻¹ hr⁻¹. If hourly nighttime respiration were this large, one would expect to find hypoxic or anoxic conditions on some sampling dates. Therefore, the fact that mid-morning DO was generally supersaturated, an indication of net autotrophic production, provides evidence to question the heterotrophy hypothesis.

Line 3. Whether lakes are heterotrophic can be inferred from the composition of dissolved inorganic carbon (DIC). The fractions in the form of dissolved carbon dioxide, bicarbonate, or carbonate can be predicted generally from pH for alkaline waters such as those found in Lake Apopka (Wetzel & Likens 1991). Essentially no free CO₂ exits with a pH > 8.0. Carbonate alkalinity occurs at pH > 8.3. Therefore, when pH is > 8.3, which is common in Lake Apopka (Fig. 1), conditions are favorable for precipitation of calcium carbonate and not outgassing of CO₂. From 1985 to 1997, pH ranged generally from 8 to 10. One would expect pH to increase during the day as DIC is utilized photosynthetically and to decrease at night when respiration produces CO₂. The diurnal change in water-column pH was relatively small for one diurnal cycle (10–11 September 1977, Biedermann 1980) with a daytime maximum of 9.2 and a nighttime minimum of 8.8. These data which are consistent with the long-term record (Fig. 1) show that the well-buffered waters in Lake Apopka were not affected greatly by nighttime respiration. Data for pH, therefore, support the case for a lake with strong autotrophic characteristics where autotrophic utilization of CO₂ is greater than heterotrophic production of CO₂.

Line 4. By definition, one of the byproducts of heterotrophy is carbon dioxide. If carbon dioxide were added to the water column as a byproduct of internal heterotrophy at the hypothesized rate, it would shift pH toward lower values. For example, Lake Apopka water contains ca. 40.8 g DIC/m³ (Gu et al. 2004). The estimated flux of CO₂ from heterotrophy (−4.49 g C m⁻² d⁻¹) equals the DIC reservoir in a 1.62-m water column every 15 days. Such a large flux of CO₂ would neutralize water-column bicarbonates and carbonates in a relatively short time and lake water pH would not be as alkaline and
Fig. 1. A thirteen-year record (1985–1997) of dissolved oxygen (DO) per cent saturation (upper) and pH (lower) in surface samples from Lake Apopka (n = 740 for DO and 603 for pH). Most samples were collected mid-morning (76% between sunrise and 11:00 AM EST). Oxygen data were affected by time of sampling ($R^2 = 0.12$, F-test, $p < 0.001$). The relationship between pH and time of sampling was significant (F-test, $p = 0.01$) but extremely weak ($R^2 = 0.01$). These data from St. Johns River Water Management District are previously unpublished.

would become a source of CO$_2$. Lake Apopka, however, has a CO$_2$ partial pressure lower than atmospheric partial pressure and, therefore, is not a source but a net sink for CO$_2$ (Gu et al. 2004, Cole et al. 1994).
Line 5. Net organic matter accumulation in sediments is an expected characteristic of autotrophic lakes (Carignan et al. 2000). Loosely consolidated, highly organic sediments have accumulated in Lake Apopka since 1947 (Schelske 2006). We hypothesize that the organic matter in these sediments originates primarily as a byproduct of phytoplankton production and has accumulated at an increasing rate in response to increased primary production driven by phosphorus enrichment (Schelske et al. 2003).

Line 6. As shown by Bachmann et al. (2006), the controversy about the heterotrophy hypothesis depends on whether hypothesized CR is valid. They ran simulations to test the conclusion by Schelske et al. (2003) that daily CR was overestimated. They found that our average respiration rate "would have to be reduced to 31% of the measured value to achieve a zero net production" and concluded that CR was not overestimated. We also ran simulations on how DO varied given different assumptions about daily CR and daily areal gross production (AGP) (data from Table 4, Schelske et al. 2003) using the following relationship:

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\text{DO}_{\text{sim}} = 2.667 \text{ (AGP} - \text{CR)}/(1.62)
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where \(\text{DO}_{\text{sim}}\) is concentration (g m\(^{-3}\)), 2.667 is a factor to convert units from C to O\(_2\), AGP and CR are in units of g C m\(^{-2}\) d\(^{-1}\), and 1.62 is mean depth in m. This relationship calculates daily ANP (daily AGP – daily CR) in terms of DO production expressed here in mg/L. We first varied daily CR. As shown by Bachmann et al. (2006), when CR is reduced 69% average \(\text{DO}_{\text{sim}}\) is 10.3 mg/L which equals average DO from lake sampling, indicating zero ANP. They did not make a calculation using the reported average daily CR. Under this condition, average \(\text{DO}_{\text{sim}}\) was –1.99 mg/L, or 12.3 mg/L less than average DO from mid-morning lake samples and \(\text{DO}_{\text{sim}}\) on individual sampling dates was negative on 14 of the 33 dates. When daily CR was reduced by 50%, \(\text{DO}_{\text{sim}}\) was 6.92 mg/L, 3.4 mg/L less than DO from lake sampling indicating ANP was negative. When daily CR was reduced by 69%, ANP was zero. To obtain a positive value for ANP would require an even larger reduction in daily CR. These simulations support our contention that CR was overestimated because daily CR and daily CR reduced by half yielded negative \(\text{DO}_{\text{sim}}\) on specific sampling dates, a condition not known to have occurred in the early 1990s.

