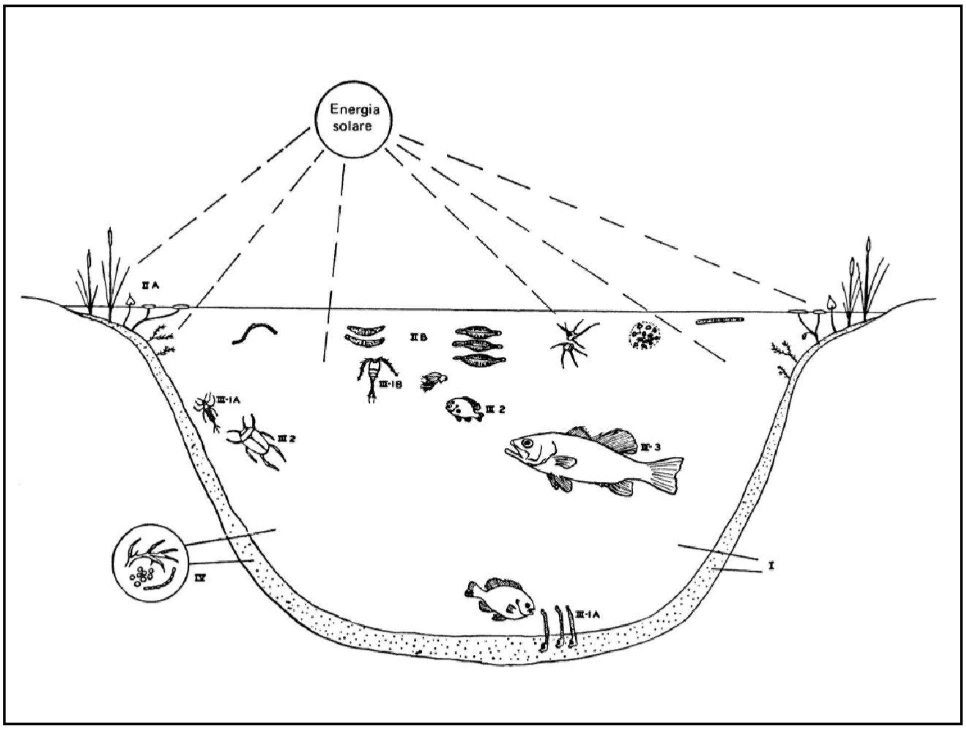
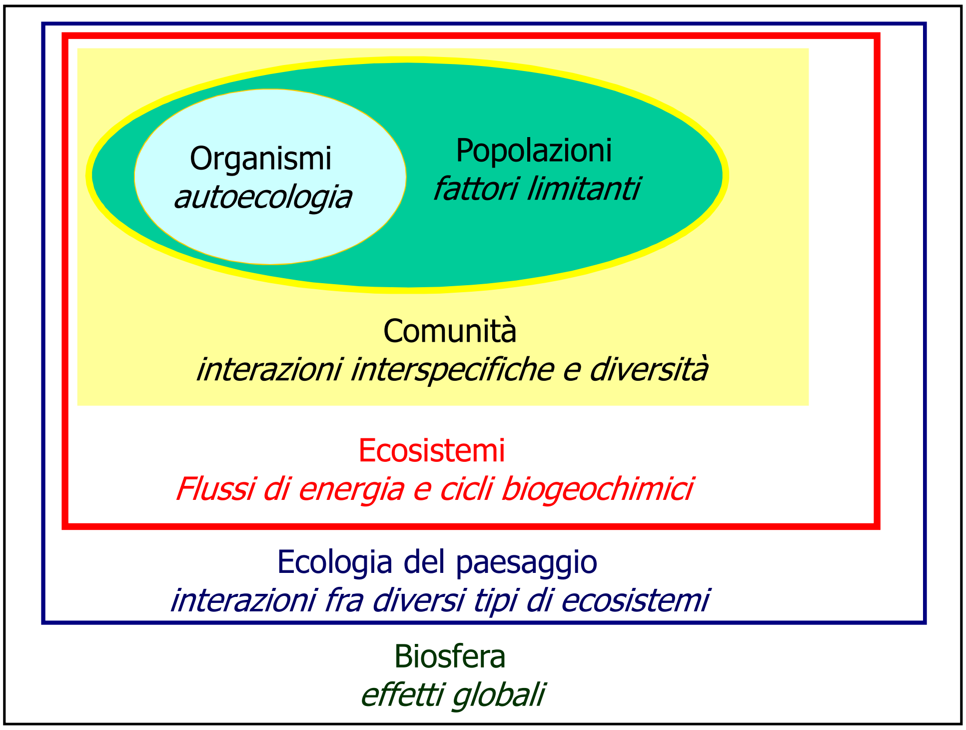
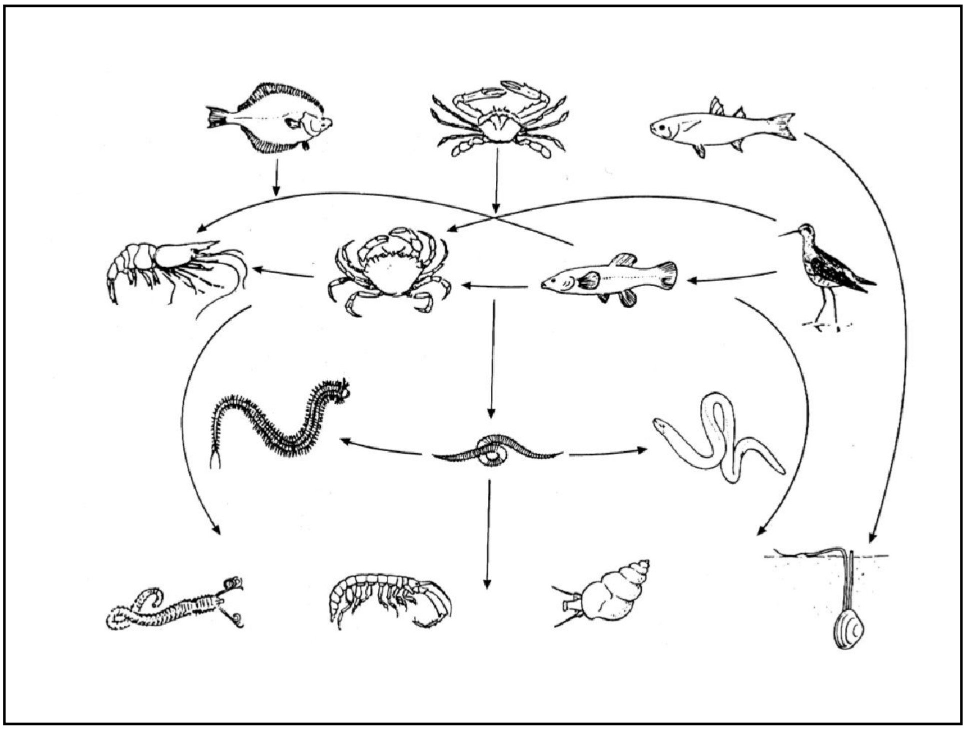
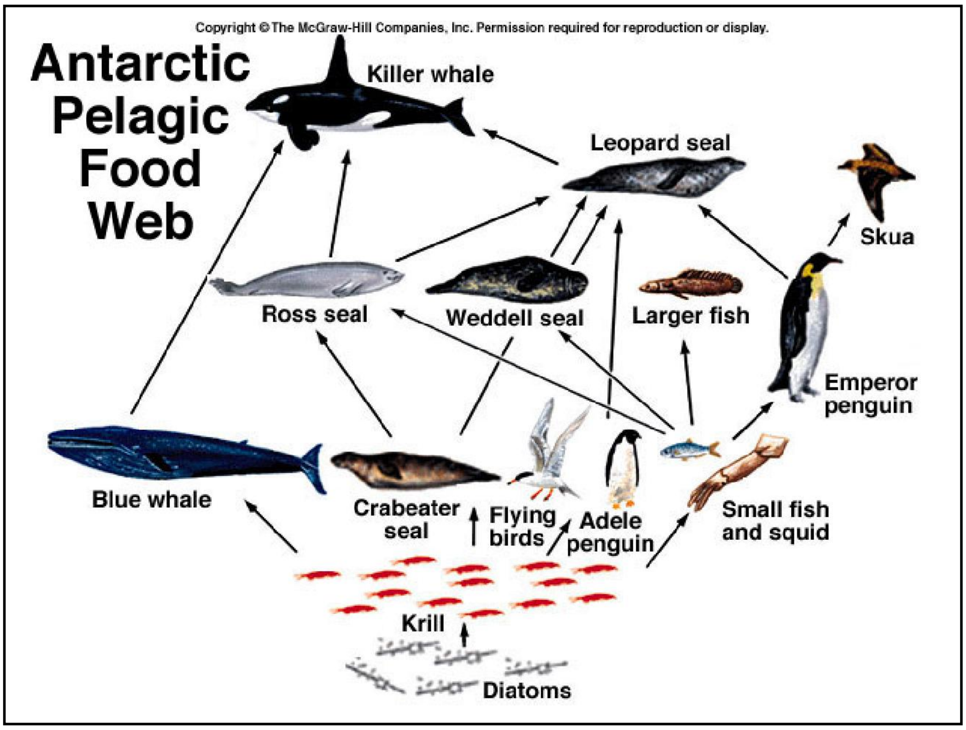

Energia solare


Organismi
autoecologia
Popolazioni
fattori limitanti
Comunità
interazioni interspecifiche e diversità
Ecosistemi
Flussi di energia e cicli biogeochimici
Ecologia del paesaggio
interazioni fra diversi tipi di ecosistemi
Biosfera
effetti globali





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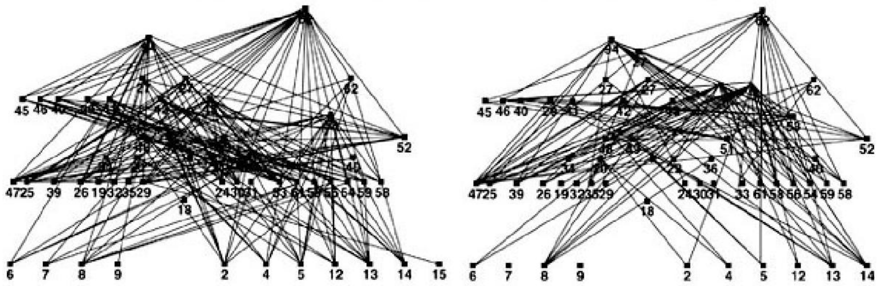
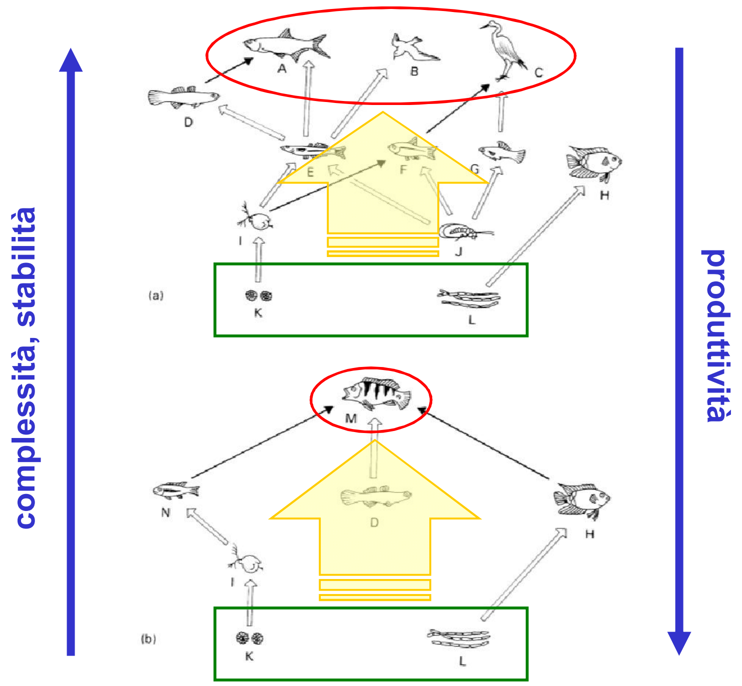
Antarctic Pelagic Food Web
Killer whale
Leopard seal
Skua
Ross seal
Weddell seal
Larger fish
Emperor penguin
Blue whale
Crabeater seal
Flying birds
Adele penguin
Small fish and squid
Krill
Diatoms

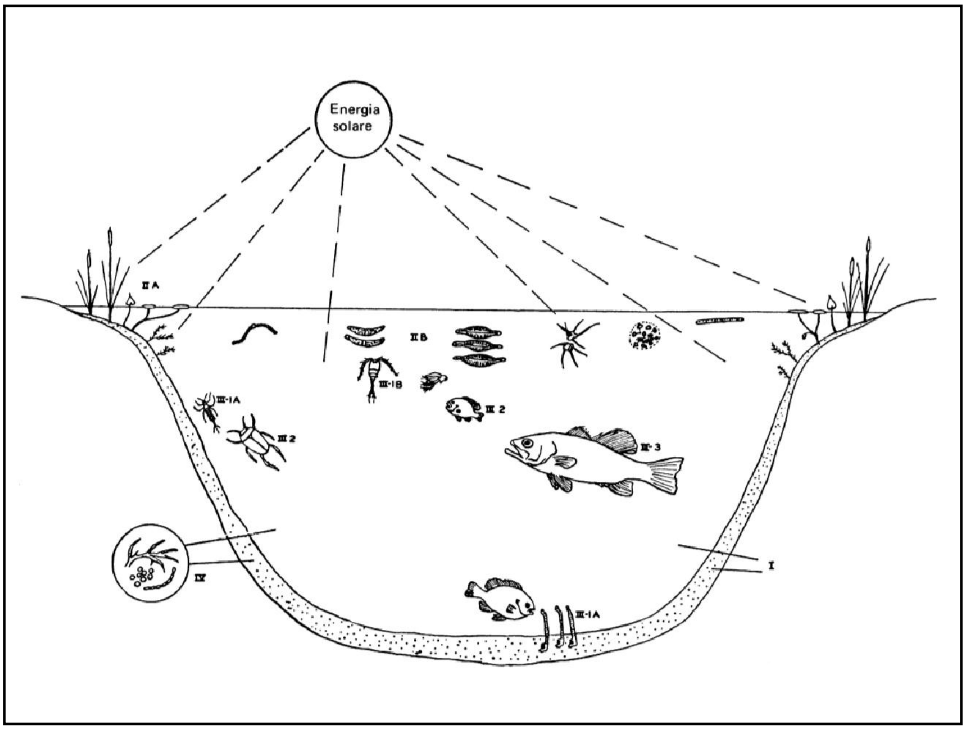
Feeding Relations of Fish

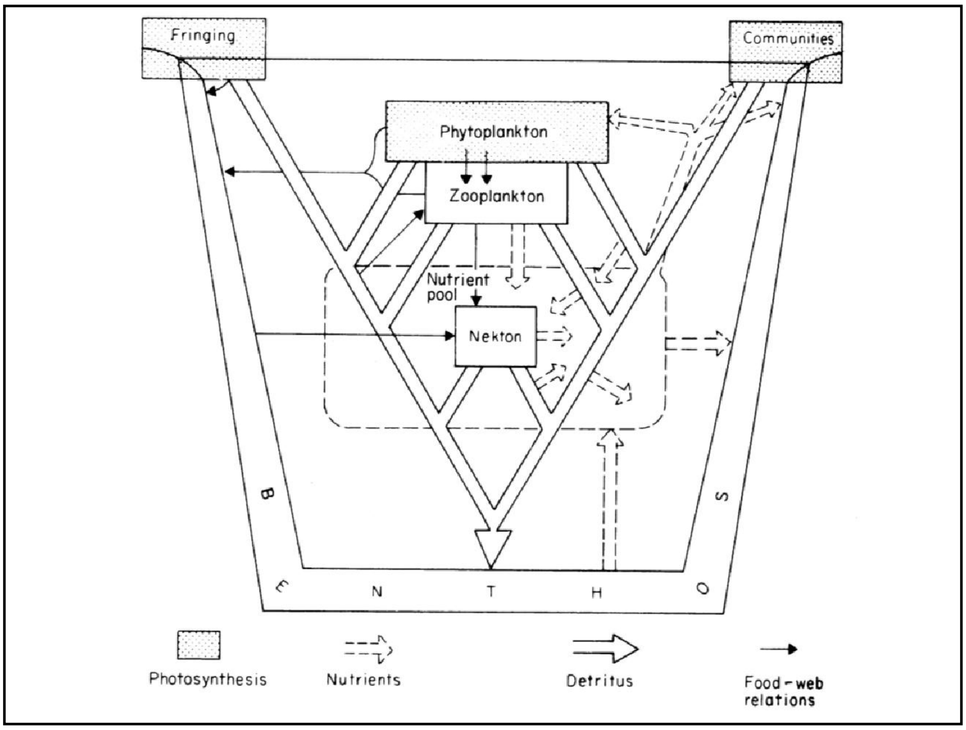


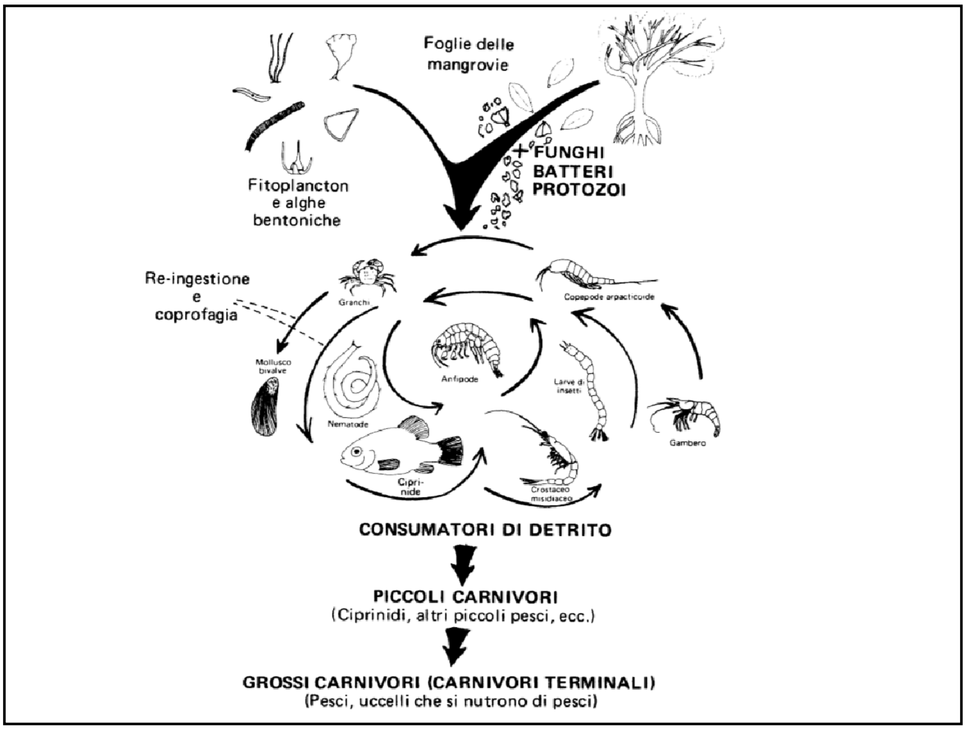
Even a food web with only 10 fish species and their foods can be very complex.

