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Kieler Meeresforschungen	Sonderheft 4	Kiel 1978

An approach to quantify the energy flow through the pelagic part of the shallow water ecosystem off Boknis Eck (Eckernförde Bay)*

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Abstract

The energy flow of the pelagic part of a shallow water ecosystem is quantified using measurements of global incident radiation, particulate organic carbon, caloric content of the particulate matter, data from other authors on primary production, zooplankton secondary net production and zooplankton tertiary net production as well as several conversion factors from the literature. – The total potential radiant energy in 1973 amounted to $3.46 \cdot 10^5$ kcal m^{-2} y^{-1}, the phytoplankton net production to $2.66 \cdot 10^3$ kcal m^{-2} y^{-1}, with an average transfer efficiency of 0.77%. The zooplankton secondary and tertiary net production were $3.58 \cdot 10^2$ and $5.49 \cdot 10^1$ kcal m^{-2} y^{-1} respectively. More than 40% of the phytoplankton net production ($1.08 \cdot 10^3$ kcal m^{-2} y^{-1}) was remineralised within the water column, 35% of the phytoplankton net production ($9.25 \cdot 10^2$ kcal m^{-2} y^{-1}) sedimented directly to the bottom. The total transfer to the sediment amounted to $1.55 \cdot 10^3$ kcal m^{-2} y^{-1} (corresponding to 58.3% of the phytoplankton primary production), the further transfer to higher trophic levels was $4.34 \cdot 10^1$ kcal m^{-2} y^{-1} or 1.6% of the phytoplankton primary production.

Zusammenfassung

Ein Quantifizierungsversuch für den Energiefluß durch den pelagischen Teil des Flachwasserökosystems bei Boknis Eck (Eckernförder Bucht)

Die Bestimmung des Energieflusses im pelagischen Teil eines Flachwasser-Ökosystems erfolgt unter Verwendung von Messungen der Globalstrahlung, des partikulären organischen Kohlenstoffes, des Kaloriengehaltes der partikulären Substanz, von Daten anderer Autoren über die Primär-, Sekundär- und Tertiärproduktion und von mehreren Umrechnungsfaktoren aus der Literatur.

Im Jahre 1973 betrug die gesamte potentiell nutzbare Strahlungsenergie $3{,}46 \cdot 10^5$ kcal m^{-2} a^{-1}, die Netto-Primärproduktion $2{,}66 \cdot 10^3$ kcal m^{-2} a^{-1}, das entspricht einer durchschnittlichen Ausnutzungsrate von 0,77%. Die Netto-Sekundärproduktion betrug $3{,}58 \cdot 10^2$ kcal m^{-2} a^{-1} und die Netto-Tertiärproduktion $5{,}49 \cdot 10^1$ kcal m^{-2} a^{-1}. Mehr als 40% der Netto-Primärproduktion ($1{,}08 \cdot 10^3$ kcal m^{-2} a^{-1}) wurden bereits im freien Wasser remineralisiert, weitere 35% ($9{,}25 \cdot 10^2$ kcal m^{-2} a^{-1}) sedimentierten direkt. Der gesamte Transport aus der Wassersäule zum Sediment

* Contribution No. 198 of the Joint Research Programme 95, Kiel University

betrug 1,55 · 10^3 kcal m^{-2} a^{-1} (oder 58,3% der Netto-Primärproduktion), der weitere Transport innerhalb des Nahrungsnetzes belief sich auf 4,34 · 10^1 kcal m^{-2} a^{-1}, das entspricht 1,6% der Netto-Primärproduktion.

Introduction

An ecosystem is governed by two dynamic processes; the cycling of matter and the flow of energy. To describe the functioning of a marine ecosystem it is necessary to take both processes into account.

Within a longer period, e. g. annual cycle, the total amount of material within a marine ecosystem is relatively constant, whereas the total amount of energy, which is mostly bound within the organic material, can vary more than an order of magnitude.