Next, we varied AGP to simulate large increases in photosynthetic activity. When AGP was doubled or tripled, average \(\text{DO}_{\text{sim}}\) was 3.52 or 9.03 mg/L, respectively. Because both values are less than average DO from lake sampling, they show that simulated AGP was too small to produce net autotrophy. The CV of mean \(\text{DO}_{\text{sim}}\) for doubled and tripled AGP was 251 and 116%, respectively. The larger CV for doubled AGP indicates a greater variation than that measured during our study. By comparison, CV for DO measured on individual sampling dates was only 17% and for daily CR reduced by 69% was only
31%. Simulations using daily CR and AGP provide strong evidence that daily CR was overestimated.

Line 7. Other available data for CR were analyzed to investigate the heterotrophy hypothesis. The smallest CR (74 mg C m⁻³ hr⁻¹) for a three-day sampling period (24 July to 26 July 1991) occurred on 25 July when a storm event reduced measured DO concentration to saturation (SCHELSKIE et al. 2003). If according to BACHMANN et al. (2000, 2006), internal heterotrophy was fueled by sediment resuspension, one would expect CR to have been large after a storm event when sediments are most likely to be resuspended. However, CR was smaller than the preceding (196 mg C m⁻³ hr⁻¹) or succeeding day (134 mg C m⁻³ hr⁻¹) and less than half the study average (174 ± 89 mg C m⁻³ hr⁻¹). This result is not surprising because regression of CR on wind speed for 33 sampling dates was not significant, neither for the day of collection nor on the two succeeding days (Table 5, SCHELSKIE et al. 2003). Also, CR varied diurnally on the second day of sampling. These data for CR obtained over a three-day period also are inconsistent with the heterotrophy hypothesis.

We disagree with the authors that standard light- and dark-bottle oxygen methods were appropriate to validate internal heterotrophy. Because photosynthetic rates were high, we limited measurements to short-time periods (avg. = 2.66 h) and only once daily (SCHELSKIE et al. 1992). This is a "standard technique" from WETZEL & LIKENS (1991). However, according to WETZEL & LIKENS (1991), the assumption that "respiration is not affected by illumination" is not valid. They state "respiration results from mitochondrial activity, which has been shown to be altered by light", and that photorespiration, CO₂ generated from glycolate metabolism, "is influenced by and proportional to oxygen concentration, light intensity, and temperature". They also state that resulting variations are not taken into account by the method and that rates of photosynthesis and community respiration fluctuate over the course of a day. We, therefore, would be remiss in not emphasizing that standard methods must be applied in soundly designed experiments that address the question of interest. We used an experimental protocol designed to estimate photosynthetic intensity and CR for one depth at midday. This design obviously was not appropriate for estimating daily spatial and temporal variability of CR in the water-column.

BACHMANN et al. (2006) conclude that error in determining respiration rates in dark bottles was not important. We agree that our DO measurements were conducted with high precision. However, as pointed out above, experimental design not error in DO measurements is the source of error in respiration measurements.

We disagree strongly that estimates of photosynthetic rates were not affected by oxygen supersaturation in light bottles. Examining DO data from light- and dark-bottle experiments, we found that average initial DO was 10.3
± 1.6 mg/L and average final DO (light level with greatest change) was 12.7 ± 1.8 mg/L for the 33 sampling dates, or an average DO increase of 2.4 mg/L for the short average period (2.66 h) represented by our experiments. During the experiments, average DO saturation increased from 126 % to 154 %. Oxygen saturation for final DO was >160 % on 14 dates and the maximum saturation was 209 %. Gas bubbles, presumably oxygen, observed in light bottles provide the basis for our earlier statement that photosynthesis was underestimated due to DO supersaturation (SCHELSKÉ et al. 2003). BIEDERMANN (1980) reached a similar conclusion. He initially incubated light- and dark-bottles for two hours. Because of high oxygen production, he purged lake waters with nitrogen gas to minimize formation of air bubbles and shortened the incubation time to one hour. WETZEL & LIKENS (1991) also comment on this problem: “under ‘pea soup’ conditions of very high algal biomass, an hour of incubation could result in supersaturated conditions”. During titration “bubbles of oxygen likely would be lost and the productivity greatly underestimated”. We believe, therefore, that AGP was underestimated because of DO supersaturation in light bottles.