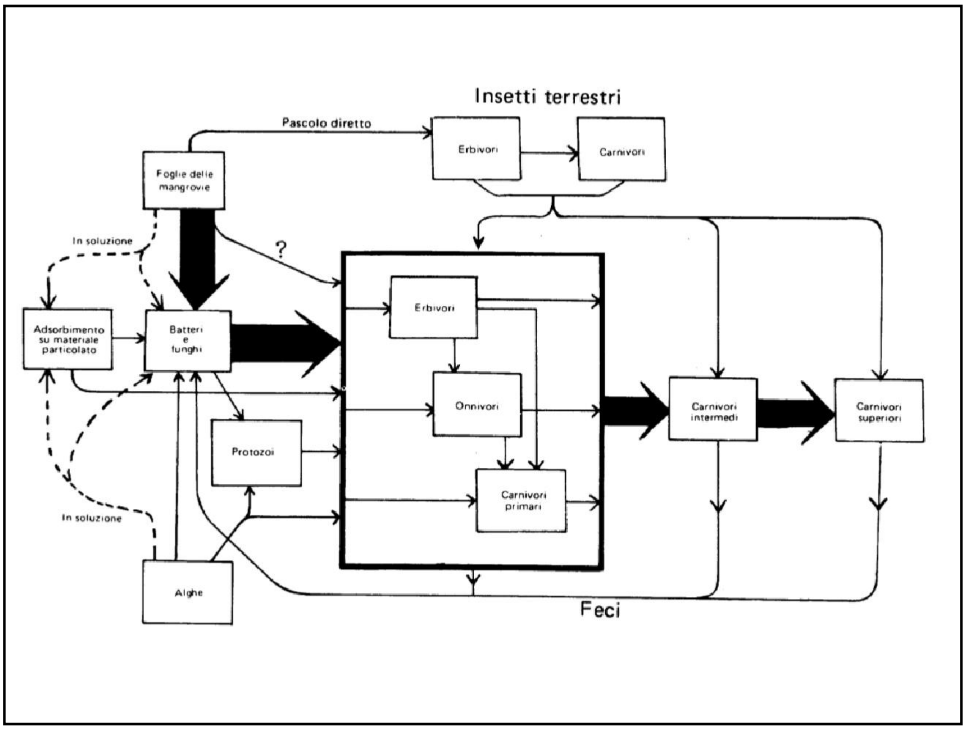
However, removing weak feeding relationships produces a more understandable picture of the community.

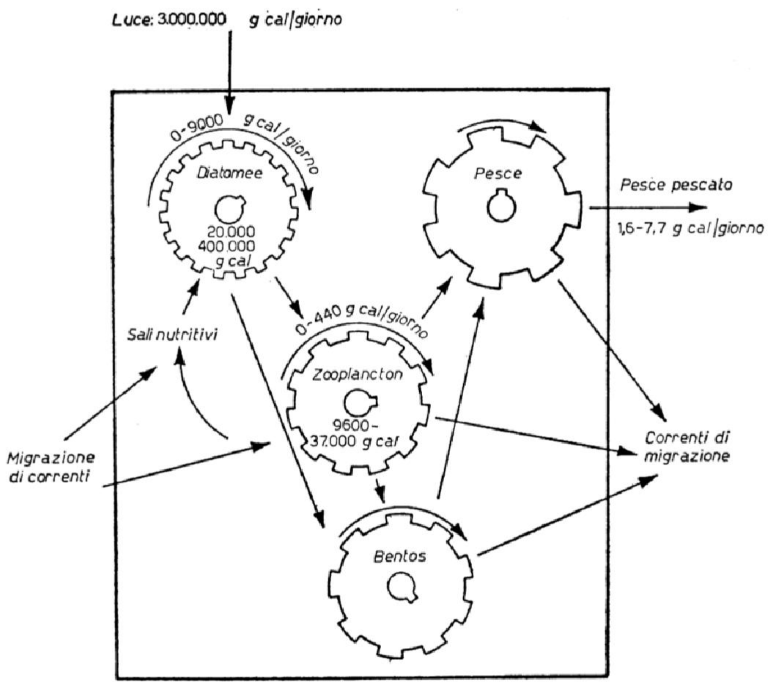



Energia
solare


Fringing
Communities
Phytoplankton
Zooplankton
Nutrient
pool
Nekton
B
E
N
T
H
O
S
Photosynthesis
Nutrients
Detritus
Food-web
relations

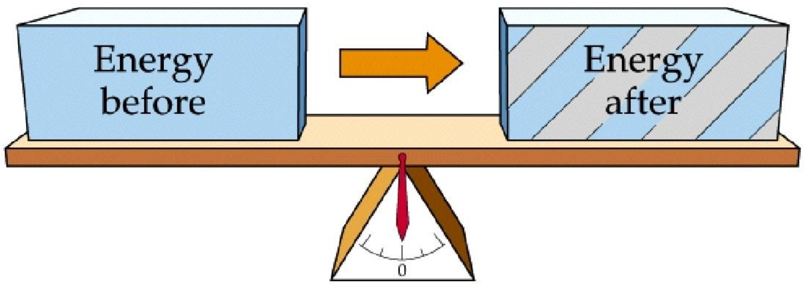

Foglie delle mangrovie
+ FUNGHI
BATTERI
PROTOZOI
Fitoplancton e alghe bentoniche
Re-ingestione e coprofagia
Granchi
Copepode arpacticoide
Mollusco bivalve
Anfipode
Larve di insetti
Nematode
Gambero
Ciprinide
Crostaceo misidiaceo
CONSUMATORI DI DETRITO
PICCOLI CARNIVORI
(Ciprinidi, altri piccoli pesci, ecc.)
GROSSI CARNIVORI (CARNIVORI TERMINALI)
(Pesci, uccelli che si nutrono di pesci)


Insetti terrestri
Pascolo diretto
Erbivori
Carnivori
Foglie delle mangrovie
In soluzione
?
Adsorbimento su materiale particolato
Batteri e funghi
Erbivori
Onnivori
Protozoi
Carnivori primari
Carnivori intermedi
Carnivori superiori
In soluzione
Alghe
Feci



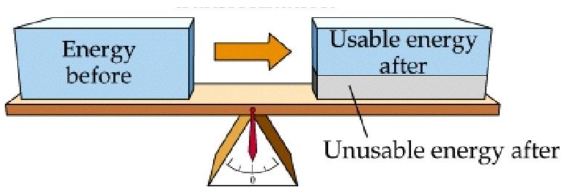
Prima legge della termodinamica

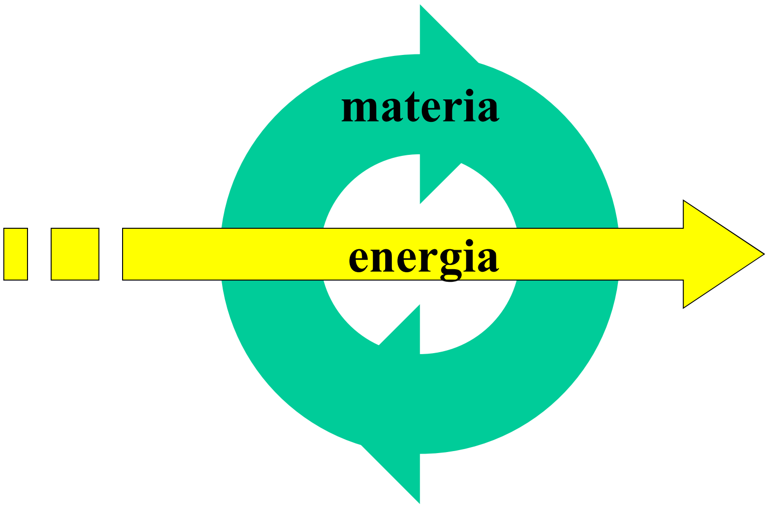
L'energia si conserva: non può essere nè creata nè distrutta, ma solo trasformata.



Seconda legge della termodinamica

Le trasformazioni dell'energia non sono mai completamente efficienti: esse comportano una parziale dissipazione sotto forma di calore (l'entropia dell'universo è costantemente in aumento).

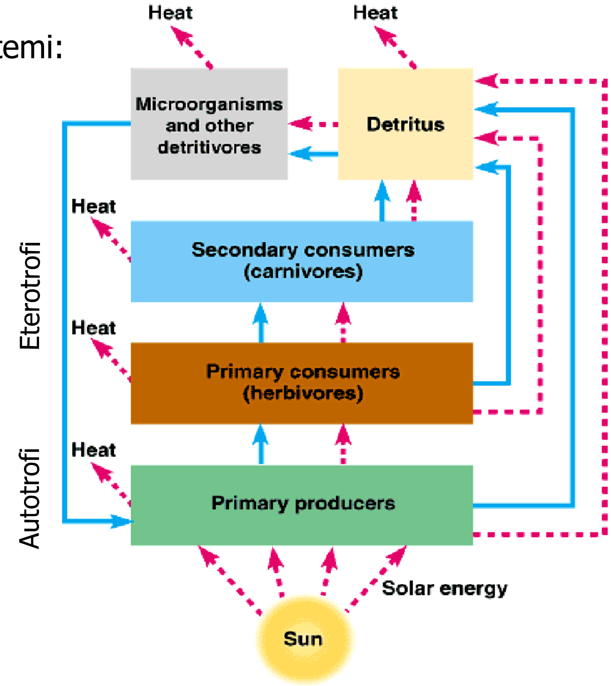


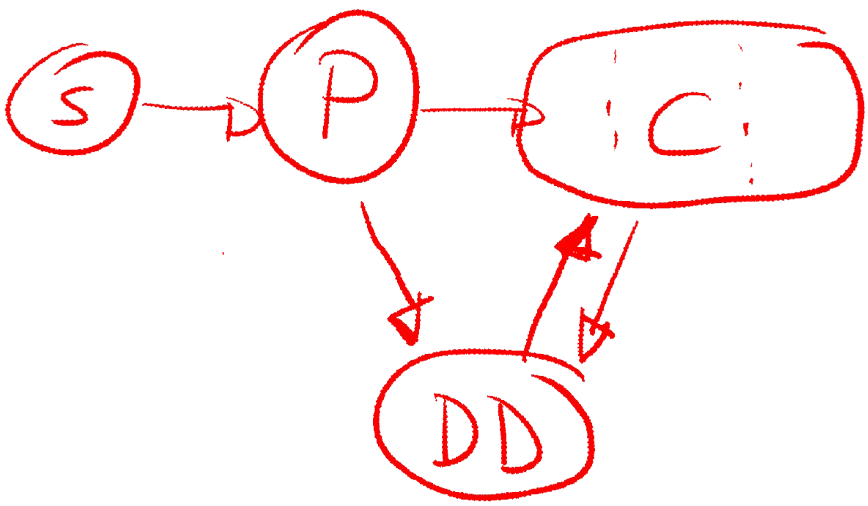


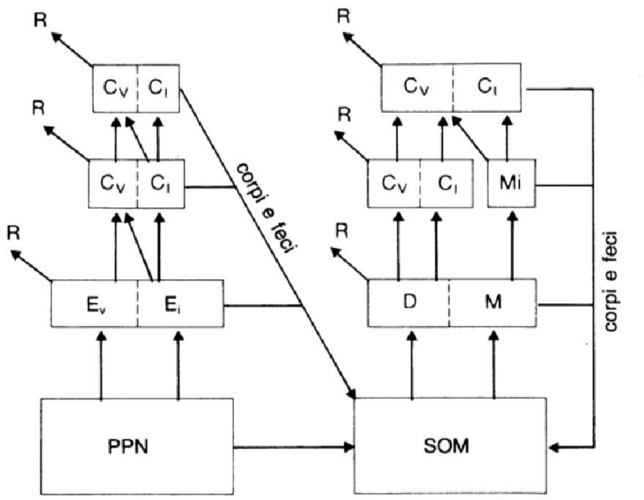
Dinamica degli ecosistemi:
1- Flussi di energia
2- Cicli biogeochimici

ENERGIA – Non puo' essere riciclata, fluisce attraverso gli ecosistemi, proviene da una fonte esterna. Entra come luce ed esce come calore.

MATERIA – Circola all'interno degli ecosistemi.



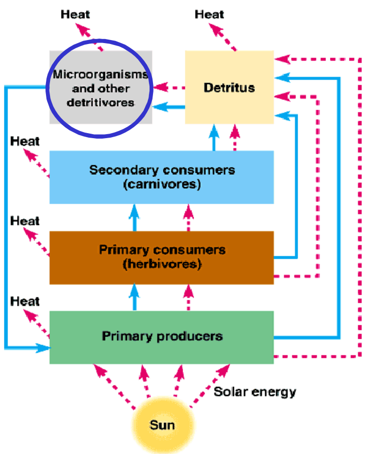


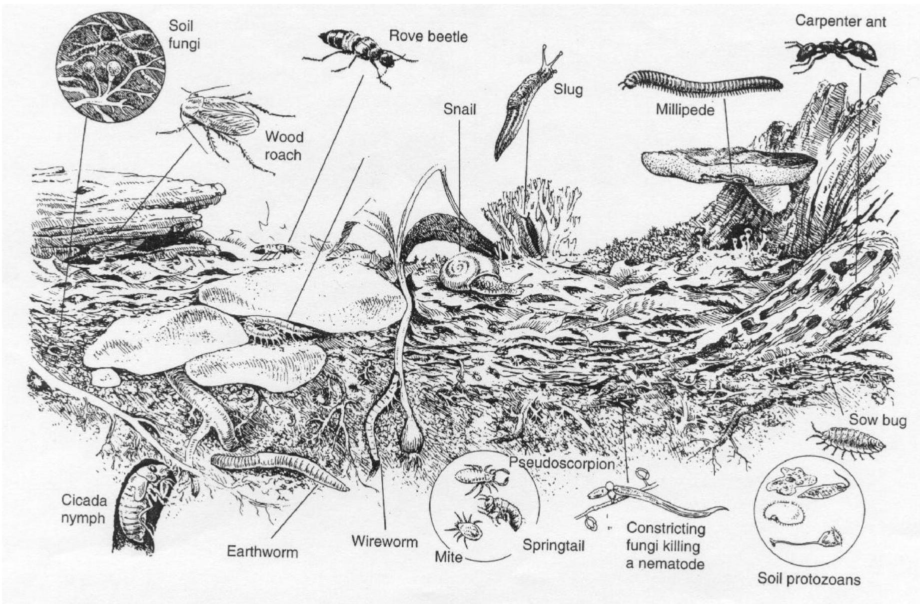


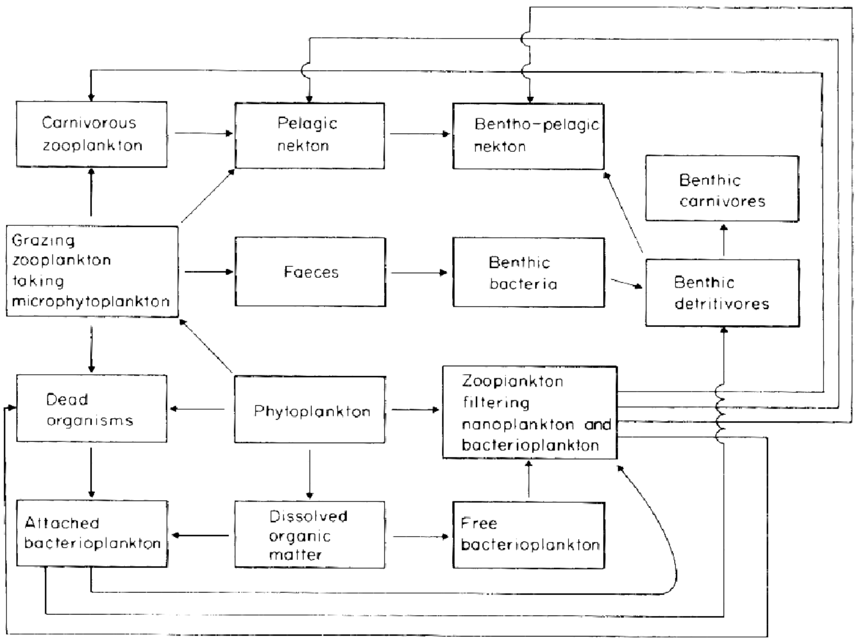
v vertebrato
i invertebrato
PPN produzione primaria netta
SOM sostanza organica morta
E erbivoro
C carnivoro
D detritivoro
M microrganismi
Mi microbivoro