The material of an ecosystem appears in different compounds: inorganic (dissolved and particulate) and organic (also dissolved and particulate) material. The living matter contributes only a small amount to the total particulate organic material. The inorganic nutrients are taken up by the phytoplankton to produce organic substances (proteins, carbohydrates and fatty acids) during photosynthesis. This organic material is the main food source for all other heterotrophic organisms within the food web. At each level certain parts of the organic material are remineralised and appear again in the inorganic nutrient pool. Finally all of the organic material is brought back into its inorganic phase by respiration or lysis of plants, animals and bacteria and hence is available for the autotrophic organisms.

Naturally this is only a generalized description. In reality the cycle of material consists of many interrelated processes 'woven' together to form a food web.

Contrary to the cycling of material, the energy flows through the ecosystem. It 'enters' the system through the process of photosynthesis. The phytoplankton uses fractions of solar energy and inorganic nutrients to produce energy-rich compounds. Bound to the organic material, the energy is transported through different trophic levels. All heterotrophic organisms live by converting this chemical energy into thermal energy. The latter leaves the ecosystem and is lost for any further biological use.

Herein an approach to quantify the amount of energy flowing through the pelagic part of the shallow water ecosystem off Boknis Eck during 1973 will be given.

The energy flow can not be measured directly. Therefore it will be calculated using some measurements and determinations of the amount of energy fixed and of the organic material present at different trophic levels. The main parameters used are global radiation (cal cm^{-2} d^{-1}), particulate organic carbon (mg C m^{-2}), caloric content of the particulate matter – seston calories (kcal m^{-2}), primary productivity (g C m^{-2} y^{-1}) and zooplankton (secondary and tertiary) production (g C m^{-2} y^{-1}) and sedimentation (kcal m^{-2} y^{-1}). Various conversion factors are taken from the literature.

Because most of the data are for the annual period, a certain simplification and a restriction to the main parts of the food web is required. That is why e. g. the amount of energy fixed in the dissolved organic material is not taken into consideration. It is assumed that this does not influence the results significantly, because most probably on an annual basis the amounts of energy taken from and supplied to the large pool of dissolved organic material by the organisms are rather similar.

Material and methods

Sampling procedure:

All sampling was carried out off Boknis Eck at the entrance of Eckernförde Bay (54° 32′ N, 10° 03′ E). The station 'Boknis Eck', with an average depth of 20 m, is situated near the deepest part of the 'Hausgarten', a restricted research area of the SFB 95 (Joint Research Programme 'Interaction Sediment – Water Column'). The station 'Boknis Eck' can be regarded as representative for the western part of the Kiel Bight (v. BODUNGEN, 1975; SMETACEK, 1975).

Between January 1973 and April 1974 the station 'Boknis Eck' was visited 46 times in intervals of 3 days to 3 weeks. Samples were taken with a hydrocast (5 l, Hydrobios Kiel) from light depths (100%, 55%, 10% and 1%) and from 20 m.

Incident radiation was measured at the weather station Schleswig with a solarigraph (KIPP and ZONEN, Netherlands) according to MOLL-GORCZYNSKI. The apparatus measures solar radiation between 350 and 1500 nm in cal cm^{-2} d^{-1}.

Caloric determinations of particulate matter were carried out with the method described by v. BRÖCKEL (1973).

Particulate organic carbon was measured with a CHN-analyzer (HEWLETT and PACKARD, 185 B).

Primary productivity data were taken from v. BODUNGEN (1975). V. BODUNGEN determined phytoplankton production using the ^{14}C-in-situ method according to STEEMANNN NIELSEN (1952, 1958). All zooplankton data were derived from MARTENS (1975, 1976). MARTENS calculated the annual secondary and tertiary production (g C m^{-2} y^{-1}) taking into account a) the observed increase of the standing stock, b) the natural mortality from sediment trap samples and c) the predation by carnivorous zooplankton.

Conversion factors:

Potential radiant energy: Only the incident radiation in the range of 380 to 750 nm (STRICKLAND, 1960; BOUGIS, 1974) can be used by phytoplankton for photosynthesis. This part of the spectrum, which corresponds approximately to visible light, is called hence 'potential radiant energy'.

The solarigraph used has a sensitivity range of 350 to 1500 nm for total global irradiation measurements, the potential radiant energy has to be calculated.