Invoking internal heterotrophy constrains tests of the heterotrophy hypothesis. It is constrained by supplies of oxygen in the water column and by supplies of organic matter in near-surface sediments. As shown above, DO supplies in the water column were not adequate to support the hypothesized magnitude of CR for some of our sampling dates. By contrast, lake waters frequently were supersaturated with DO during routine sampling (Fig. 1). If hypothesized high rates of CR were valid, one would expect hypoxia or anoxia to have occurred frequently. Another constraint, can sediment resuspension provide the requisite supply of organic matter for internal heterotrophy? The calculated quantity of historic macrophyte sediments that must be processed for hypothesized internal heterotrophy amounts to a lake-basin average of 7.2 cm yr⁻¹ (SCHELSKÉ 2006). A basin average may be misleading because in 1996 pre-1947 sediments on 37 % of the lake basin were overlain by at least 47 cm of post-1947 sediments. Accumulation of flocculent sediments, therefore, is such that internal heterotrophy as proposed becomes a self-attenuating process (SCHELSKÉ & KENNEY 2001). A final constraint, what fraction of organic matter in historic macrophyte sediments is labile? It was assumed in calculations of organic matter consumption that all organic matter in macrophyte sediments is labile.

We believe that a conceptual model of internal heterotrophy would be useful in future studies. The heterotrophy hypothesis states that the source of organic matter for internal heterotrophy is derived from macrophyte sediments deposited before 1947. The authors have advanced a mechanism by which macrophyte sediments are “liquefied” to form “fluid mud”. “Fluid mud” can then in turn be resuspended and provide an internal source of organic matter.
for heterotrophy. There is no discussion, however, of how organic matter is processed during heterotrophy. One can assume that the first trophic interaction is mediated microbiologically and that subsequent trophic interactions are based on organic matter fixed by microbes. Beyond this step, we can only speculate about the fate of this organic matter. We might assume that subsequent processing of organic matter yields recalcitrant organic compounds that are sedimented, a characteristic of Lindemann trophic dynamics. However, calculations used here and in SCHELSKE (2006) assume that all the historic organic matter is processed and degraded to carbon dioxide. In addition, we have difficulty in specifying the physical factors in a conceptual model that provides sediment liquefaction of the magnitude (basin-wide average equal to 7.2 cm yr\textsuperscript{-1}) mandated by the heterotrophy hypothesis. BACHMANN et al. (2005, 2006) offer no insights about these relationships.

Some critical aspects and unresolved issues that bear directly on the heterotrophy hypothesis should be tested with additional study. For example, experimental studies to measure factors that control degradation of sediment organic matter could be designed. Such studies could investigate the role of physical, chemical, and biological factors. Intuitively, our prediction is that degradation of organic matter in macrophyte sediments would be slow and insignificant compared to rates mandated by the heterotrophy hypothesis. This prediction is based on the hypothesis that organic matter in macrophyte sediments is largely recalcitrant, not labile. Additional analysis of historic data is not likely to resolve the controversy about internal heterotrophy – new approaches and new experimental evidence are required to test the heterotrophy hypothesis. Finally, a model of phytoplankton production that incorporates realistic estimates of spatial and temporal variability in CR might be instructive.

One of the lessons from this controversy is that other studies of primary production in aquatic systems may not have considered all assumptions underlying so-called “standard techniques”. Experimentalists and consumers of “standard” data should be aware of the consequences of inherent assumptions. In particular, we show here that assumptions, real or implied, about ecosystem respiration should be carefully evaluated (see WETZEL & LIKENS 1991). It is beyond the scope of this paper to evaluate and discuss the complexity of spatial and temporal variability in CR. BACHMANN et al. (2000, 2006) support the case for heterotrophy by extrapolating short-term results for CR at one depth in the photic zone to daily estimates for the entire water mass. We would like to point out, however, that WETZEL & LIKENS (1991) caution against such an extrapolation. They point out that it would be invalid to extrapolate CR estimated at midday to 24-hr estimates. In the case of Lake Apopka, that such extrapolations are highly unreliable can be demonstrated readily by indirect methods. This may not be the case in systems with lower rates of primary production.
In summary, we present a number of independent lines of evidence to either reject or seriously question the heterotrophy hypothesis. We also believe that any one of several of these and other arguments may provide the basis for rejecting the proposed hypothesis. Taken together, the arguments substantiate the case that Lake Apopka in the early 1990s, when our experiments were conducted (Schelske et al. 1992, 2003), was characterized by hypereutrophy and net autotrophy and not by net heterotrophy.

References