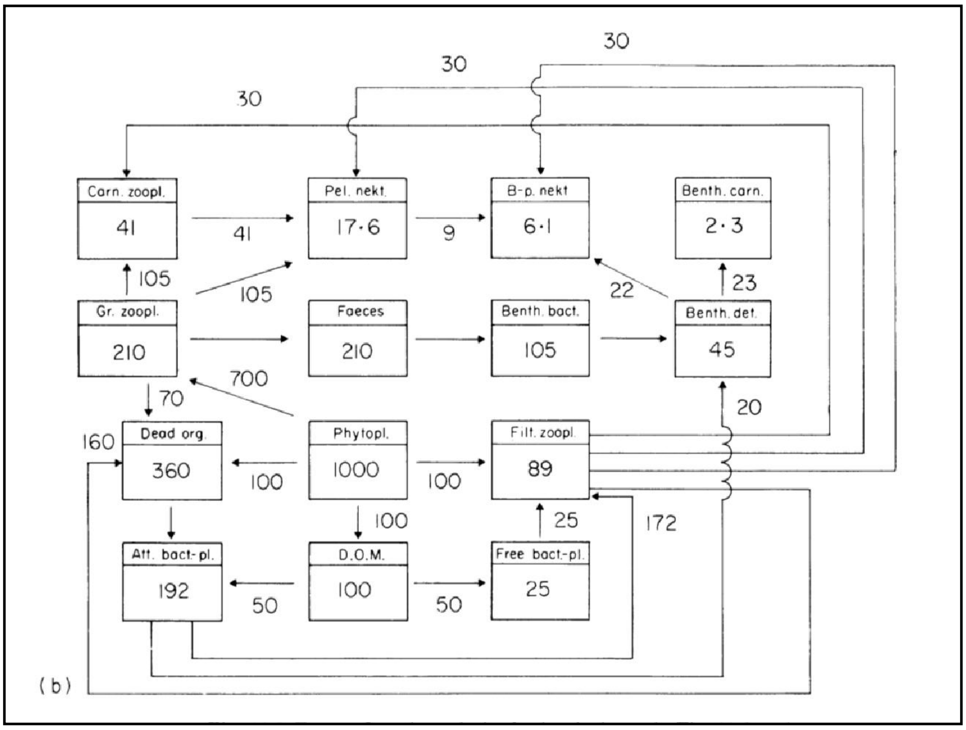
Interconnessioni fra livelli trofici:

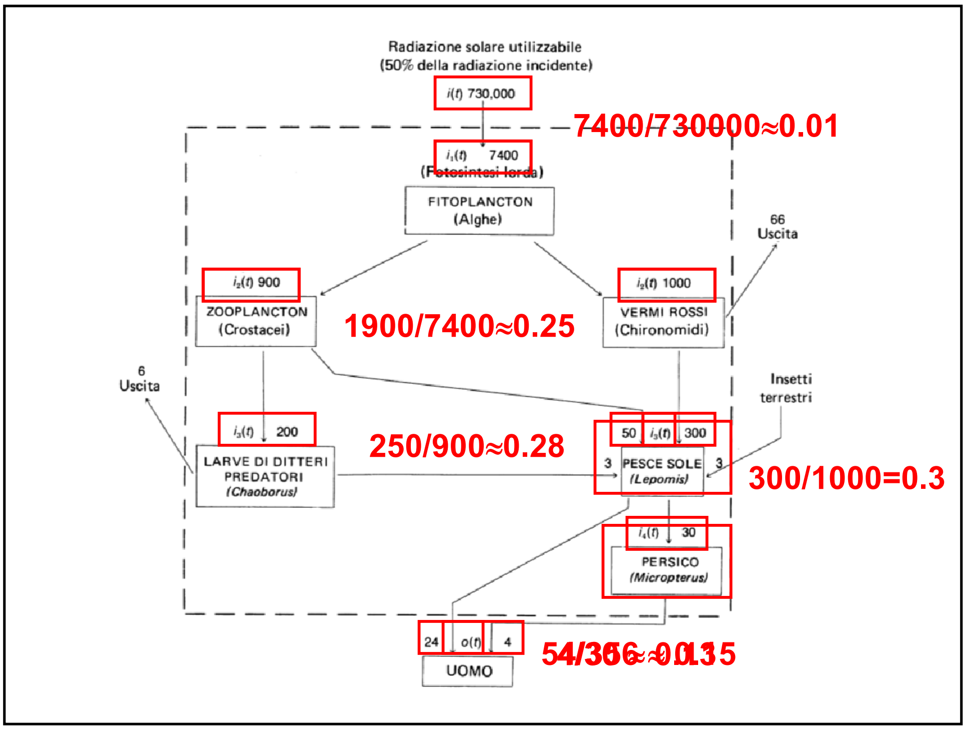
- Tutti i livelli trofici sono connessi fra loro attreverso i decompositori.
- Batteri e funghi riciclano gli elementi che costituiscono la materia organica, decomponendola.
- Senza decomposizione non ci sarebbe vita.

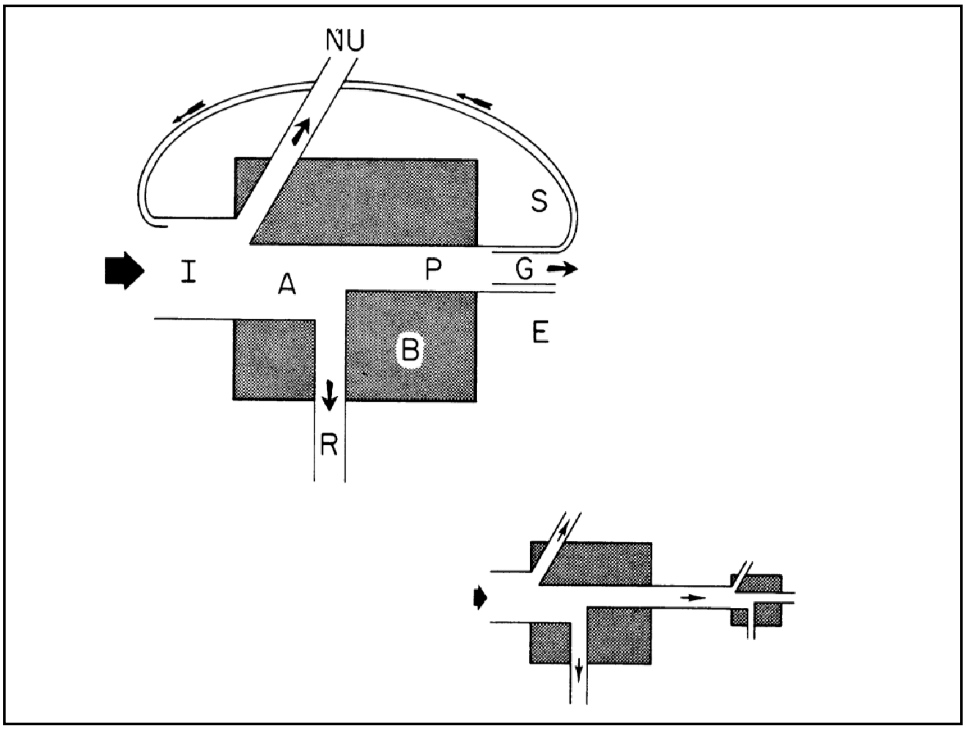


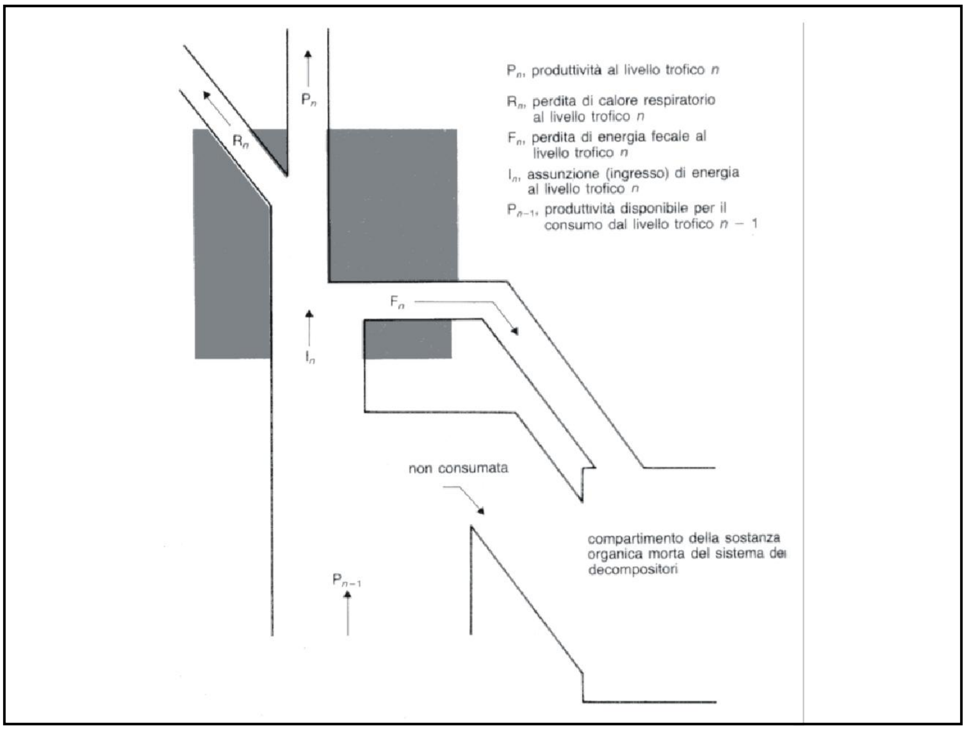

Soil fungi
Rove beetle
Carpenter ant
Slug
Snail
Millipede
Wood roach
Sow bug
Pseudoscorpion
Cicada nymph
Constricting fungi killing a nematode
Earthworm
Wireworm
Mite
Springtail
Soil protozoans

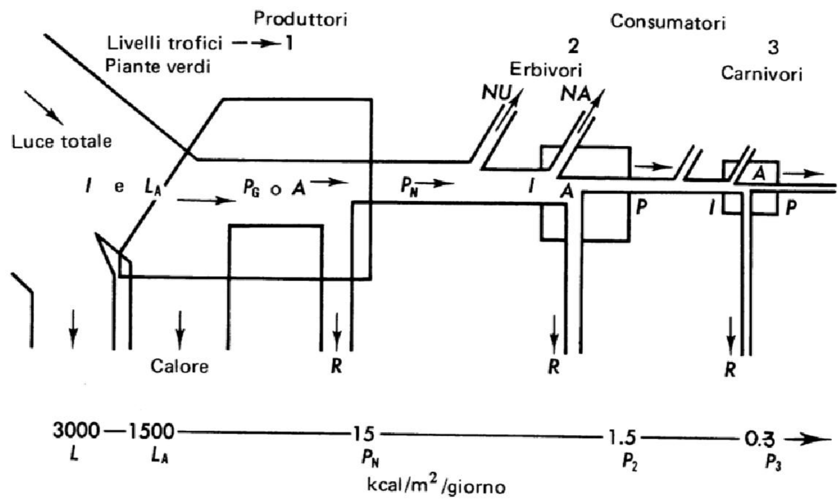

Carnivorous zooplankton
Pelagic nekton
Bentho-pelagic nekton
Benthic carnivores
Grazing zooplankton taking microphytoplankton
Faeces
Benthic bacteria
Benthic detritivores
Dead organisms
Phytoplankton
Zooplankton filtering nanoplankton and bacterioplankton
Attached bacterioplankton
Dissolved organic matter
Free bacterioplankton

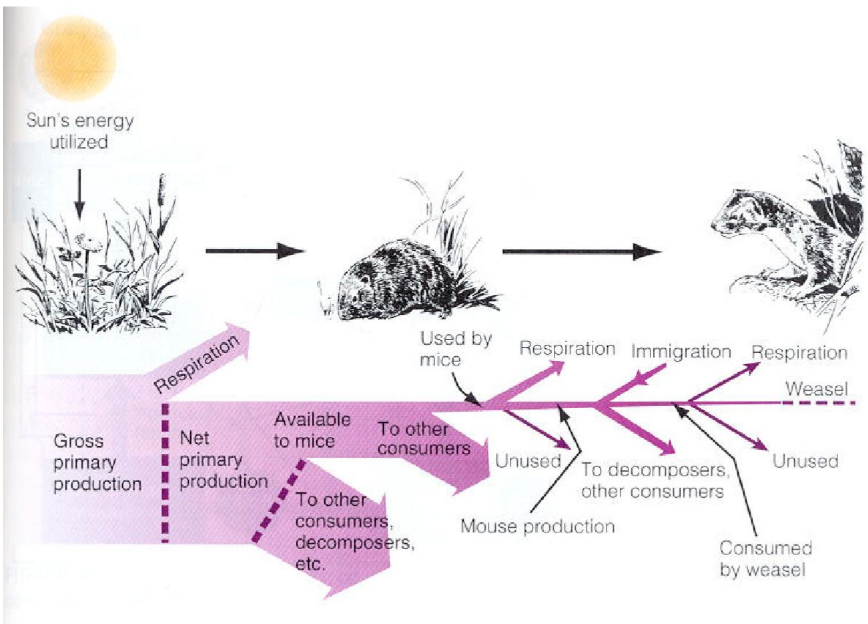

30
30
30
Carn. zoopl.
41
41
Pel. nekt.
17·6
9
B-p. nekt
6·1
Benth. carn.
2·3
105
105
22
23
Gr. zoopl.
210
Faeces
210
Benth. bact.
105
Benth. det.
45
70
700
20
160
Dead org.
360
100
Phytopl.
1000
100
Filt. zoopl.
89
100
25
172
Att. bact-pl.
192
50
D.O.M.
100
50
Free bact-pl.
25
(b)


Radiazione solare utilizzabile
(50% della radiazione incidente)
i(t) 730,000
7400/730000≈0.01
i1(t) 7400
FITOPLANCTON
(Alghe)
66
Uscita
i2(t) 900
ZOOPLANCTON
(Crostacei)
1900/7400≈0.25
i2(t) 1000
VERMI ROSSI
(Chironomidi)
6
Uscita
Insetti
terrestri
i3(t) 200
250/900≈0.28
50
i3(t)
300
LARVE DI DITTERI
PREDATORI
(Chaoborus)
3
PESCE SOLE
(Lepomis)
3
300/1000=0.3
i4(t) 30
PERSICO
(Micropterus)
24
o(t)
4
UOMO

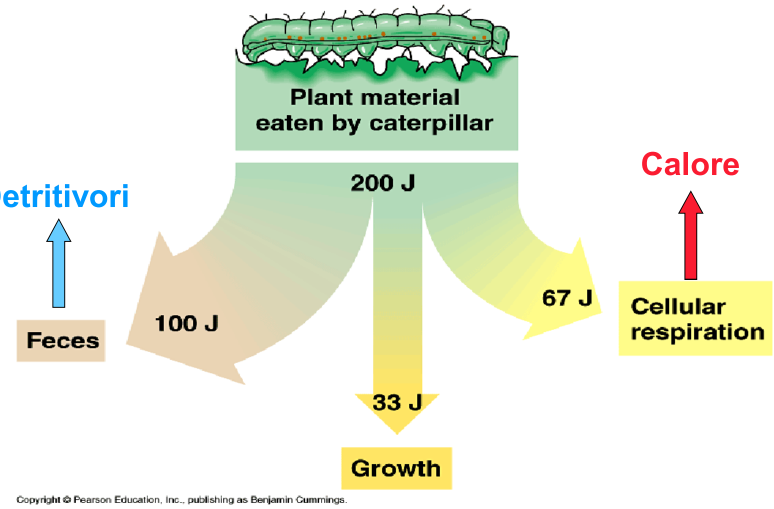

NU
S
I
A
P
G
E
B
R

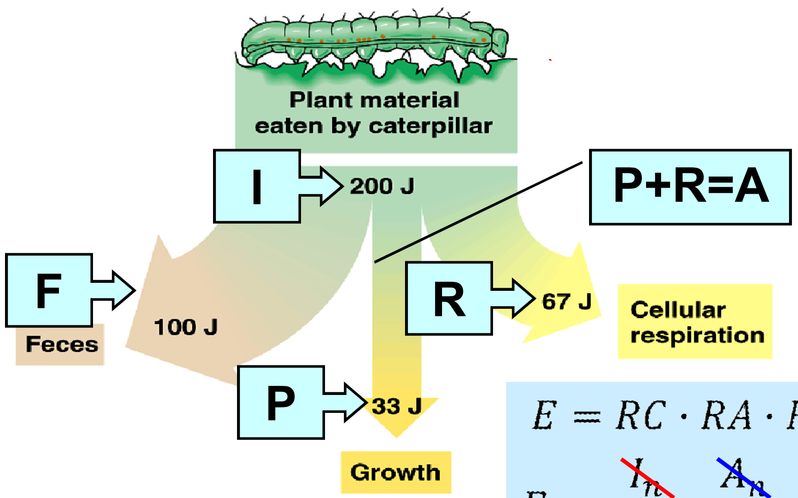

P_n
R_n
F_n
I_n
P_n, produttività al livello trofico n
R_n, perdita di calore respiratorio al livello trofico n
F_n, perdita di energia fecale al livello trofico n
I_n, assunzione (ingresso) di energia al livello trofico n
P_{n-1}, produttività disponibile per il consumo dal livello trofico $n-1$
non consumata
compartimento della sostanza organica morta del sistema dei decompositori
P_{n-1}


Produttori
Livelli trofici → 1
Piante verdi
Consumatori
2
Erbivori
3
Carnivori
NU
NA
Luce totale
I e L_A
P_G o A
P_N
I
A
P
I
A
P
Calore
R
R
R
3000 — 1500 — 15 — 1.5 — 0.3
L
L_A
P_N
P_2
P_3
kcal/m^2/giorno


Sun's energy utilized
Respiration
Gross primary production
Net primary production
Available to mice
To other consumers
To other consumers, decomposers, etc.
Used by mice
Respiration
Immigration
Respiration
Weasel
Unused
To decomposers, other consumers
Unused
Mouse production
Consumed by weasel