According to several authors (EDMONDSON, 1956; RYTHER, 1956; McALLISTER et al., 1961; ANDERSON, 1967; TALLING, 1971, TILZER, 1972; BOUGIS, 1974; STEEMANN NIELSEN, 1974) between 42.5 and 52.3% of the incident radiation can be used by phytoplankton. According to these authors, the value of 45% given by ANDERSON (1967) is an average value.

For the calculation of the potential radiant energy it is assumed that 45% of the incident radiation measured can be used by phytoplankton to produce energy-rich substances.

An additional loss of energy is due to the reflection of the irradiation at the air-water interface. The amount of reflected energy depends on the angle of incidence for direct sunlight, the cloud cover of the sky and the wave action.

With increasing angle of incidence (from 5 to 90°) the amount of energy reflected decreases (from 40 to 3%) (SVERDRUP, 1953). A cloudy sky amounts to a more diffusive radiation with less reflection. With increasing wave action due to stronger winds, the reflection of the incident radiation increases, specially due to air bubbles building up near the water surface.

RYTHER (1956), STRICKLAND (1958), TALLING (1971) and PARSONS and TAKAHASHI (1973) give values of 5 to 30% for the loss of radiant energy due to reflection at the water surface. According to TALLING (1971) 10% is an average value.

Thus the potential radiant energy is calculated as 45% of the global irradiation minus 10% as a reflection loss.

Phytoplankton production:

The transformation of radiant energy into chemical energy by phytoplankton during the photosynthesis is hence called 'phytoplankton production' and given in energetic terms (kcal m^{-2}). It is not possible to measure this transformation of energy directly. Furthermore it is not possible, to determine the amount of energy bound within a given phytoplankton population, because there is no method available to separate living phytoplankton cells from detritus with all its organic and inorganic compounds. Therefore the input of energy by phytoplankton is calculated using the data for particulate organic carbon (g C m^{-2}), ^{14}C production (mg C m^{-2} d^{-1}) and caloric content of the particulate matter (seston calories) (kcal m^{-2}), with the assumption that the relationship of particulate organic carbon to produced particulate organic carbon (carbon content of seston to organic carbon produced by phytoplankton) is equal to the relationship of seston calories to the input of energy (caloric content of seston to energy uptake by phytoplankton):

$$\frac{\text{particulate organic carbon} : {}^{14}\text{C-production}}{\text{seston calories} : \text{input of energy}} =$$

This assumption includes that the relations of caloric to carbon content are equal for living phytoplankton and detritus, although phytoplankton has a higher energetic content per carbon than detritus. Therefore values gained with this equation for the energy input of phytoplankton are slightly too low.

The data of v. BODUNGEN for the ^{14}C production are somewhere between the gross and net production (STRICKLAND, 1960), most probably closer to the net production (ANTIA et al., 1963; McALLISTER et al., 1961). The ^{14}C method does not consider production of released organic material. This production of dissolved organic carbon can reach considerable amounts. Depending on the physiological state of the phytoplankton population it is somewhere between 2 and 90% of the particulate organic carbon produced (KROGH, 1931; ANTIA et al. 1963; DUURSMA, 1965; WEBER and MOORE, 1967; ANDERSON and ZEUTSCHEL, 1970).

Therefore the obtained data for the energy input of phytoplankton are regarded to be similar to the net production and are hence referred to as 'phytoplankton net production'.

Zooplankton production:

MARTENS (1975, 1976) calculated the secondary and tertiary net production and the sedimentation rate for the second and third level of the food web. His data are presented in g C m^{-2} y^{-1}.

The relation between organic carbon and dry weight and between organic substances and dry weight are assumed to be 45 and 85% respectively (PARSONS and TAKAHASHI, 1973).

According to WINBERG (1971) the caloric content of organic material within 'aquatic animals' is 5.6 cal mg^{-1} (in the range of 4.74 to 6.42 cal mg^{-1}). Data from other authors and own measurements are in agreement with this value (RICHMAN, 1958; PLATT et al., 1969; CUMMINS and WUYCHECK, 1971).

The energy input of the secondary and tertiary zooplankton, furtheron called 'secondary net production' and 'tertiary net production' and the sedimentation of the second and the third level of the food web are converted into energetic equivalents (kcal m^{-2} y^{-1}) using the above mentioned data: net production (kcal m^{-2} y^{-1}) = net production (g C m^{-2} y^{-1}) × 2.22 × 0,85 × 5.6.

