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Original Achievements Leading Inductively Towards Quantitative Evaluation of Detritus Food Chains in the Marine Food Web

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Abstract : Representative studies conducted originally to the reasonable assessment on significance of detritus food chains in the marine food web for the stability of marine ecosystems have been reviewed from the point of views of both (1) the feeding types of animals comprising the food web, and (2) the energy flow among marine communities in the world oceans.

The former view is evident from the fact that many marine animal species do not conform to specific trophic levels, and the ability of a given species to utilize alternative foods has a great buffering action which tends to stabilize population sizes in the complex marine ecosystem communities.

The latter can be evaluated by comparing the potential solar energy available for primary production in the world oceans, the actual primary productivity measured in the world oceans, and the possible productivity calculated from the commercial fish catch.

Carbon Budget of the Marine Ecosystem Assuming Predominance of the Grazing Food Chains

As in any ecosystem of the Biosphere, the food chains in the marine ecosystem have been shown to be of two basic types; (1) the grazing food chain, which starts from a plant base to grazing herbivores, and on to carnivores, and (2) the detritus food chain, which goes from dead organic matter to heterotrophic microorganisms, and then to detritivores and their predators.

Even at present, most textbooks and encyclopedias describe the grazing food chains as being predominant in the marine ecosystem in contrast with the predominance of detritus food chains in terrestrial ecosystems. The greatest symbolic illustration of this concept goes back to a famous picture of the marine food web in "The nature of oceanic life" by ISAACS in *Scientific American* (1969). With this conventional agreement that the grazing food chains

are predominant in the marine ecosystem, many sophisticated efforts have been made among the greatest authorities to estimate the solar energy available to the marine community in the world oceans (OPPENHEIMER ed., 1968).

Here, based on the solar energy available for photosynthesis in the world oceans, the theoretically maximum productivity of the oceans is calculated as 1.6×10^{11} tons of carbon per year.

Next, this theoretically maximum productivity of the oceans is examined by comparing it with the actual primary productivity measured in the marine ecosystem. As referred to primary production measured actually at different regions of seas and oceans, the annual productivity measured in the world oceans should be summarized as 5.3×10^{10} tons of carbon; that is roughly one third of the theoretical maximum productivity of the world oceans.

Finally, the theoretically maximum productivity of the oceans is examined also by comparing with the primary productivity

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calculated from the commercial fish catch in the world oceans, based on the transfer of food energy with repeated eating and being eaten through a series of prey-predator relationships leading back to the energy source of primary producers in the marine ecosystem.

For this calculation, the amount of commercial fish catch in 1961 was from FAO Fisheries Statistics, by assuming three links in the food chain, with a 5% ecological transfer efficiency. The efficiency is one of the minimal estimations (STEELE ed., 1970), but it must be appropriate in this calculations because there is much energy consumption for the seeking and chasing of a prey by a predator in such an oligotrophic environment as most parts of the oceans. Thus the annual productivity is evaluated as 5.8×10^{10} tons of carbon, that is pretty close to the annual productivity measured in the world oceans.

The conclusion was made at the symposium (OPPENHEIMER ed., 1968) that the annual primary productivity is getting to be within an order of magnitude of the maximum productivity possible, and that the actual harvest of fishery products from the world oceans is getting very close to what is being put into the world oceans. However, we must realize that the estimation by the actual measurement of primary productivity is based only on the phytoplankton, from which transformation of the grazing food chains starts. We must recall also that the actual harvest of fisheries products from the world oceans in 1961 was half of that in the 1980s (FAO, 1991). The cybernetic system of biological productivity in the oceans should not be so inefficient in the utilization of solar energy to be as low as one third of the theoretical maximum productivity!

Carbon Budget of the Marine Ecosystem With Both Grazing and Detritus Food Chains

The conventional agreement that the grazing food chains could be predominant in the marine ecosystem is definitely inadequate because phytoplankters are shown not to be harvested efficiently by grazing zooplankters (PORTER, 1973). Chains of diatoms are broken while they are grasped by zooplankton, and a part of diatoms is damaged and lost. Rough

estimates of the grazing efficiency of phytoplankton by zooplankton under natural conditions vary from 90% to 50%. Zooplankters graze an over-abundance of phytoplankton food, far in excess of their needs, and excrete half or more as faecal pellets. This semi-digested phytoplankton detritus has been reported to often form a significant fraction of particulate organic materials in coastal waters (STRICKLAND, 1965).

Virus infection has been shown recently as another important factor to make phytoplankton flow directly into the ocean debris (*e.g.*, SUTTLE *et al.*, 1991), since a high abundance of viruses were found in aquatic environments by BERGH *et al.* (1989).