Produzione secondaria





Rendimento di consumo: $RC=I_n/P_{n-1}$

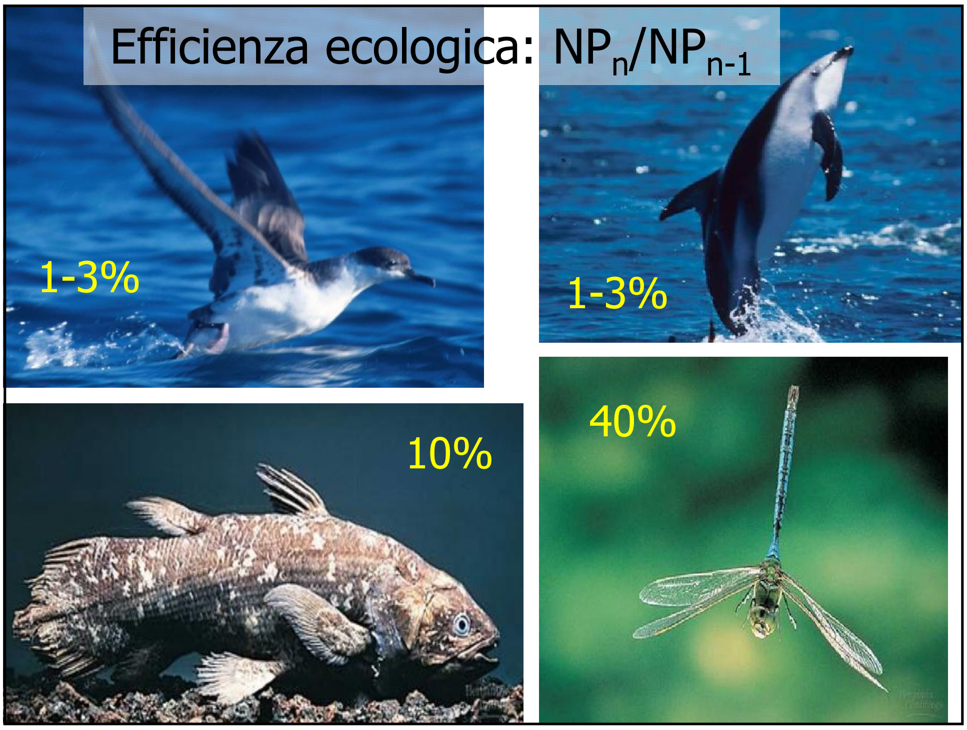
Rendimento di assimilazione: $RA=A_n/I_n$

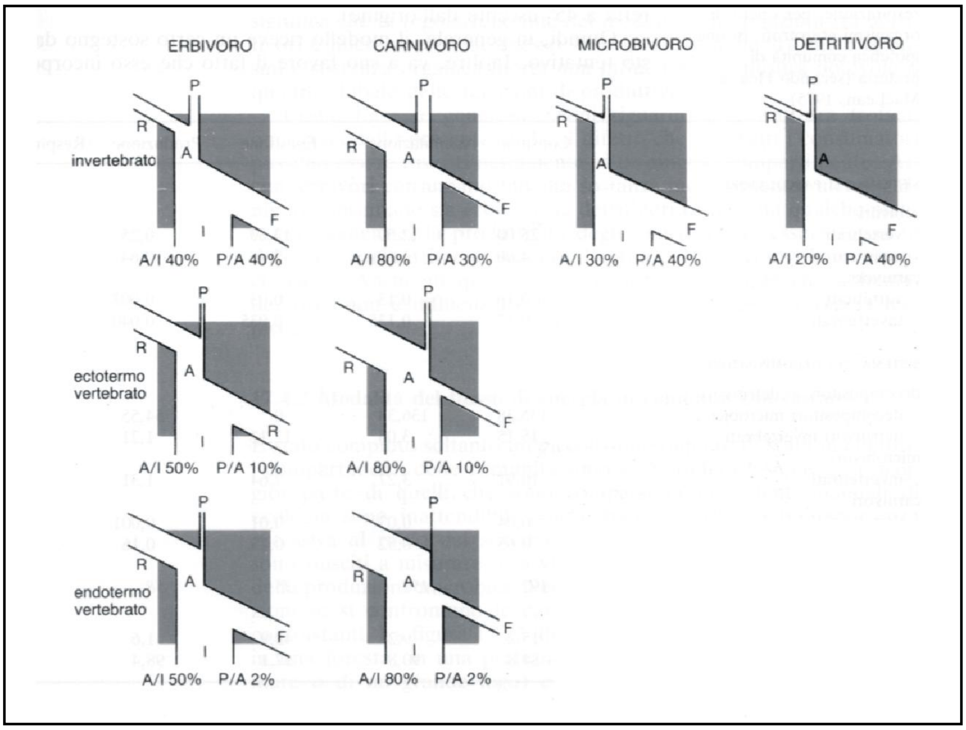
Rendimento di produzione: $RP=P_n/A_n$

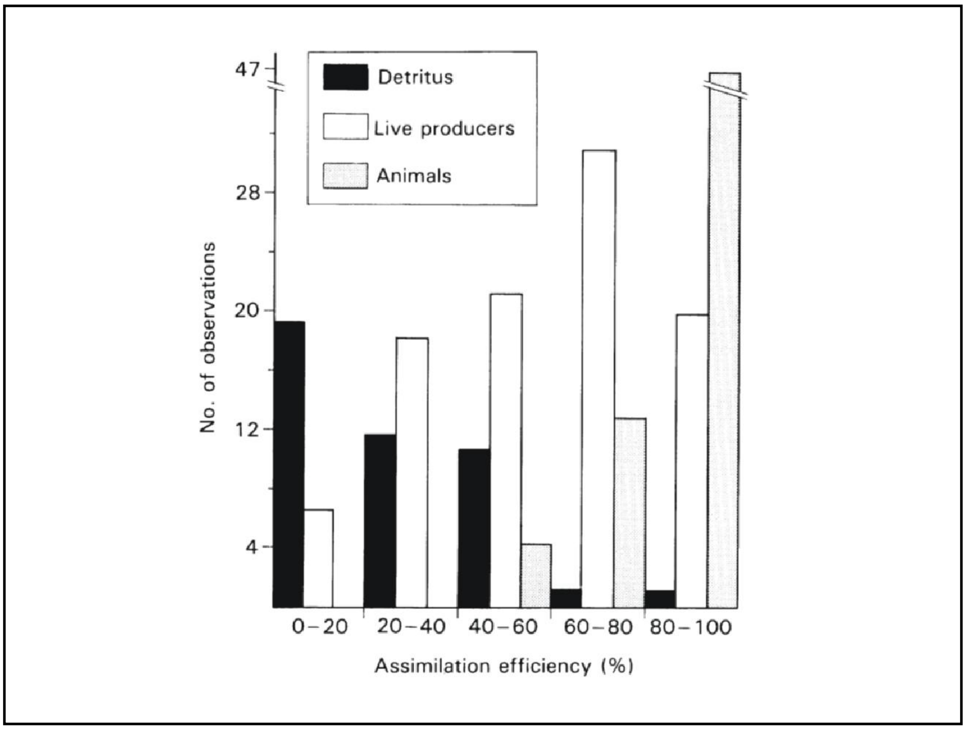
$$E = RC \cdot RA \cdot RP$$

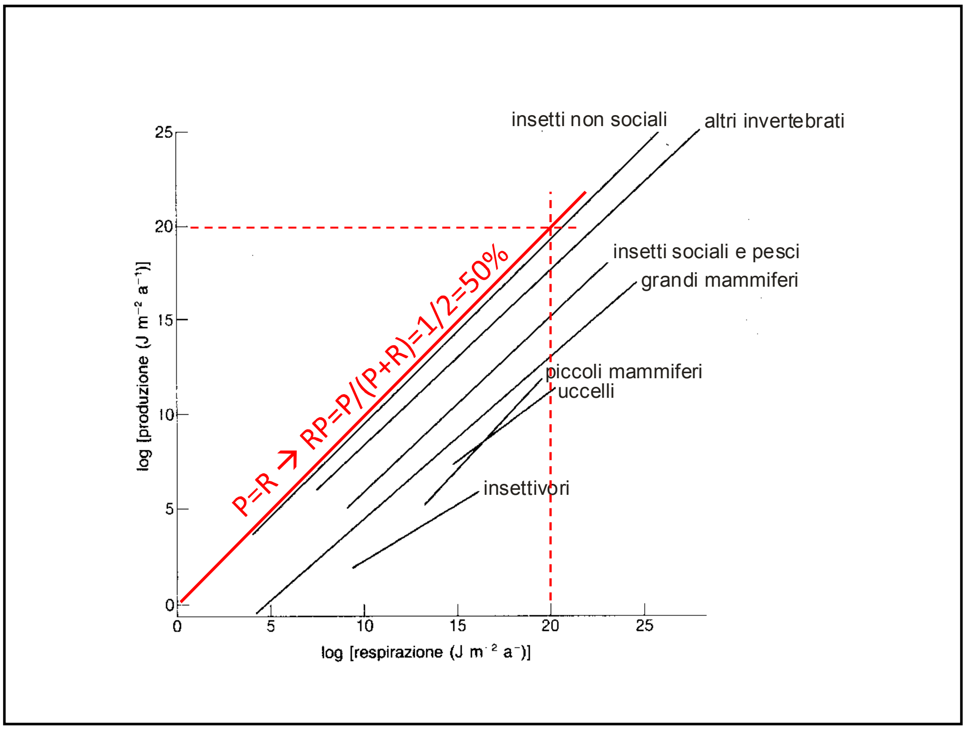
$$E = \frac{\cancel{I_n}}{P_{n-1}} \cdot \frac{\cancel{A_n}}{\cancel{I_n}} \cdot \frac{P_n}{\cancel{A_n}}$$

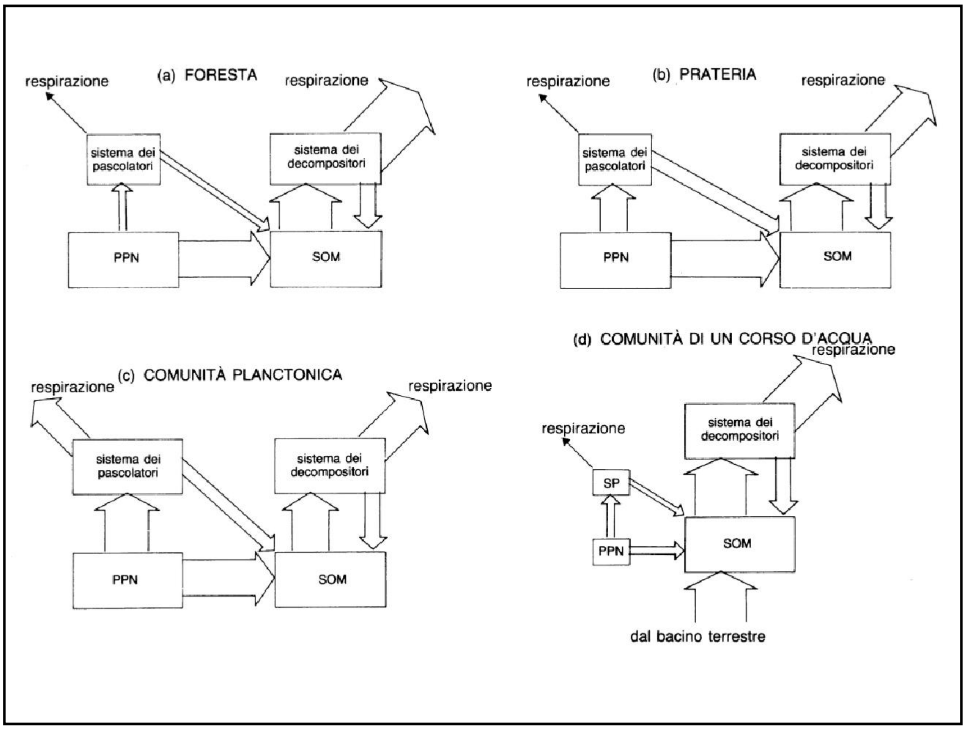
$$E = \frac{P_n}{P_{n-1}}$$

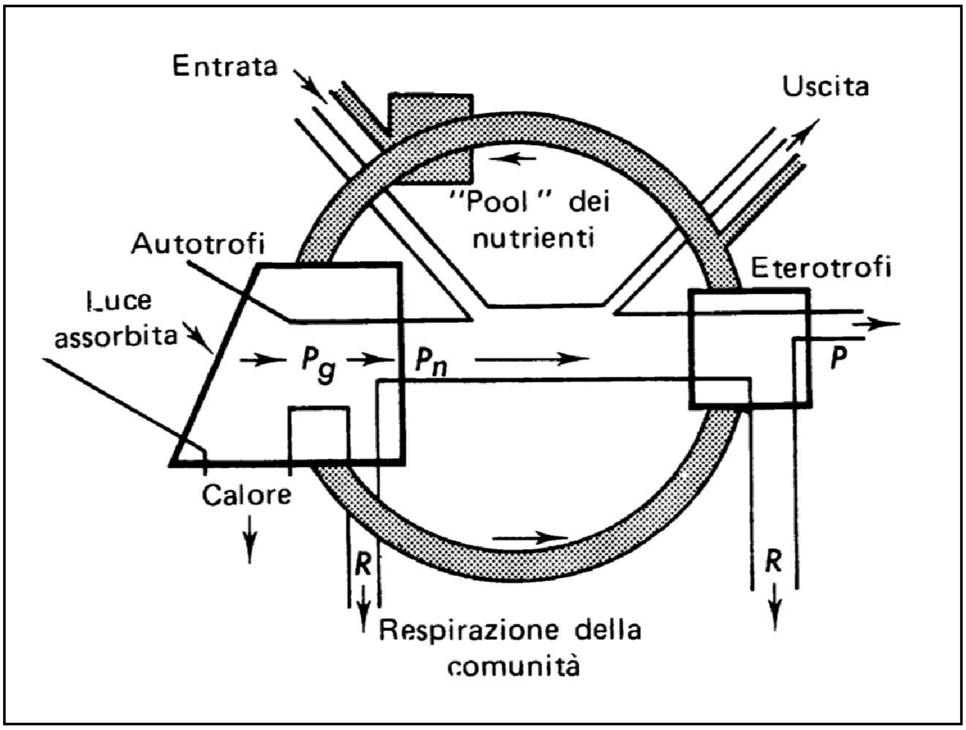

Efficienza ecologica: NP_n/NP_{n-1}
1-3%
1-3%
10%
40%

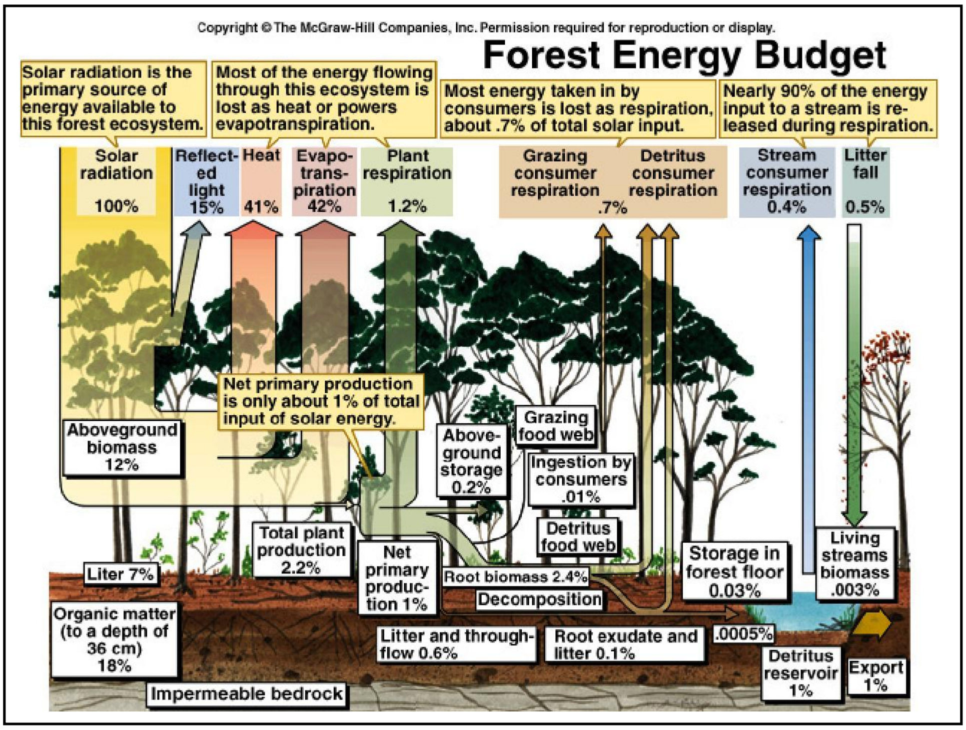

ERBIVORO
CARNIVORO
MICROBIVORO
DETRITIVORO
invertebrato
A/I 40% P/A 40%
A/I 80% P/A 30%
A/I 30% P/A 40%
A/I 20% P/A 40%
ectotermo vertebrato
A/I 50% P/A 10%
A/I 80% P/A 10%
endotermo vertebrato
A/I 50% P/A 2%
A/I 80% P/A 2%
P
R
A
I
F


Detritus
Live producers
Animals
No. of observations
47
28
20
12
4
0–20
20–40
40–60
60–80
80–100
Assimilation efficiency (%)


insetti non sociali
altri invertebrati
insetti sociali e pesci
grandi mammiferi
piccoli mammiferi
uccelli
insettivori
P=R → RP=P/(P+R)=1/2=50%
log [produzione (J m⁻² a⁻¹)]
log [respirazione (J m⁻² a⁻¹)]
25
20
15
10
5
0


(a) FORESTA
respirazione
respirazione
sistema dei pascolatori
sistema dei decompositori
PPN
SOM
(b) PRATERIA
respirazione
respirazione
sistema dei pascolatori
sistema dei decompositori
PPN
SOM
(c) COMUNITÀ PLANCTONICA
respirazione
respirazione
sistema dei pascolatori
sistema dei decompositori
PPN
SOM
(d) COMUNITÀ DI UN CORSO D'ACQUA
respirazione
respirazione
sistema dei decompositori
SP
PPN
SOM
dal bacino terrestre