Results and Discussion

The hydrographical conditions during 1973 were rather unstable. Due to wind induced turbulence and an increased short term in – and outflow of low and high salinity water from the Baltic Proper and the Skagerrak respectively, no stable halocline could be observed over a longer period, which is normally present during late summer (v. BODUNGEN, 1975). A detailed description of hydrographical and chemical conditions and of primary productivity in the western part of Kiel Bight is given by v. BODUNGEN (1975).

These unstable conditions influenced the annual phytoplankton succession. A very detailed description of the composition and the organic content of the different phytoplankton populations can be obtained from SMETACEK (1975). The total number of phytoplankton blooms in 1973 increased to nine, compared to 1972 where only 5 phytoplankton blooms could be observed. The nine blooms of 1973 were less distinct in their composition. The total amount of energy fixed and of organic material produced during 1973 was similar to the data obtained for other years.

The total irradiation is shown in Fig. 1 as the daily radiation (small dots) and the seven days running mean with one day lag (large dots). Remarkable is the fast increase within a few days at the beginning of March and the great variability of the daily irradiation within short periods. A more detailed description is given by v. BRÖCKEL (1975).

The calculated potential radiant energy is shown in Fig. 2. The total amount of potential radiant energy in 1973 was $3.46 \cdot 10^5$ kcal m^{-2} y^{-1}. V. BODUNGEN presented his data for different seasons of the year. To get more informations from the data under consideration here the same classification is taken to present the data for potential radiant energy and for phytoplankton net production. The periods of the different seasons according to v. BODUNGEN (1975) are:

winter	15.11.–15. 2.	93 days
spring	16. 2.–31. 5.	105 days
summer	1. 6.–31. 8.	92 days
autumn	1. 9.–13.11,	75 days

This classification is chosen, because the first spring bloom occurs mainly in the second half of February and the last autumn bloom may last until the beginning of November. In Tab. 1 the potential radiant energy (for the periods of winter 1972/73 to winter 1973/74) is presented as well as the annual value. Note that the sum of all periods yield a higher value than the annual one, because there are two winters included.

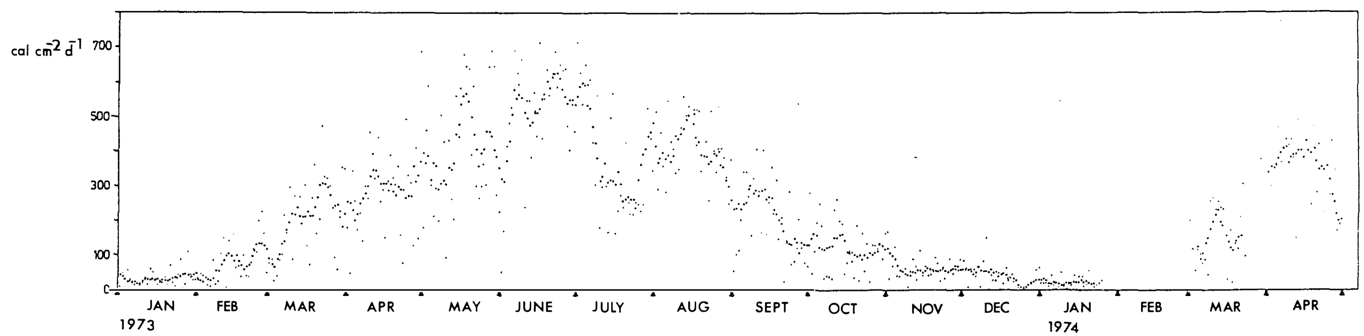

Figure 1

Global radiation, January 1973 to April 1974 (in cal cm⁻² d⁻¹) small dots: daily values large dots: seven days running mean with one day lag