Entrata
Uscita
"Pool" dei nutrienti
Autotrofi
Eterotrofi
Luce assorbita
Pg
Pn
P
Calore
R
R
Respirazione della comunità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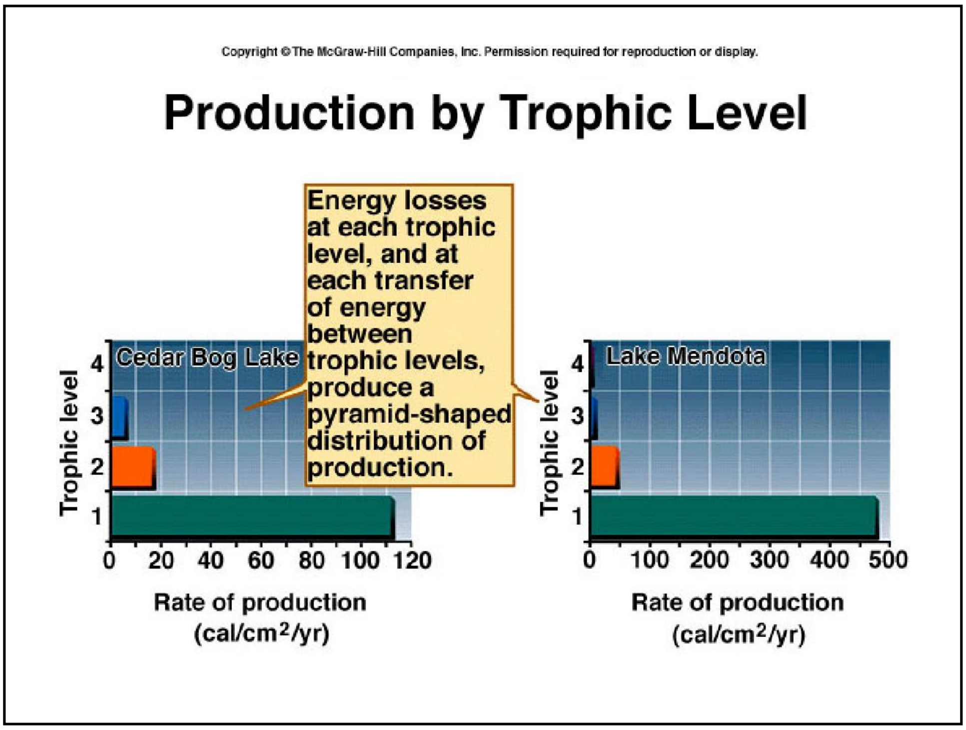
Forest Energy Budget
Solar radiation is the primary source of energy available to this forest ecosystem.
Most of the energy flowing through this ecosystem is lost as heat or powers evapotranspiration.
Most energy taken in by consumers is lost as respiration, about .7% of total solar input.
Nearly 90% of the energy input to a stream is re-leased during respiration.
Solar radiation 100%
Reflect-ed light 15%
Heat 41%
Evapo-trans-piration 42%
Plant respiration 1.2%
Grazing consumer respiration
Detritus consumer respiration
.7%
Stream consumer respiration 0.4%
Litter fall 0.5%
Net primary production is only about 1% of total input of solar energy.
Aboveground biomass 12%
Above-ground storage 0.2%
Grazing food web
Ingestion by consumers .01%
Detritus food web
Total plant production 2.2%
Net primary produc-tion 1%
Root biomass 2.4%
Decomposition
Storage in forest floor 0.03%
Living streams biomass .003%
Liter 7%
Organic matter (to a depth of 36 cm) 18%
Litter and through-flow 0.6%
Root exudate and litter 0.1%
.0005%
Detritus reservoir 1%
Export 1%
Impermeable bedrock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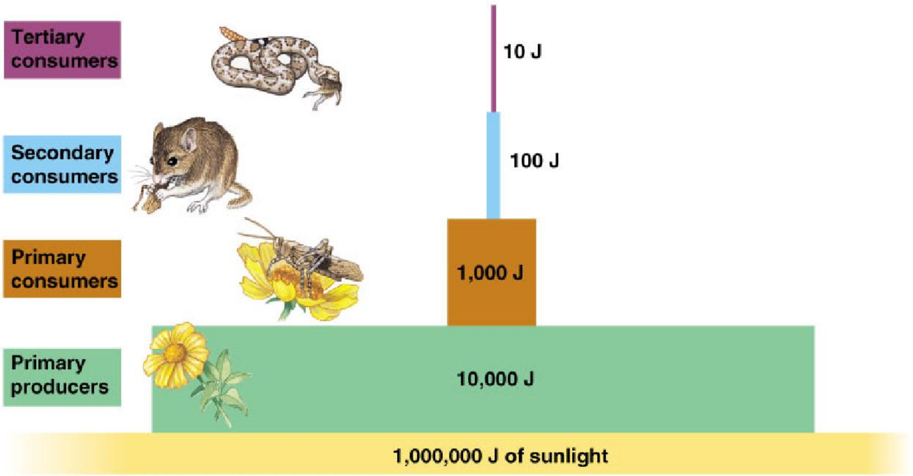
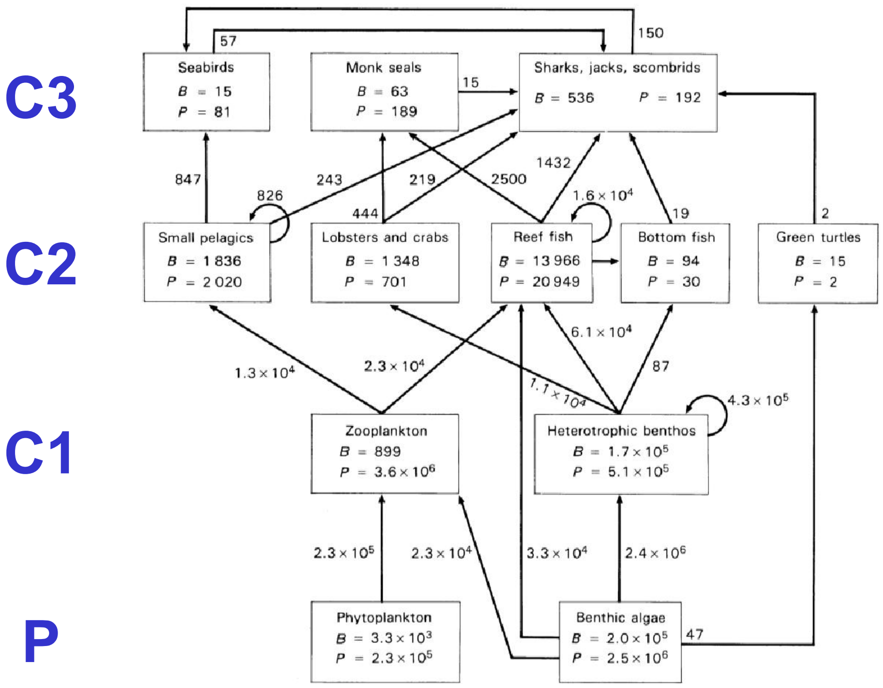
Production by Trophic Level
Energy losses at each trophic level, and at each transfer of energy between trophic levels, produce a pyramid-shaped distribution of production.
Cedar Bog Lake
Trophic level
1
2
3
4
0 20 40 60 80 100 120
Rate of production (cal/cm2/yr)
Lake Mendota
Trophic level
1
2
3
4
0 100 200 300 400 500
Rate of production (cal/cm2/yr)

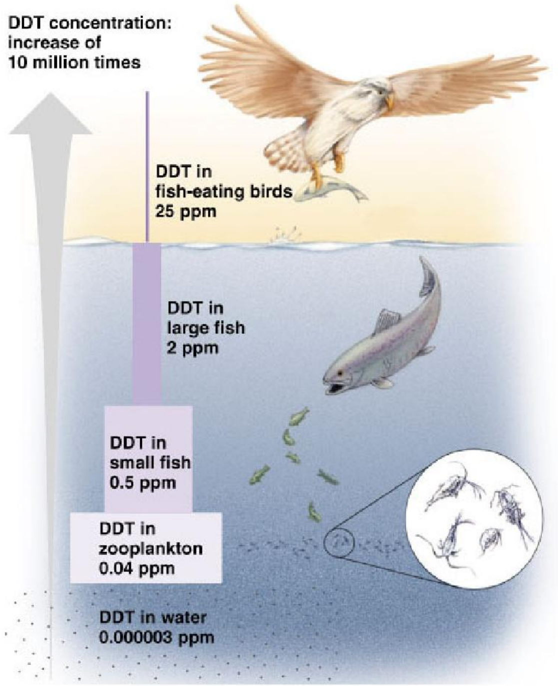


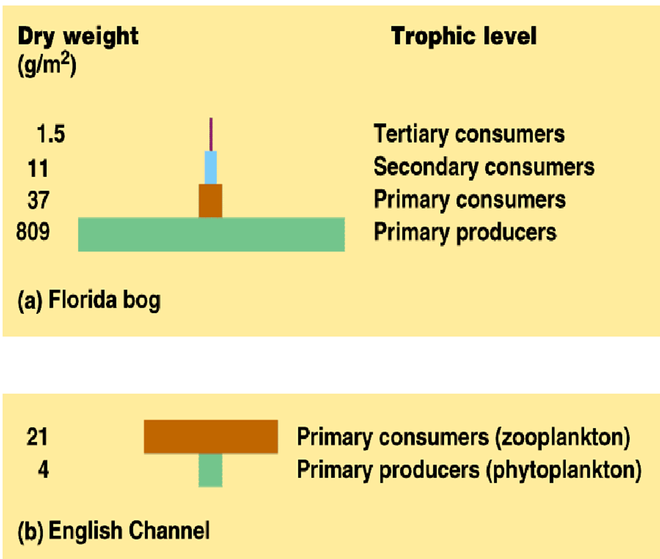
Tertiary consumers
Secondary consumers
Primary consumers
Primary producers
10 J
100 J
1,000 J
10,000 J
1,000,000 J of sunlight

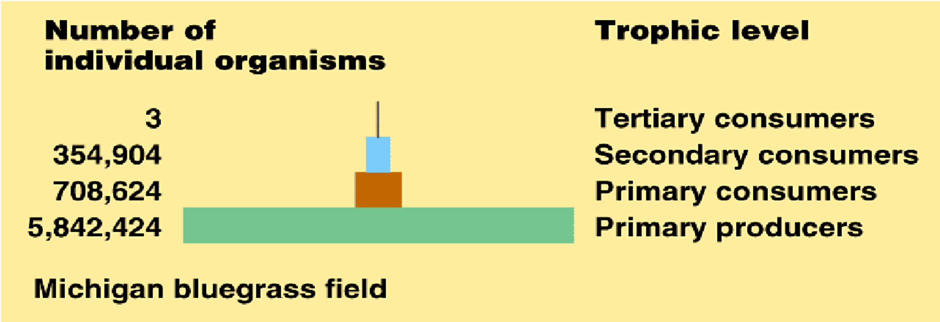


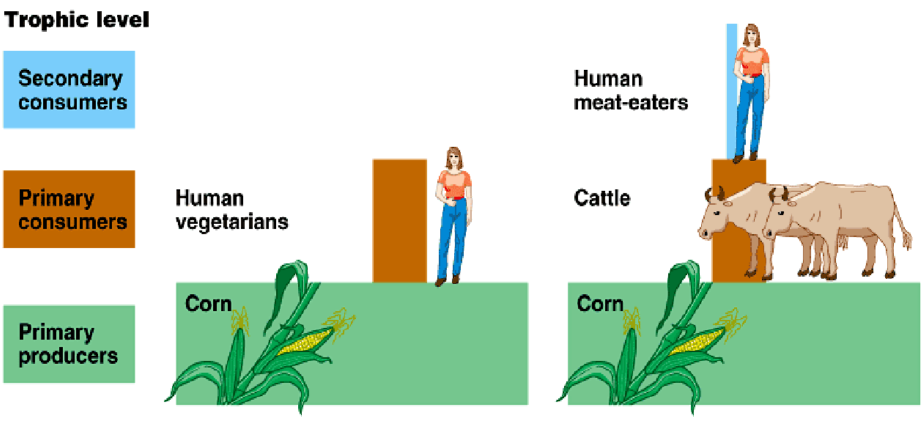
C3
C2
C1
P
Seabirds
B = 15
P = 81
Monk seals
B = 63
P = 189
Sharks, jacks, scombrids
B = 536 P = 192
Small pelagics
B = 1 836
P = 2 020
Lobsters and crabs
B = 1 348
P = 701
Reef fish
B = 13 966
P = 20 949
Bottom fish
B = 94
P = 30
Green turtles
B = 15
P = 2
Zooplankton
B = 899
P = 3.6 × 10^6
Heterotrophic benthos
B = 1.7 × 10^5
P = 5.1 × 10^5
Phytoplankton
B = 3.3 × 10^3
P = 2.3 × 10^5
Benthic algae
B = 2.0 × 10^5
P = 2.5 × 10^6
57
150
15
847
826
243
219
2500
1432
1.6 × 10^4
444
19
2
1.3 × 10^4
2.3 × 10^4
6.1 × 10^4
87
1.1 × 10^4
4.3 × 10^5
2.3 × 10^5
2.3 × 10^4
3.3 × 10^4
2.4 × 10^6
47

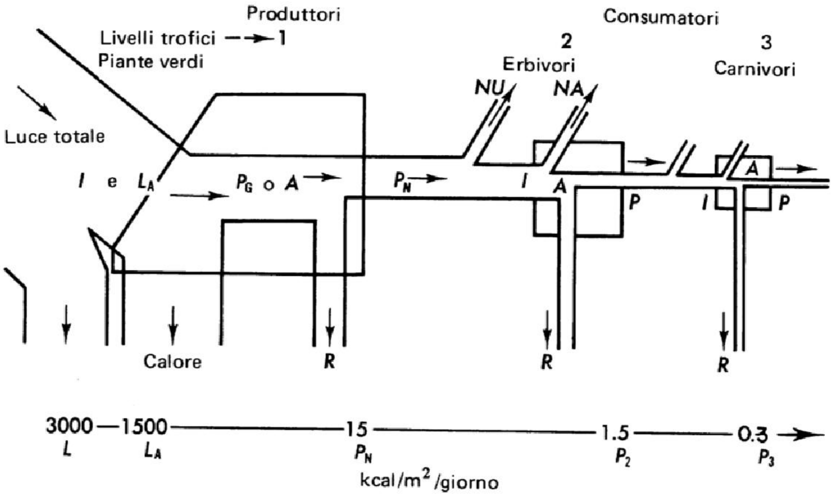
Magnificazione biologica






Number of individual organisms
Trophic level
3
354,904
708,624
5,842,424
Tertiary consumers
Secondary consumers
Primary consumers
Primary producers
Michigan bluegrass field


Trophic level
Secondary consumers
Primary consumers
Primary producers
Human vegetarians
Corn
Human meat-eaters
Cattle
Corn



THE TROPHIC-DYNAMIC ASPECT OF ECOLOGY

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Recent progress in the study of aquatic food-cycle relationships invites a reappraisal of certain ecological tenets. Quantitative productivity data provide a basis for enunciating certain trophic principles, which, when applied to a series of successional stages, shed new light on the dynamics of ecological succession.

"COMMUNITY" CONCEPTS

A chronological review of the major viewpoints guiding synecological thought indicates the following stages: (1) the static species-distributional viewpoint; (2) the dynamic species-distributional viewpoint, with emphasis on successional phenomena; and (3) the trophic-dynamic viewpoint. From either species-distributional viewpoint, a lake, for example, might be considered by a botanist as containing several distinct plant aggregations, such as marginal emergent, floating-leafed, submerged, benthic, or phytoplankton communities, some of which might even be considered as "climax" (cf. Tutin, '41). The associated animals would be "biotic factors" of the plant environment, tending to limit or modify the development of the aquatic plant communities. To a strict zoologist, on the other hand, a lake would seem to contain animal communities roughly coincident with the plant communities, although the "associated vegetation" would be considered merely as a part of the environment[1] of the animal community. A more "bio-ecological" species-distributional approach would recognize both the plants and animals as co-constituents of restricted "biotic" communities, such as "plankton communities," "benthic communities," etc., in which members of the living community "co-act" with each other and "react" with the non-living environment (Clements and Shelford, '39; Carpenter, '39, '40; T. Park, '41). Coactions and reactions are considered by bio-ecologists to be the dynamic effectors of succession.

The trophic-dynamic viewpoint, as adopted in this paper, emphasizes the relationship of trophic or "energy-availing" relationships within the community-unit to the process of succession. From this viewpoint, which is closely allied to Vernadsky's "biogeochemical" approach (cf. Hutchinson and Wollack, '40) and to the "oekologische Sicht" of Friederichs ('30), a lake is considered as a primary ecological unit in its own right, since all the lesser "communities" mentioned above are dependent upon other components of the lacustrine food cycle (cf. figure 1) for their very existence. Upon further consideration of the trophic cycle, the discrimination between living organisms as parts of the "biotic community" and dead organisms and inorganic nutritives as parts of the "environment" seems arbitrary and unnatural. The difficulty of drawing clear-cut lines between the living *community* and the non-living *environment* is illustrated by the difficulty of determining the status of a slowly dying pondweed covered with periphytes, some of which are also continually dying. As indicated in figure 1, much of the non-living nascent ooze is rapidly reincorporated through "dis-

[1] The term *habitat* is used by certain ecologists (Clements and Shelford, '39; Haskell, '40; T. Park, '41) as a synonym for *environment* in the usual sense and as here used, although Park points out that most biologists understand "habitat" to mean "simply the place or niche that an animal or plant occupies in nature" in a species-distributional sense. On the other hand, Haskell, and apparently also Park, use "environment" as synonymous with the *cosmos*. It is to be hoped that ecologists will shortly be able to reach some sort of agreement on the meanings of these basic terms.

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solved nutrients" back into the living "biotic community." This constant organic-inorganic cycle of nutritive substance is so completely integrated that to consider even such a unit as a lake primarily as a biotic community appears to force a "biological" emphasis upon a more basic functional organization.

This concept was perhaps first expressed by Thienemann ('18), as a result of his extensive limnological studies on the lakes of North Germany. Allee ('34) expressed a similar view, stating: "The picture than finally emerges . . . is of a sort of superorganismic unity not alone between the plants and animals to form biotic communities, but also between the biota and the environment." Such a concept is inherent in the term *ecosystem*, proposed by Tansley ('35) for the fundamental ecological unit.[2] Rejecting the terms "complex organism" and "biotic community," Tansley writes, "But the more fundamental conception is, as it seems to me, the whole *system* (in the sense of physics), including not only the organism-complex, but also the whole complex of physical factors forming what we call the environment of the biome. . . . It is the systems so formed which, from the point of view of the ecologist, are the basic units of nature on the face of the earth. . . . These *ecosystems*, as we may call them, are of the most various kinds and sizes. They form one category of the multitudinous physical systems of the universe, which range from the universe as a whole down to the atom." Tansley goes on to discuss the ecosystem as a category of rank equal to the "biome" (Clements, '16), but points out that the term can also be used in a general sense, as is the word "community." The *ecosystem* may be formally defined as the system composed of physical-chemical-biological processes active within a space-time unit of any magnitude, i.e., the biotic community *plus* its abiotic environment. The concept of the ecosystem is believed by the writer to be of fundamental importance in interpreting the data of dynamic ecology.

[2] The ecological system composed of the "biocoenosis + biotop" has been termed the *holocoen* by Friederichs ('30) and the *biosystem* by Thienemann ('39).

Trophic Dynamics

Qualitative food-cycle relationships

Although certain aspects of food relations have been known for centuries, many processes within ecosystems are still very incompletely understood. The basic process in trophic dynamics is the transfer of energy from one part of the ecosystem to another. All function, and indeed all life, within an ecosystem depends upon the utilization of an external source of energy, solar radiation. A portion of this incident energy is transformed by the process of photosynthesis into the structure of living organisms. In the language of community economics introduced by Thienemann ('26), autotrophic plants are *producer* organisms, employing the energy obtained by photosynthesis to synthesize complex organic substances from simple inorganic substances. Although plants again release a portion of this potential energy in catabolic processes, a great surplus of organic substance is accumulated. Animals and heterotrophic plants, as *consumer* organisms, feed upon this surplus of potential energy, oxidizing a considerable portion of the consumed substance to release kinetic energy for metabolism, but transforming the remainder into the complex chemical substances of their own bodies. Following death, every organism is a potential source of energy for saprophagous organisms (feeding directly on dead tissues), which again may act as energy sources for successive categories of consumers. Heterotrophic bacteria and fungi, representing the most important saprophagous consumption of energy, may be conveniently differentiated from animal consumers as special-

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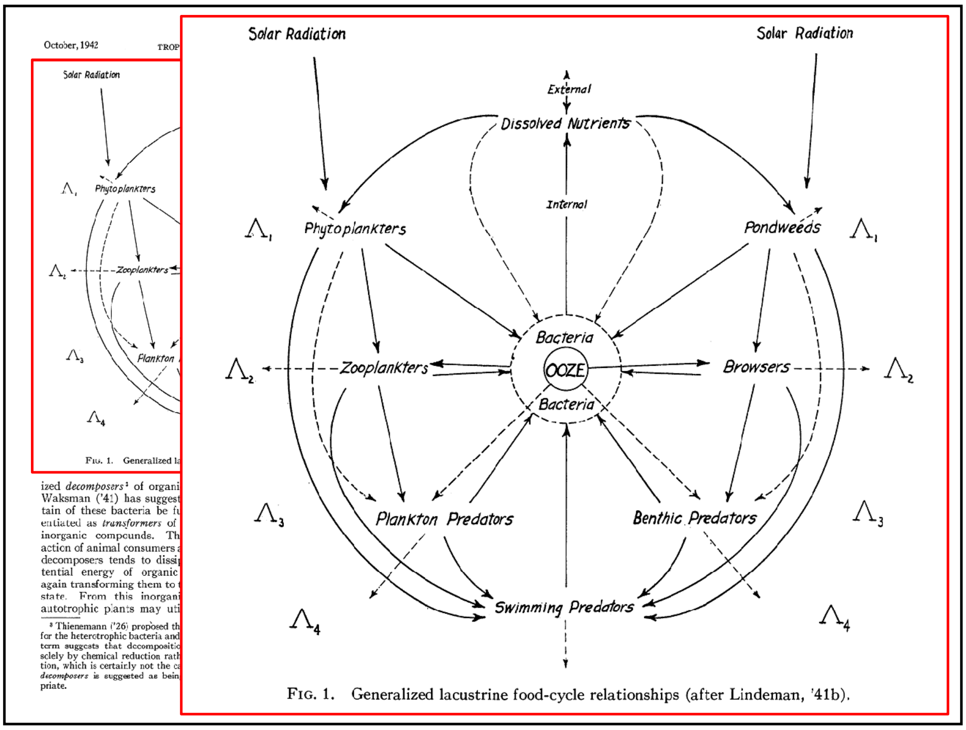

FIG. 1. Generalized lacustrine food-cycle relationships (after Lindeman, '41b).

usual prey are only periodically abundant. This ability on the part of predators, which tends to make the higher trophic levels of a food cycle less discrete than the lower, increases the difficulties of analyzing the energy relationships in this portion of the food cycle, and may also tend to "shorten the food-chain."

Fundamental food cycle variations in different ecosystems may be observed by comparing lacustrine and terrestrial cycles. Although dissolved nutrients in the lake water and in the ooze correspond directly with those in the soil, the autotrophic producers differ considerably in form. Lacustrine producers include macrophytic pondweeds, in which massive supporting tissues are at a minimum, and microphytic phytoplankters, which in larger lakes definitely dominate the production of organic substance. Terrestrial producers are predominantly multicellular plants containing much cellulose and lignin in various types of supporting tissues. Terrestrial herbivores, belonging to a great number of specialized food groups, act as *primary consumers* (sensu Jacot, '40) of organic substance; these groups correspond to the "browsers" of aquatic ecosystems. Terrestrial predators may be classified as more remote (secondary, tertiary, quaternary, etc.) consumers, according to whether they prey upon herbivores or upon other predators; these correspond roughly to the benthic predators and swimming predators, respectively, of a lake. Bacterial and fungal decomposers in terrestrial systems are concentrated in the humus layer of the soil; in lakes, where the "soil" is overlain by water, decomposition takes place both in the water, as organic particles slowly settle, and in the benthic "soil." Nutrient salts are thus freed to be reutilized by the autotrophic plants of both ecosystems.

The striking absence of terrestrial "life-forms" analogous to plankters[4] (cf. figure 1) indicates that the terrestrial food cycle is essentially "mono-cyclic" with macrophytic producers, while the lacustrine cycle, with two "life-forms" of producers, may be considered as "bi-cyclic." The marine cycle, in which plankters are the only producers of any consequence, may be considered as "mono-cyclic" with microphytic producers. The relative absence of massive supporting tissues in plankters and the very rapid completion of their life cycle exert a great influence on the differential productivities of terrestrial and aquatic systems. The general convexity of terrestrial systems as contrasted with the concavity of aquatic substrata results in striking trophic and successional differences, which will be discussed in a later section.

Productivity

Definitions.—The quantitative aspects of trophic ecology have been commonly expressed in terms of the productivity of the food groups concerned. Productivity has been rather broadly defined as the general rate of production (Riley, '40, and others), a term which may be applied to any or every food group in a given ecosystem. The problem of productivity as related to biotic dynamics has been critically analyzed by G. E. Hutchinson ('42) in his recent book on limnological principles. The two following paragraphs are quoted from Hutchinson's chapter on "The Dynamics of Lake Biota":

> The dynamics of lake biota is here treated as primarily a problem of energy transfer . . . the biotic utilization of solar energy entering the lake surface. Some of this energy is transformed by photosynthesis into the structure of phytoplankton organisms, representing an energy content which may be expressed as Λ_1 (first level). Some of the phytoplankters will be eaten by

[4] Francé ('13) developed the concept of the *edaphon*, in which the soil microbiota was represented as the terrestrial equivalent of aquatic plankton. This concept appears to have a number of adherents in this country. The author feels that this analogy is misleading, as the edaphon, which has almost no producers, represents only a dependent side-chain of the terrestrial cycle, and is much more comparable to the lacustrine microbenthos than to the plankton.

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zooplankters (energy content Λ_2), which again will be eaten by plankton predators (energy content Λ_3). The various successive levels (i.e., stages[5]) of the food cycle are thus seen to have successively different energy contents ($\Lambda_1, \Lambda_2, \Lambda_3$, etc.).

Considering any food-cycle level Λ_n, energy is entering the level and is leaving it. The rate of change of the energy content Λ_n therefore may be divided into a positive and a negative part:

$$\frac{d\Lambda_n}{dt} = \lambda_n + \lambda_n',$$

where λ_n is by definition positive and represents the rate of contribution of energy from Λ_{n-1} (the previous level) to Λ_n, while λ_n' is negative and represents the sum of the rate of energy dissipated from Λ_n and the rate of energy content handed on to the following level Λ_{n+1}. The more interesting quantity is λ_n which is defined as the true *productivity* of level Λ_n. In practice, it is necessary to use mean rates over finite periods of time as approximations to the mean rates $\lambda_0, \lambda_1, \lambda_2$. . . .

In the following pages we shall consider the quantitative relationships of the following productivities: λ_0 (rate of incident solar radiation), λ_1 (rate of photosynthetic production), λ_2 (rate of primary or herbivorous consumption), λ_3 (rate of secondary consumption or primary predation), and λ_4 (rate of tertiary consumption). The total amount of organic structure formed per year for any level Λ_n, which is commonly expressed as the annual "yield," actually represents a value uncorrected for dissipation of energy by (1) respiration, (2) predation, and (3) post-mortem decomposition. Let us now consider the quantitative aspects of these losses.

Respiratory corrections.—The amount of energy lost from food levels by catabolic processes (respiration) varies considerably for the different stages in the life histories of individuals, for different levels in the food cycle and for different seasonal temperatures. In terms of annual production, however, individual deviates cancel out and respiratory differences between food groups may be observed.

Numerous estimates of average respiration for photosynthetic producers may be obtained from the literature. For terrestrial plants, estimates range from 15 per cent (Pütter, re Spoehr, '26) to 43 per cent (Lundegårdh, '24) under various types of natural conditions. For aquatic producers, Hicks ('34) reported a coefficient of about 15 per cent for Lemna under certain conditions. Wimpenny ('41) has indicated that the respiratory coefficient of marine producers in polar regions (diatoms) is probably much less than that of the more "animal-like" producers (peridinians and coccolithophorids) of warmer seas, and that temperature may be an important factor in determining respiratory coefficients in general. Juday ('40), after conducting numerous experiments with Manning and others on the respiration of phytoplankters in Trout Lake, Wisconsin, concluded that under average conditions these producers respire about ⅓ of the organic matter which they synthesize. This latter value, 33 per cent, is probably the best available respiratory coefficient for lacustrine producers.

Information on the respiration of aquatic primary consumers is obtained from an illuminating study by Ivlev ('39a) on the energy relationships of *Tubifex*. By means of ingenious techniques, he determined calorific values for assimilation and growth in eleven series of experiments. Using the averages of his calorific values, we can make the following simple calculations: *assimilation* (16.77 cal.) − *growth* (10.33 cal.) = *respiration* (6.44 cal.), so that respiration in terms of growth $= \frac{6.44}{10.33} = 62.30$ per cent. As a check on the growth stage of these worms, we find that $\frac{\text{growth}}{\text{assimilation}} = 61.7$ per cent, a value in good agreement with the classical conclusions of Needham ('31, III, p. 1655) with respect to embryos: the efficiency of all developing embryos is numerically similar, between 60 and 70 per cent, and

[5] The term *stage*, in some respects preferable to the term *level*, cannot be used in this trophic sense because of its long-established usage as a successional term (cf. p. 23).

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independent of temperature within the range of biological tolerance. We may therefore conclude that the worms were growing at nearly maximal efficiency, so that the above respiratory coefficient is nearly minimal. In the absence of further data, we shall tentatively accept 62 per cent as the best available respiratory coefficient for aquatic herbivores.

The respiratory coefficient for aquatic predators can be approximated from data of another important study by Ivlev ('39b), on the energy transformations in predatory yearling carp. Treating his calorific values as in the preceding paragraph, we find that *ingestion* (1829 cal.) − *defecation* (454 cal.) = *assimilation* (1375 cal.), and *assimilation* − *growth* (573 cal.) = *respiration* (802 cal.), so that respiration in terms of growth $= \frac{802}{573} = 140$ per cent, a much higher coefficient than that found for the primary consumer, *Tubifex*. A rough check on this coefficient was obtained by calorific analysis of data on the growth of yearling green sunfishes (*Lepomis cyanellus*) published by W. G. Moore ('41), which indicate a respiratory coefficient of 120 per cent with respect to growth, suggesting that these fishes were growing more efficiently than those studied by Ivlev. Since Moore's fishes were fed on a highly concentrated food (liver), this greater growth efficiency is not surprising. If the maximum growth efficiency would occur when $\frac{\text{growth}}{\text{assimilation}}$ = 60–70 per cent (AEE of Needham, '31), the AEE of Moore's data (about 50 per cent) indicates that the minimum respiratory coefficient with respect to growth might be as low as 100 per cent for certain fishes. Food-conversion data from Thompson ('41) indicate a minimum respiratory coefficient of less than 150 per cent for young black bass (*Huro salmoides*) at 70° F., the exact percentage depending upon how much of the ingested food (minnows) was assimilated. Krogh ('41) showed that predatory fishes have a higher rate of respiration than the more sluggish herbivorous species; the respiratory rate of *Esox* under resting conditions at 20° C. was 3½ times that of *Cyprinus*. The form of piscian growth curves (cf. Hile, '41) suggests that the respiratory coefficient is much higher for fishes towards the end of their normal life-span. Since the value obtained from Ivlev (above) is based on more extensive data than those of Moore, we shall tentatively accept 140 per cent as an average respiratory coefficient for aquatic predators.

Considering that predators are usually more active than their herbivorous prey, which are in turn more active than the plants upon which they feed, it is not surprising to find that respiration with respect to growth in producers (33 per cent), in primary consumers (62 per cent) and in secondary consumers (>100 per cent) increases progressively. These differences probably reflect a trophic principle of wide application: the percentage loss of energy due to respiration is progressively greater for higher levels in the food cycle.

Predation corrections.—In considering the predation losses from each level, it is most convenient to begin with the highest level, Λ_n. In a mechanically perfect food cycle composed of organically discrete levels, this loss by predation obviously would be zero. Since no natural food cycle is so mechanically constituted, some "cannibalism" within such an arbitrary level can be expected, so that the actual value for predation loss from Λ_n probably will be somewhat above zero. The predation loss from level Λ_{n-1} will represent the total amount of assimilable energy passed on into the higher level (i.e., the true productivity, λ_n), plus a quantity representing the average content of substance killed but not assimilated by the predator, as will be discussed in the following section. The predation loss from level Λ_{n-2} will likewise represent the total amount of assimilable energy passed on to the next

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level (i.e., λ_{n-1}), plus a similar factor for unassimilated material, as illustrated by the data of tables II and III. The various categories of parasites are somewhat comparable to those of predators, but the details of their energy relationships have not yet been clarified, and cannot be included in this preliminary account.

Decomposition corrections.—In conformity with the principle of Le Chatelier, the energy of no food level can be completely extracted by the organisms which feed upon it. In addition to the energy represented by organisms which survive to be included in the "annual yield," much energy is contained in "killed" tissues which the predators are unable to digest and assimilate. Average coefficients of indigestible tissues based largely of th… of the "crude fib… chemical analyses … ('22), are as follow…

Nannoplankters. . . . .
Algal mesoplankters. .
Mature pondweeds. . .
Primary consumers. . .
Secondary consumers.
Predatory fishes. . . . .

Corrections for … would certainly b… though the data a… rant a generalizatio… increasing digestibi… levels, particularly … ponents of aquatic cycles.

Ogni sistema tende a reagire ad una modifica impostagli dall'esterno minimizzandone gli effetti.

The loss of energy due to premature death from non-predatory causes usually must be neglected, since such losses are exceedingly difficult to evaluate and under normal conditions probably represent relatively small components of the annual production. However, considering that these losses may assume considerable proportions at any time, the above "decomposition coefficients" must be regarded as correspondingly minimal.

Following non-predated death, every organism is a potential source of energy for myriads of bacterial and fungal saprophages, whose metabolic products provide simple inorganic and organic solutes reavailable to photosynthetic producers. These saprophages may also serve as energy sources for successive levels of consumers, often considerably supplementing the normal diet of herbivores (ZoBell and Feltham, '38). Jacot ('40) considered saprophage-feeding or coprophagous animals as "low" primary consumers, but the writer believes that in the present state of our knowledge a quantitative subdivision of primary consumers is unwarranted.

Application.—The value of these theoretical energy relationships can be illustrated by analyzing data of the three ecosystems for which relatively comprehensive productivity values have been published (table I). The summary ac…

…count of Brujewicz ('39) on "the dynamics of living matter in the Caspian Sea" leaves much to be desired, as bottom animals are not differentiated into their relative food levels, and the basis for determining the annual production of phytoplankters (which on theoretical grounds appears to be much too low) is not clearly explained. Furthermore, his values are stated in terms of thousands of tons of dry weight for the Caspian Sea as a whole, and must be roughly transformed to calories per square centimeter of surface area. The data for Lake Mendota, Wisconsin, are

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taken directly from a general summary (Juday, '40) of the many productivity studies made on that eutrophic lake. The data for Cedar Bog Lake, Minnesota, are taken from the author's four-year analysis (Lindeman, '41b) of its food-cycle dynamics. The calorific values in table I, representing annual production of organic matter, are uncorrected for energy losses.

TABLE II. *Productivity values for the Cedar Bog Lake food cycle, in g-cal/cm²/year, as corrected by using the coefficients derived in the preceding sections.*

Trophic level	Uncorrected productivity	Respiration	Predation	Decomposition	Corrected productivity
Producers: Λ_1	70.4±10.14	23.4	14.8	2.8	111.3
Primary consumers: Λ_2	7.0±1.07	4.4	3.1	0.3	14.8
Secondary consumers: Λ_3	1.3±0.43*	1.8	0.0	0.0	3.1

* This value includes the productivity of the small cyprinoid fishes found in the lake.