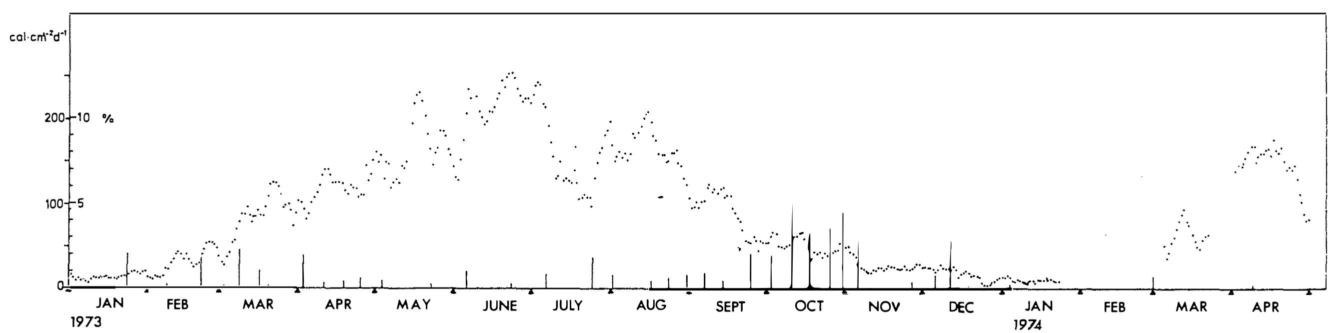

Figure 2

Potential radiant energy (seven days running mean with one day lag in cal cm⁻² d⁻¹) and the efficiency rates of the phytoplankton (columns), January 1973 to April 1974

Table 1
Potential radiant energy, phytoplankton net production and transfer efficiency for 1973 and its seasons

	Potential radiant energy (kcal m^{-2})	Phytoplankton net production (kcal m^{-2})	Transfer efficiency (%)
1973	$34.64 \cdot 10^4$	$2.66 \cdot 10^3$	0.77
Winter 72/73	$1.31 \cdot 10^4$	$0.07 \cdot 10^3$	0.55
Spring 73	$11.98 \cdot 10^4$	$0.64 \cdot 10^3$	0.54
Summer 73	$16.51 \cdot 10^4$	$1.44 \cdot 10^3$	0.87
Autumn 73	$4.50 \cdot 10^4$	$0.58 \cdot 10^3$	1.28
Winter 73/74	$1.54 \cdot 10^4$	$0.09 \cdot 10^3$	0.59

A rapid increase of potential radiant energy from winter 1972/73 to spring 1973 can be seen ($1.31 \cdot 10^4$ to $11.98 \cdot 10^4$ kcal m^{-2}), a further increase from spring to summer ($11.98 \cdot 10^4$ to $16.51 \cdot 10^4$ kcal m^{-2}), is followed by a sharp decline towards the autumn (to $4.50 \cdot 10^4$ kcal m^{-2}) and another smaller decrease of the usual low winter value ($1.54 \cdot 10^4$ kcal m^{-2}).

In energetic terms phytoplankton net production for 1973 amounted to $2.66 \cdot 10^3$ kcal m^{-2} y^{-1}. The average transfer efficiency between the potential radiant energy and the phytoplankton net production was 0.77%. In Tab. 1 the phytoplankton net production and the transfer efficiencies during the different seasons are presented. It is remarkable that transfer efficiencies do not increase between winter and spring (0.55 and 0.54% respectively), whereas a steady increase towards the autumn can be observed (Fig. 2). The highest transfer efficiency for 1973 was 5.3% on October 10th. It seems that due to the decrease towards the end of autumn potential radiant energy becomes the limiting factor for the phytoplankton growth. Although the phytoplankton population is able to use a relative high amount of the available energy it is not enough to support a further development of the population.

According to STRICKLAND (1965) the transfer efficiencies for productive and less productive oceans are about 5.0 and 1.0% respectively. Data given by other authors (cited by v. BRÖCKEL, 1975) are in the same range as the values presented here.

In 1973 the secondary and tertiary net production amounted to $3.58 \cdot 10^2$ and $5.49 \cdot 10^1$ kcal m^{-2} y^{-1} respectively.