Correcting for the energy losses due to respiration, predation and decomposition, as discussed in the preceding sections, casts a very different light on the relative productivities of food levels. The calculation of corrections for the Cedar Bog Lake values for producers, primary consumers and secondary consumers are given in table II. The application of similar corrections to the energy values for the food levels of the Lake Mendota food cycle given by Juday ('40), as shown in table III, indicates that Lake Mendota is much more productive of producers and primary consumers than is Cedar Bog Lake, while the production of secondary consumers is of the same order of magnitude in the two lakes.

In calculating total productivity for Lake Mendota, Juday ('40) used a blanket correction of 500 per cent of the annual production of all consumer levels for "metabolism," which presumably includes both respiration and predation. Thompson ('41) found that the "carry-

TABLE III. *Productivity values for the Lake Mendota food cycle, in g-cal/cm²/year, as corrected by using coefficients derived in the preceding sections, and as given by Juday ('40).*

Trophic Level	Uncorrected productivity	Respiration	Predation	Decomposition	Corrected productivity	Juday's corrected productivity
Producers: Λ_1	321*	107	42	10	480	428
Primary consumers: Λ_2	24	15	2.3	0.3	41.6	144
Secondary consumers: Λ_3	1†	1	0.3	0.0	2.3	6
Tertiary consumers: Λ_4	0.12	0.2	0.0	0.0	0.3	0.7

* Hutchinson ('42) gives evidence that this value is probably too high and may actually be as low as 250.

† Apparently such organisms as small "forage" fishes are not included in any part of Juday's balance sheets. The inclusion of these forms might be expected to increase considerably the productivity of secondary consumption.

ing-capacity" of lakes containing mostly carp and other "coarse" fishes (primarily Λ_3), was about 500 per cent that of lakes containing mostly "game" fishes (primarily Λ_4), and concluded that "this difference must be about one complete link in the food chain, since it usually requires about five pounds of food to produce one pound of fish." While such high "metabolic losses" may hold for tertiary and quaternary predators under certain field conditions, the physiological experiments previously cited indicate much lower respiratory coefficients. Even when predation and decomposition corrections are included, the resultant productivity values are less than half those obtained by using Juday's coefficient. Since we have shown that the necessary corrections vary progressively with the different food levels, it seems probable that Juday's "coefficient of metabolism" is much too high for primary and secondary consumers.

Biological efficiency

The quantitative relationships of any food-cycle level may be expressed in terms of its efficiency with respect to lower levels. Quoting Hutchinson's ('42)

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Secondary consumers: Λ_3	1†	1	0.3	0.0	2.3	6
Tertiary consumers: Λ_4	0.12	0.2	0.0	0.0	0.3	0.7

definition, "the efficiency of the productivity of any level (Λ_n) relative to the productivity of any previous level (Λ_m) is defined as $\frac{\lambda_n}{\lambda_m}100$. If the rate of solar energy entering the ecosystem is denoted as λ_0, the efficiencies of all levels may be referred back to this quantity λ_0." In general, however, the most interesting efficiencies are those referred to the previous level's productivity (λ_{n-1}), or those expressed as $\frac{\lambda_n}{\lambda_{n-1}}100$. These latter may be termed the *progressive efficiencies* of the various food-cycle levels, indicating for each level the degree of utilization of its potential food supply or energy source. All efficiencies discussed in the following pages are progressive efficiencies, expressed in terms of relative productivities $\left(\frac{\lambda_n}{\lambda_{n-1}}100\right)$. It is important to remember that efficiency and productivity are not synonymous. Productivity is a rate (i.e., in the units here used, cal/cm²/year), while efficiency, being a ratio, is a dimensionless number. The points of reference for any efficiency value should always be clearly stated.

The progressive efficiencies $\left(\frac{\lambda_n}{\lambda_{n-1}}100\right)$ for the trophic levels of Cedar Bog Lake and Lake Mendota, as obtained from the productivities derived in tables II and III, are presented in table IV. In view of the uncertainties concerning some

TABLE IV. *Productivities and progressive efficiencies in the Cedar Bog Lake and Lake Mendota food cycles, as g-cal/cm²/year*

	Cedar Bog Lake		Lake Mendota	
	Productivity	Efficiency	Productivity	Efficiency
Radiation	≦118,872		118,872	
Producers: Λ_1	111.3	0.10%	480*	0.40%
Primary consumers: Λ_2	14.8	13.3%	41.6	8.7%
Secondary consumers: Λ_3	3.1	22.3%	2.3†	5.5%
Tertiary consumers: Λ_4	—	—	0.3	13.0%

* Probably too high; see footnote of table III.

† Probably too low; see footnote of table III.

of the Lake Mendota productivities, no definite conclusions can be drawn from their relative efficiencies. The Cedar Bog Lake ratios, however, indicate that the progressive efficiencies increase from about 0.10 per cent for production, to 13.3 per cent for primary consumption, and to 22.3 per cent for secondary consumption. An uncorrected efficiency of tertiary consumption of 37.5 per cent ± 3.0 per cent (for the weight ratios of "carnivorous" to "forage" fishes in Alabama ponds) is indicated in data published by Swingle and Smith ('40). These progressively increasing efficiencies may well represent a fundamental trophic principle, namely, that the consumers at progressively higher levels in the food cycle are progressively more efficient in the use of their food supply.

At first sight, this generalization of increasing efficiency in higher consumer groups would appear to contradict the previous generalization that the loss of energy due to respiration is progressively greater for higher levels in the food cycle. These can be reconciled by remembering that increased activity of predators considerably increases the chances of encountering suitable prey. The ultimate effect of such antagonistic principles would present a picture of a predator completely wearing itself out in the process of completely exterminating its prey, a very improbable situation. However, Elton ('27) pointed out that food-cycles rarely have more than five trophic levels. Among the several factors involved, increasing respiration of successive levels of predators contrasted with their successively increasing efficiency of predation appears to be important in restricting the number of trophic levels in a food cycle.

The effect of increasing temperature is alleged by Wimpenny ('41) to cause a decreasing consumer/producer ratio, presumably because he believes that the "acceleration of vital velocities" of consumers at increasing temperatures is more rapid than that of producers. He

TABLE IV. *Productivities and progressive efficiencies in the Cedar Bog Lake and Lake Mendota food cycles, as g-cal/cm²/year*

	Cedar Bog Lake		Lake Mendota	
	Productivity	Efficiency	Productivity	Efficiency
Radiation	≦118,872		118,872	
Producers: Λ_1	111.3	0.10%	480*	0.40%
Primary consumers: Λ_2	14.8	13.3%	41.6	8.7%
Secondary consumers: Λ_3	3.1	22.3%	2.3†	5.5%
Tertiary consumers: Λ_4	—	—	0.3	13.0%

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cites as evidence Lohmann's ('12) data for relative *numbers* (not biomass) of Protophyta, Protozoa and Metazoa in the centrifuge plankton of "cool" seas (741:73:1) as contrasted with tropical areas (458:24:1). Since Wimpenny himself emphasizes that many metazoan plankters are larger in size toward the poles, these data do not furnish convincing proof of the allegation. The data given in table IV, since Cedar Bog Lake has a much higher mean annual water temperature than Lake Mendota, appear to contradict Wimpenny's generalization that consumer/producer ratios fall as the temperature increases.

The Eltonian pyramid

The general relationships of higher food-cycle levels to one another and to community structure were greatly clarified following recognition (Elton, '27) of the importance of size and of numbers in the animals of an ecosystem. Beginning with primary consumers of various sizes, there are as a rule a number of food-chains radiating outwards in which the probability is that predators will become successively larger, while parasites and hyper-parasites will be progressively smaller than their hosts. Since small primary consumers can increase faster than larger secondary consumers and are so able to support the latter, the animals at the base of a food-chain are relatively abundant while those toward the end are progressively fewer in number. The resulting arrangement of sizes and numbers of animals, termed the pyramid of Numbers by Elton, is now commonly known as the Eltonian Pyramid. Williams ('41), reporting on the "floor fauna" of the Panama rain forest, has recently published an interesting example of such a pyramid, which is reproduced in figure 2.

The Eltonian Pyramid may also be expressed in terms of biomass. The weight of all predators must always be much lower than that of all food animals, and the total weight of the latter much lower than the plant production (Bodenheimer, '38). To the human ecologist, it is noteworthy that the population density of the essentially vegetarian Chinese, for example, is much greater than that of the more carnivorous English.

The principle of the Eltonian Pyramid has been redefined in terms of productivity by Hutchinson (unpublished) in the following formalized terms: the rate of production cannot be less and will almost certainly be greater than the rate of primary consumption, which in turn cannot be less and will almost certainly be greater than the rate of secondary consumption, which in turn . . . , etc. The energy-relationships of this principle may be epitomized by means

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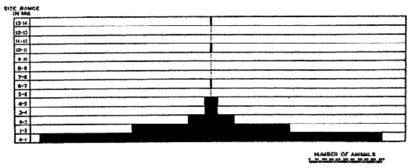

FIG. 2. Eltonian pyramid of numbers, for floor-fauna invertebrates of the Panama rain forest (from Williams, '41).

of the productivity symbol λ, as follows:

$$\lambda_0 > \lambda_1 > \lambda_2 \ldots > \lambda_n.$$

This rather obvious generalization is confirmed by the data of all ecosystems analyzed to date.

TROPHIC-DYNAMICS IN SUCCESSION

Dynamic processes within an ecosystem, over a period of time, tend to produce certain obvious changes in its species-composition, soil characteristics and productivity. Change, according to Cooper ('26), is the essential criterion of succession. From the trophic-dynamic viewpoint, succession is the process of development in an ecosystem, brought about primarily by the effects of the organisms on the environment and upon each other, towards a relatively stable condition of equilibrium.

It is well known that in the initial phases of hydrarch succession (oligotrophy → eutrophy) productivity increases rapidly; it is equally apparent that the colonization of a bare terrestrial area represents a similar acceleration in productivity. In the later phases of succession, productivity increases much more slowly. As Hutchinson and Wollack ('40) pointed out, these generalized changes in the rate of production may be expressed as a sigmoid curve showing a rough resemblance to the growth curve of an organism or of a homogeneous population.

Such smooth logistic growth, of course, is seldom found in natural succession, except possibly in such cases as bare areas developing directly to the climax vegetation type in the wake of a retreating glacier. Most successional seres consist of a number of *stages* ("recognizable, clearly-marked subdivisions of a given sere"—W. S. Cooper), so that their productivity growth-curves will contain undulations corresponding in distinctness to the distinctness of the stages. The presence of stages in a successional sere apparently represents the persistent influence of some combination of limiting factors, which, until they are overcome by species-substitution, etc., tend to decrease the acceleration of productivity and maintain it at a more constant rate. This tendency towards *stage-equilibrium* of productivity will be discussed in the following pages.

Productivity in hydrarch succession

The descriptive dynamics of hydrarch succession is well known. Due to the essentially concave nature of the substratum, lake succession is internally complicated by a rather considerable influx of nutritive substances from the drainage basin surrounding the lake. The basins of lakes are gradually filled with sediments, largely organogenic, upon which a series of vascular plant stages successively replace one another until a more or less stable (climax) stage is attained. We are concerned here, however, primarily with the productivity aspects of the successional process.

Eutrophication. — Thienemann ('26) presented a comprehensive theoretical discussion of the relation between lake succession and productivity, as follows: In oligotrophy, the pioneer phase, productivity is rather low, limited by the amount of dissolved nutrients in the lake water. Oxygen is abundant at all times, almost all of the synthesized organic matter is available for animal food; bacteria release dissolved nutrients from the remainder. Oligotrophy thus has a very "thrifty" food cycle, with a relatively high "efficiency" of the consumer populations. With increasing influx of nutritives from the surrounding drainage basin and increasing primary productivity (λ_1), oligotrophy is gradually changed through mesotrophy to eutrophy, in which condition the production of organic matter (λ_1) exceeds that which can be oxidized (λ_1') by respiration, predation and bacterial decomposition. The oxygen supply of the hypolimnion becomes depleted, with disastrous effects on the oligotroph-

conditioned bottom fauna. Organisms especially adapted to endure temporary anaerobiosis replace the oligotrophic species, accompanied by anaerobic bacteria which during the stagnation period cause reduction rather than oxidation of the organic detritus. As a result of this process, semi-reduced organic ooze, or *gytija*, accumulates on the bottom. As oxygen supply thus becomes a limiting factor of productivity, relative efficiency of the consumer groups in utilizing the synthesized organic substance becomes correspondingly lower.

The validity of Thienemann's interpretation, particularly regarding the trophic mechanisms, has recently been challenged by Hutchinson ('41, '42), who states that three distinct factors are involved: (1) the edaphic factor, representing the potential nutrient supply (primarily phosphorus) in the surrounding drainage basin; (2) the age of the lake at any stage, indicating the degree of utilization of the nutrient supply; and (3) the morphometric character at any stage, dependent on both the original morphometry of the lake basin and the age of the lake, and presumably influencing the oxygen concentration in the hypolimnion. He holds that true eutrophication takes place only in regions well supplied with nutrients, lakes in other regions developing into "ideotrophic types." The influx of phosphorus is probably very great in the earliest phases, much greater than the supply of nitrogen, as indicated by very low N/P ratios in the earliest sediments (Hutchinson and Wollack, '40). A large portion of this phosphorus is believed to be insoluble, as a component of such mineral particles as apatite, etc., although certainly some of it is soluble. The supply of available nitrogen increases somewhat more slowly, being largely dependent upon the fixation of nitrogen by micro-organisms either in the lake or in the surrounding soils. The photosynthetic productivity (λ_1) of lakes thus increases rather rapidly in the early phases, its quantitative value for lakes with comparable edaphic nutrient supplies being dependent on the morphometry (mean depth). Since deep lakes have a greater depth range for plankton photosynthesis, abundant oxygen and more chance for decomposition of the plankton detritus before reaching the bottom, such deep lakes may be potentially as productive as shallower lakes, in terms of unit surface area. Factors tending to lessen the comparative productivity of deep lakes are (1) lower temperature for the lake as a whole, and (2) greater dilution of nutrients in terms of volume of the illuminated "trophogenic zone" of the lake. During eutrophication in a deep lake, the phosphorus content of the sediment falls and nitrogen rises, until a N/P ratio of about 40/1 is established. "The decomposition of organic matter presumably is always liberating some of this phosphorus and nitrogen. Within limits, the more organic matter present the easier will be such regeneration. It is probable that benthic animals and anion exchange play a part in such processes" (Hutchinson, '42). The progressive filling of the lake basin with sediments makes the lake shallower, so that the oxygen supply of the hypolimnion is increasingly, and finally completely, exhausted during summer stagnation. Oxidation of the sediments is less complete, but sufficient phosphorus is believed to be regenerated from the ooze surface so that productivity in terms of surface area remains relatively constant. The nascent ooze acts as a trophic buffer, in the chemical sense, tending to maintain the productivity of a lake in stage-equilibrium (*typological equilibrium* of Hutchinson) during the eutrophic stage of its succession.

The concept of eutrophic stage-equilibrium seems to be partially confused (cf. Thienemann, '26; Hutchinson and Wollack, '40) with the theoretically ideal condition of complete *trophic equilibrium*, which may be roughly defined as the dynamic state of continuous, complete utilization and regeneration of chemical nutrients in an ecosystem, without loss or gain from the outside, under a periodically constant energy source—such as might be found in a perfectly balanced aquarium or terrarium. Natural ecosystems may tend to approach a state of trophic equilibrium under certain conditions, but it is doubtful if any are sufficiently autochthonous to attain, or maintain, true trophic equilibrium for any length of time. The biosphere as a whole, however, as Vernadsky ('29, '39) so vigorously asserts, may exhibit a high degree of true trophic equilibrium.

The existence of prolonged eutrophic stage-equilibrium was first suggested as a result of a study on the sediments of Grosser Plöner See in Germany (Groschopf, '36). Its significance was recognized by Hutchinson and Wollack ('40), who based their critical discussion on chemical analyses (ibid.) and pollen analyses (Deevey, '39) of the sediments of Linsley Pond, Connecticut. They reported a gradual transition from oligotrophy to eutrophy (first attained in the oak-hemlock pollen period), in which stage the lake has remained for a very long time, perhaps more than 4000 years. They report indications of a comparable eutrophic stage-equilibrium in the sediments of nearby Upper Linsley Pond (Hutchinson and Wollack, unpublished). Similar attainment of stage-equilibrium is indicated in a preliminary report on the sediments of Lake Windermere in England (Jenkin, Mortimer and Pennington, '41). Every stage of a sere is believed to possess a similar stage-equilibrium of variable duration, although terrestrial stages have not yet been defined in terms of productivity.

The trophic aspects of eutrophication cannot be determined easily from the sediments. In general, however, the ratio of organic matter to the silt washed into the lake from the margins affords an approximation of the photosynthetic productivity. This undecomposed organic matter, representing the amount of energy which is lost from the food cycle, is derived largely from level Λ_1, as plant structures in general are decomposed less easily than animal structures. The quantity of energy passed on into consumer levels can only be surmised from undecomposed fragments of organisms which are believed to occupy those levels. Several types of animal "microfossils" occur rather consistently in lake sediments, such as the carapaces and post-abdomens of certain cladocerans, chironomid head-capsules, fragments of the phantom-midge larva *Chaoborus*, snail shells, polyzoan statoblasts, sponge spicules and rhizopod shells. Deevey ('42), after making comprehensive microfossil and chemical analyses of the sediments of Linsley Pond, suggested that the abundant half-carapaces of the planktonic browser *Bosmina* afford "a reasonable estimate of the quantity of zooplankton produced" and that "the total organic matter of the sediment is a reasonable estimate of the organic matter produced by phytoplankton and littoral vegetation." He found a striking similarity in the shape of the curves representing *Bosmina* content and total organic matter plotted against depth, which, when plotted logarithmically against each other, showed a linear relationship expressed by an empirical power equation. Citing Hutchinson and Wollack ('40) to the effect that the developmental curve for organic matter was analogous to that for the development of an organism, he pressed the analogy further by suggesting that the increase of zooplankton (*Bosmina*) with reference to the increase of organic matter (λ_1) fitted the formula $y = bx^k$ for allometric growth (Huxley, '32), "where y = *Bosmina*, x = total organic matter, b = a constant giving the value of y when $x = 1$, and k = the 'allometry constant,' or the slope of the line when a double log plot is made." If we represent the organic matter produced as λ_1 and further assume that *Bosmina* represents the primary consumers (λ_2), neglecting benthic browsers,

the formula becomes $\lambda_2 = b\lambda_1^k$. Whether this formula would express the relationship found in other levels of the food cycle, the development of other stages, or other ecosystems, remains to be demonstrated.[6] Stratigraphic analyses in Cedar Bog Lake (Lindeman and Lindeman, unpublished) suggest a roughly similar increase of both organic matter and *Bosmina* carapaces in the earliest sediments. In the modern senescent lake, however, double logarithmic plottings of the calorific values for λ_1 against λ_2, and λ_2 against λ_3, for the four years studied, show no semblance of linear relationship, i.e., do not fit any power equation. If Deevey is correct in his interpretation of the Linsley Pond microfossils, allometric growth would appear to characterize the phases of pre-equilibrium succession as the term "growth" indeed implies.

The relative duration of eutrophic stage-equilibrium is not yet completely understood. As exemplified by Linsley Pond, the relation of stage-equilibrium to succession is intimately concerned with the trophic processes of (1) external influx and efflux (partly controlled by climate), (2) photosynthetic productivity, (3) sedimentation (partly by physiographic silting) and (4) regeneration of nutritives from the sediments. These processes apparently maintain a relatively constant ratio to each other during the extended equilibrium period. Yet the food cycle is not in true trophic equilibrium, and continues to fill the lake with organic sediments. *Succession* is continuing, at a rate corresponding to the rate of sediment accumulation. In the words of Hutchinson and Wollack ('40), "this means that during the equilibrium period the lake, through the internal activities of its biocoenosis, is continually approaching a condition when it ceases to be a lake."

Senescence.—As a result of long-continued sedimentation, eutrophic lakes attain senescence, first manifested in bays and wind-protected areas. Senescence is usually characterized by such pond-like conditions as (1) tremendous increase in shallow littoral area populated with pondweeds and (2) increased marginal invasion of terrestrial stages. Cedar Bog Lake, which the author has studied for several years, is in late senescence, rapidly changing to the terrestrial stages of its succession. On casual inspection, the massed verdure of pondweeds and epiphytes, together with sporadic algal blooms, appears to indicate great photosynthetic productivity. As pointed out by Wesenberg-Lund ('12), littoral areas of lakes are virtual hothouses, absorbing more radiant energy per unit volume than deeper areas. At the present time the entire aquatic area of Cedar Bog Lake is essentially littoral in nature, and its productivity per cubic meter of water is probably greater than at any time in its history. However, since radiant energy (λ_0) enters a lake only from the surface, productivity must be defined in terms of surface area. In these terms, the present photosynthetic productivity pales into insignificance when compared with less advanced lakes in similar edaphic regions; for instance, λ_1 is less than ⅓ that of Lake Mendota, Wisconsin (cf. table IV). These facts attest the essential accuracy of Welch's ('35) generalization that productivity declines greatly during senescence. An interesting principle demonstrated in Cedar Bog Lake (Lindeman, '41b) is that during late lake senescence general productivity (λ_n) is increasingly influenced by climatic factors, acting through

[6] It should be mentioned in this connection that Meschkat ('37) found that the relationship of population density of tubificids to organic matter in the bottom of a polluted "Buhnenfeld" could be expressed by the formula $y = a^x$, where y represents the population density, x is the "determining environmental factor," and a is a constant. He pointed out that for such an expression to hold the population density must be maximal. Hentschel ('36), on less secure grounds, suggested applying a similar expression to the relationship between populations of marine plankton and the "controlling factor" of their environment.

water level changes, drainage, duration of winter ice, snow cover, etc., to affect the presence and abundance of practically all food groups in the lake.

Terrestrial stages.—As an aquatic ecosystem passes into terrestrial phases, fluctuations in atmospheric factors increasingly affect its productivity. As succession proceeds, both the species-composition and the productivity of an ecosystem increasingly reflect the effects of the regional climate. Qualitatively, these climatic effects are known for soil morphology (Joffe, '36), autotrophic vegetation (Clements, '16), fauna (Clements and Shelford, '39) and soil microbiota (Braun-Blanquet, '32), in fact for every important component of the food cycle. Quantitatively, these effects have been so little studied that generalizations are most hazardous. It seems probable, however, that productivity tends to increase until the system approaches maturity. Clements and Shelford ('39, p. 116) assert that both plant and animal productivity is generally greatest in the subclimax, except possibly in the case of grasslands. Terrestrial ecosystems are primarily convex topographically and thus subject to a certain nutrient loss by erosion, which may or may not be made up by increased availability of such nutrients as can be extracted from the "C" soil horizon.

Successional productivity curves.—In recapitulating the probable photosynthetic productivity relationships in hydrarch succession, we shall venture to diagram (figure 3) a hypothetical hydrosere, developing from a moderately deep lake in a fertile cold temperate region under relatively constant climatic conditions. The initial period of oligotrophy is believed to be relatively short (Hutchinson and Wollack, '40; Lindeman, '41a), with productivity rapidly increasing until eutrophic stage-equilibrium is attained. The duration of high eutrophic productivity depends upon the mean depth of the basin and upon the rate of sedimentation, and productivity fluctuates about a high eutrophic mean until the lake becomes too shallow for maximum growth of phytoplankton or regeneration of nutrients from the ooze. As the lake becomes shallower and more senescent, productivity is increasingly influenced by climatic fluctuations and

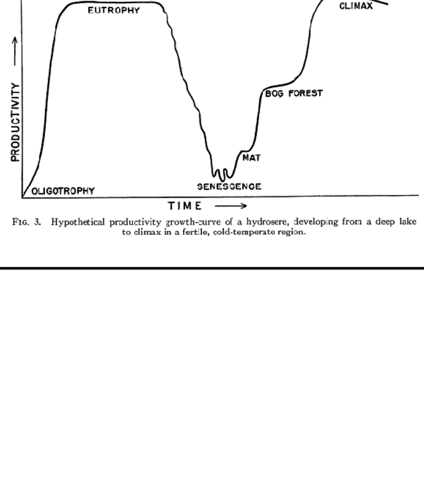

FIG. 3. Hypothetical productivity growth-curve of a hydrosere, developing from a deep lake to climax in a fertile, cold-temperate region.

gradually declines to a minimum as the lake is completely filled with sediments.

The terrestrial aspects of hydrarch succession in cold temperate regions usually follow sharply defined, distinctive stages. In lake basins which are poorly drained, the first stage consists of a mat, often partly floating, made up primarily of sedges and grasses or (in more coastal regions) such heaths as *Chamaedaphne* and *Kalmia* with certain species of sphagnum moss (cf. Rigg, '40). The mat stage is usually followed by a bog forest stage, in which the dominant species is *Larix laricina*, *Picea mariana* or *Thuja occidentalis*. The bog forest stage may be relatively permanent ("edaphic" climax) or succeeded to a greater or lesser degree by the regional climax vegetation. The stage-productivities indicated in figure 3 represent only crude relative estimates, as practically no quantitative data are available.

Efficiency relationships in succession

The successional changes of photosynthetic efficiency in natural areas (with respect to solar radiation, i.e., $\left.\frac{\lambda_1}{\lambda_0}\,100\right)$ have not been intensively studied. In lake succession, photosynthetic efficiency would be expected to follow the same course deduced for productivity, rising to a more or less constant value during eutrophic stage-equilibrium, and declining during senescence, as suggested by a photosynthetic efficiency of at least 0.27 per cent for eutrophic Lake Mendota (Juday, '40) and of 0.10 per cent for senescent Cedar Bog Lake. For the terrestrial hydrosere, efficiency would likewise follow a curve similar to that postulated for productivity.

Rough estimates of photosynthetic efficiency for various climatic regions of the earth have been summarized from the literature by Hutchinson (unpublished). These estimates, corrected for respiration, do not appear to be very reliable because of imperfections in the original observations, but are probably of the correct order of magnitude. The mean photosynthetic efficiency for the sea is given as 0.31 per cent (after Riley, '41). The mean photosynthetic efficiency for terrestrial areas of the earth is given as 0.09 per cent ± 0.02 per cent (after Noddack, '37), for forests as 0.16 per cent, for cultivated lands as 0.13 per cent, for steppes as 0.05 per cent, and for deserts as 0.004 per cent. The mean photosynthetic efficiency for the earth as a whole is given as 0.25 per cent. Hutchinson has suggested (cf. Hutchinson and Lindeman, '41) that numerical efficiency values may provide "the most fundamental possible classification of biological formations and of their developmental stages."

Almost nothing is known concerning the efficiencies of consumer groups in succession. The general chronological increase in numbers of *Bosmina* carapaces with respect to organic matter and of *Chaoborus* fragments with respect to *Bosmina* carapaces in the sediments of Linsley Pond (Deevey, '42) suggests progressively increasing efficiencies of zooplankters and plankton predators. On the other hand, Hutchinson ('42) concludes from a comparison of the P : Z (phytoplankton : zooplankton) biomass ratios of several oligotrophic alpine lakes, ca 1 : 2 (Ruttner, '37), as compared with the ratios for Linsley Pond, 1 : 0.22 (Riley, '40) and three eutrophic Bavarian lakes, 1 : 0.25 (Heinrich, '34), that "as the phytoplankton crop is increased the zooplankton by no means keeps pace with the increase." Data compiled by Deevey ('41) for lakes in both mesotrophic (Connecticut) and eutrophic regions (southern Wisconsin), indicate that the deeper or morphometrically "younger" lakes have a lower ratio of bottom fauna to the standing crop of plankton (10–15 per cent) than the shallower lakes which have attained eutrophic equilibrium (22–27 per cent). The ratios for senescent Cedar Bog Lake, while not directly comparable because of its essentially littoral nature, are even higher. These meager data suggest that the efficiencies of consumer groups may increase throughout the aquatic phases of succession.

For terrestrial stages, no consumer efficiency data are available. A suggestive series of species-frequencies in mesarch succession was published by Vera Smith-Davidson ('32), which indicated greatly increasing numbers of arthropods in successive stages approaching the regional climax. Since the photosynthetic productivity of the stages probably also increased, it is impossible to determine progressive efficiency relationships. The problems of biological efficiencies present a practically virgin feld, which appears to offer abundant rewards for studies guided by a trophic-dynamic viewpoint.

In conclusion, it should be emphasized that the trophic-dynamic principles indicated in the following summary cannot be expected to hold for every single case, in accord with the known facts of biological variability. *à priori*, however, these principles appear to be valid for the vast majority of cases, and may be expected to possess a statistically significant probability of validity for any case selected at random. Since the available data summarized in this paper are far too meager to establish such generalizations on a statistical basis, it is highly important that further studies be initiated to test the validity of these and other trophic-dynamic principles.

SUMMARY

1. Analyses of food-cycle relationships indicate that a biotic community cannot be clearly differentiated from its abiotic environment; the *ecosystem* is hence regarded as the more fundamental ecological unit.

2. The organisms within an ecosystem may be grouped into a series of more or less discrete trophic levels (Λ_1, Λ_2, Λ_3, . . . Λ_n) as producers, primary consumers, secondary consumers, etc., each successively dependent upon the preceding level as a source of energy, with the producers (Λ_1) directly dependent upon the rate of incident solar radiation (productivity λ_0) as a source of energy.

3. The more remote an organism is from the initial source of energy (solar radiation), the less probable that it will be dependent solely upon the preceding trophic level as a source of energy.

4. The progressive energy relationships of the food levels of an "Eltonian Pyramid" may be epitomized in terms of the productivity symbol λ, as follows:

$$\lambda_0 > \lambda_1 > \lambda_2 \ldots > \lambda_n.$$

5. The percentage loss of energy due to respiration is progressively greater for higher levels in the food cycle. Respiration with respect to growth is about 33 per cent for producers, 62 per cent for primary consumers, and more than 100 per cent for secondary consumers.

6. The consumers at progressively higher levels in the food cycle appear to be progressively more efficient in the use of their food supply. This generalization can be reconciled with the preceding one by remembering that increased activity of predators considerably increases the chances of encountering suitable prey.

7. Productivity and efficiency increase during the early phases of successional development. In lake succession, productivity and photosynthetic efficiency increase from oligotrophy to a prolonged eutrophic stage-equilibrium and decline with lake senescence, rising again in the terrestrial stages of hydrarch succession.

8. The progressive efficiencies of consumer levels, on the basis of very meager data, apparently tend to increase throughout the aquatic phases of succession.

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Jenkin, B. M., C. H. Mortimer, and W. Pennington. 1941. The study of lake deposits. Nature, 147: 496–500.

Joffe, J. S. 1936. Pedology. New Brunswick, New Jersey. Rutgers Univ. Press.

Juday, C. 1922. Quantitative studies of the bottom fauna in the deeper waters of Lake Mendota. Trans. Wisconsin Acad. Sci., Arts, Lett., 20: 461–493.

——. 1940. The annual energy budget of an inland lake. Ecology, 21: 438–450.

Krogh, A. 1941. The Comparative Physiology of Respiratory Mechanisms. Philadelphia. Univ. Pennsylvania Press.

Lindeman, R. L. 1941a. The developmental history of Cedar Creek Bog, Minnesota. Amer. Midl. Nat., 25: 101–112.

——. 1941b. Seasonal food-cycle dynamics in a senescent lake. Amer. Midl. Nat., 26: 636–673.

Lohmann, H. 1912. Untersuchungen über das Pflanzen- und Tierleben der Hochsee, zugleich ein Bericht über die biologischen Arbeiten auf der Fahrt der "Deutschland" von Bremerhaven nach Buenos Aires. Veröffentl. d. Inst. f. Meereskunde, N.F., A. Geogr.-naturwissen. Reihe, Heft 1, 92 pp.

Lundegårdh, H. 1924. Kreislauf der Kohlensäure in der Natur. Jena. G. Fischer.

Meschkat, A. 1937. Abwasserbiologische Untersuchungen in einem Buhnenfeld unterhalb Hamburgs. Arch. Hydrobiol., 31: 399–432.

Moore, W. G. 1941. Studies on the feeding habits of fishes. Ecology, 22: 91–95.

Needham, J. 1931. Chemical Embryology. 3 vols. N. Y. Cambridge University Press.

Noddack, W. 1937. Der Kohlenstoff im Haushalt der Natur. Zeitschr. angew. Chemie, 50: 505–510.

Park, Thomas. 1941. The laboratory population as a test of a comprehensive ecological system. Quart. Rev. Biol., 16: 274–293, 440–461.

Rigg, G. B. 1940. Comparisons of the development of some Sphagnum bogs of the Atlantic coast, the interior, and the Pacific coast. Amer. Jour. Bot., 27: 1–14.

Riley, G. A. 1940. Limnological studies in Connecticut. III. The plankton of Linsley Pond. Ecol. Monogr., 10: 279–306.

——. 1941. Plankton studies. III. Long Island Sound. Bull. Bingham Oceanogr. Coll. 7 (3): 1–93.

Ruttner, F. 1937. Limnologische Studien an einigen Seen der Ostalpen. Arch. Hydrobiol., 32: 167–319.

Smith-Davidson, Vera. 1932. The effect of seasonal variability upon animal species in a deciduous forest succession. Ecol. Monogr., 2: 305–334.

Spoehr, H. A. 1926. Photosynthesis. N. Y. Chemical Catalogue Co.

Swingle, H. S., and E. V. Smith. 1940. Experiments on the stocking of fish ponds. Trans. North Amer. Wildlife Conf., 5: 267–276.

Tansley, A. G. 1935. The use and abuse of vegetational concepts and terms. Ecology, 16: 284–307.

Thienemann, A. 1918. Lebensgemeinschaft und Lebensraum. Naturw. Wochenschrift, N.F., 17: 282–290, 297–303.

——. 1926. Der Nahrungskreislauf im Wasser. Verh. deutsch. Zool. Ges., 31: 29–79. (or) Zool. Anz. Suppl., 2: 29–79.

——. 1939. Grundzüge einen allgemeinen Oekologie. Arch. Hydrobiol., 35: 267–285.

Thompson, D. H. 1941. The fish production of inland lakes and streams. Symposium on Hydrobiology, pp. 206–217. Madison. Univ. Wisconsin Press.

Tutin, T. G. 1941. The hydrosere and current concepts of the climax. Jour. Ecol. 29: 268–279.

Vernadsky, V. I. 1929. La biosphere. Paris. Librairie Felix Alcan.

——. 1939. On some fundamental problems of biogeochemistry. Trav. Lab. Biogeochem. Acad. Sci. URSS, 5: 5–17.

Waksman, S. A. 1941. Aquatic bacteria in relation to the cycle of organic matter in lakes. Symposium on Hydrobiology, pp. 86–105. Madison. Univ. Wisconsin Press.

Welch, P. S. 1935. Limnology. N. Y. McGraw-Hill Co.

Wesenberg-Lund, C. 1912. Über einige eigentümliche Temperaturverhaltnisse in der Litoralregion. . . . Internat. Rev. ges. Hydrobiol. u. Hydrogr., 5: 287–316.

Williams, E. C. 1941. An ecological study of the floor fauna of the Panama rain forest. Bull. Chicago Acad. Sci., 6: 63–124.

Wimpenny, R. S. 1941. Organic polarity: some ecological and physiological aspects. Quart. Rev. Biol., 16: 389–425.

ZoBell, C. E., and C. B. Feltham. 1938. Bacteria as food for certain marine invertebrates. Jour. Marine Research, 1: 312–327.

ADDENDUM

While this, his sixth completed paper, was in the press, Raymond Lindeman died after a long illness on 29 June, 1942, in his twenty-seventh year. While his loss is grievous to all who knew him, it is more fitting here to dwell on the achievements of his brief working life. The present paper represents a synthesis of Lindeman's work on the modern ecology and past history of a small senescent lake in Minnesota. In studying this locality he came to realize, as others before him had done, that the most profitable method of analysis lay in reduction of all the interrelated biological events to energetic terms.

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