CUSHING (1973) calculated the 'transfer coefficient' (the efficiency between the net production of two following trophic levels) for the Indian Ocean to 2 to 34%. PARSONS and TAKAHASHI (1973) named the transfer efficiency 'ecological efficiency' and presented data in the range of 10 to 20%, with an average value of 15%. RYTHER (1969) gives a correlation between the number of trophic levels within an ecosystem and its efficiency rates:

	trophic levels	transfer efficiencies %
oceanic	5	10
coastal	3	15
upwelling	1.5	20

Here the transfer efficiencies corresponding to the primary production, the secondary net production and the tertiary net production are 13.5% (between the first and the second trophic level) and 15.3% (between the second and third trophic level) respectively.
The calculated energy uptake of secondary and tertiary producers requires a higher ingestion of energy rich organic material. With the assumption, that the zooplankton uses its ingested food for respiration, net production and production of fecal pellets in relation of 1:1:1 – a similar value is presented by STEELE (1974) for a North Sea copepod – then uptake is three times as high as net production. Using this assumption secondary zooplankton ingested 40.2% of the phytoplankton net production and tertiary zooplankton 46.1% of the secondary net production (corresponding to 6.2% of the phytoplankton net production).

The sedimentation (natural mortality) of secondary and tertiary zooplankton was calculated to $1.93 \cdot 10^2$ and $1.45 \cdot 10^1$ kcal m^{-2} y^{-1} (corresponding to 7.3 and 0.5% of phytoplankton net production) respectively.

According to ITURRIAGA (1977) a substantial amount of particulate organic material, for which the phytoplankton net production is the main source, is remineralised within the euphotic zone in very short periods. In his experiments 10 to 15% of natural phytoplankton material was remineralised within a day. GOCKE (pers. comm.) calculated the bacterial production of Kiel Bay to 23% of the phytoplankton production.

Bacteria have a high efficiency (relation of ingested food to incorporated material) of 60 to 70% (ITURRIAGA, 1977). Therefore it seems reasonable to assume that about 25% of the phytoplankton net production is remineralised already in the water column by bacteria, corresponding to $6.65 \cdot 10^2$ kcal m^{-2} y^{-1}.

The remaining 35% of the phytoplankton net production ($9.25 \cdot 10^2$ kcal m^{-2} y^{-1}) are not consumed within the water column, but sink directly to the sediment, where this matter serves as a food source for the benthic heterotrophic organisms. According to v. BRÖCKEL (1975) and MARTENS (1975, 1976) there was no substantial grazing on the first spring bloom and on the last two autumn blooms. A few days after the end of the spring bloom, scuba divers observed (v. BODUNGEN et al., 1974) a few centimeter thick 'green carpet', obviously mainly the remains of the former phytoplankton population, lying on the sediment.

Therefore it seems reasonable to assume that 35% of the phytoplankton net production sink directly to the sediment surface.

In Fig. 3 the ecosystem off Boknis Eck within a 20 m water column is presented. In 1973 the total amount of potential radiant energy was $3.46 \cdot 10^5$ kcal m^{-2} y^{-1} of which 0.77% were fixed within the phytoplankton net production (corresponding to $2.66 \cdot 10^3$ kcal m^{-2} y^{-1}). Nearly 35% of the phytoplankton net production sedimented directly ($9.25 \cdot 10^2$ kcal m^{-2} y^{-1}), about 41% of the phytoplankton net production were remineralised within the water column: by bacterial activities (25% or $6.65 \cdot 10^2$ kcal m^{-2} y^{-1}), by secondary zooplankton respiration (13.5% or $3.58 \cdot 10^2$ kcal m^{-2} y^{-1}) and by tertiary zooplanktion respiration (2.1% or $5.49 \cdot 10^1$ kcal m^{-2} y^{-1}). $1.07 \cdot 10^3$ kcal m^{-2} y^1 or 40.2% of the phytoplankton net production were ingested by secondary zooplankton, of which $1.65 \cdot 10^2$ kcal m^{-2} y^{-1} were taken up by the tertiary zooplankton. The further transfer within the pelagic food web was $4.34 \cdot 10^1$ kcal m^{-2} y^{-1} corresponding to 1.6% of the phytoplankton net production. The total input to the sediment amounted to $1.55 \cdot 10^3$ kcal m^{-2} y^{-1} (corresponding to 58.3% of the phytoplankton net production), of which $5.51 \cdot 10^2$ kcal m^{-2} y^{-1} were derived from secondary zooplankton and $6.94 \cdot 10^1$ kcal m^{-2} y^{-1} from tertiary zooplankton.

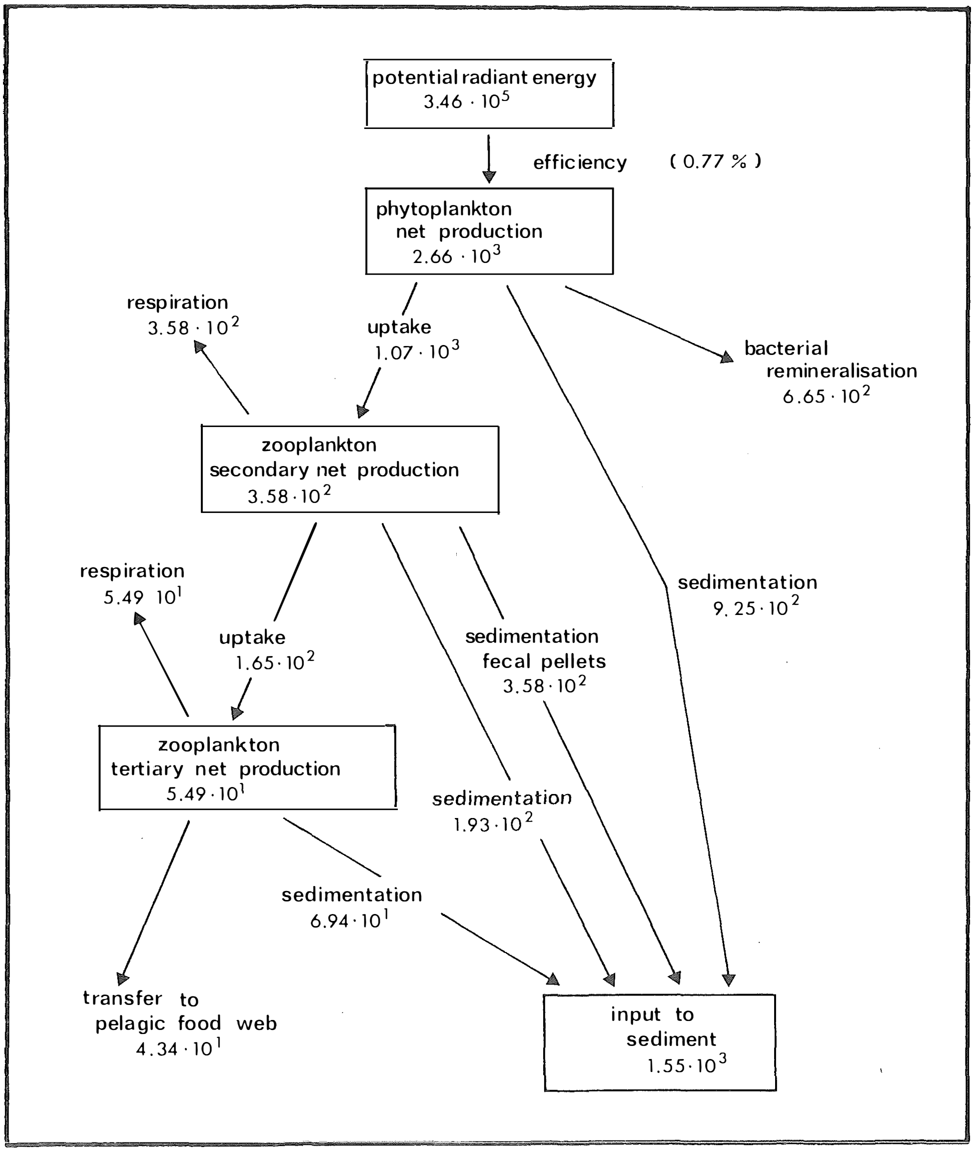

Figure 3

The energy flow in the pelagic part of the ecosystem off Boknis Eck, Eckernförde Bay, for the 20 m water column in 1973 in kcal m^{-2} y^{-1}

The data presented above are only part of the results of direct measurements. The greater part is derived from assumptions and through calculations using conversion factors which represent only general relationships. To get a more realistic picture of the energy flow of the ecosystem more details are required e. g. about the amount of energy fixed at different levels of the food web, the respiration rates of heterotrophic organisms, the sedimentation rate of organic material and the energy requirements of the benthic part of the ecosystem.

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