Ever since the first aggressive claim with scientific evidences by STRICKLAND (RILEY ed., 1963) to make conservative ecologists realize that the greater fraction of organic material in the oceans is comprised of non-living debris, marine macrophytes have received attention as a major potential source of the particulate and dissolved organic matter in sea water, because less than 5% of macrophytes production has been determined to enter the marine food web by direct grazing, in spite of the fact that the macrophytic communities and mangroves of coastal regions tend to develop to be highly productive (*e.g.*, up to 2,000 gC m⁻² per year). The evidence that marine macrophytes generate debris rather than enter the grazing food chains has thus been recognized in many species of kelps, sea grasses, rockweeds, marsh grasses and mangrove (MANN, 1972). With a careful assessment of annual primary production of these major marine macrophyte systems, the production range have been estimated from 50 to 2,000 gC per square meter, and certain kelp beds are more productive than the most productive land, such as an intensively managed alfalfa field! MANN (1972) concluded that the macrophyte fringe of the oceans has an intensity of production which is up to 40 times the intensity of phytoplankton production. Assuming that the area of macrophyte fringe occupies the coastal region above 10 m deep, the fringe dominates 1.0% of the world oceans, *i.e.*, based on 7.6% area of continental shelf in the oceans (KOSSINNA, 1921) and

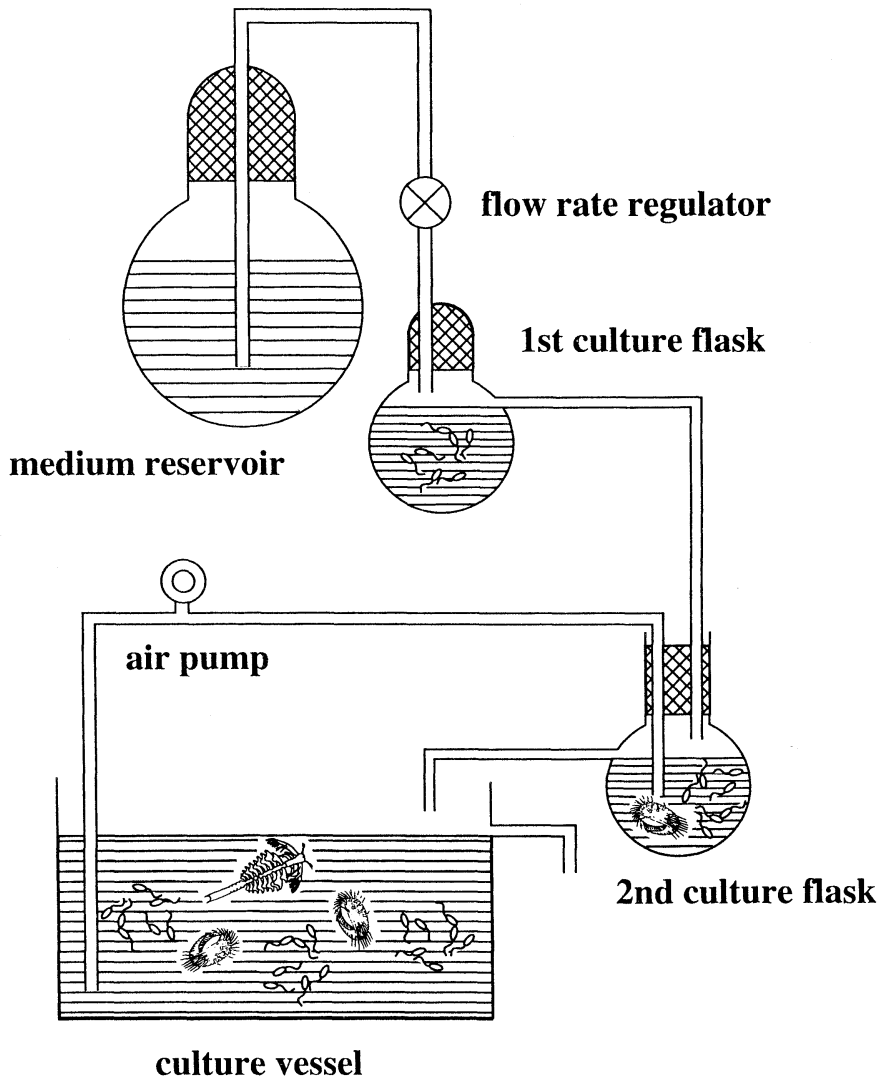
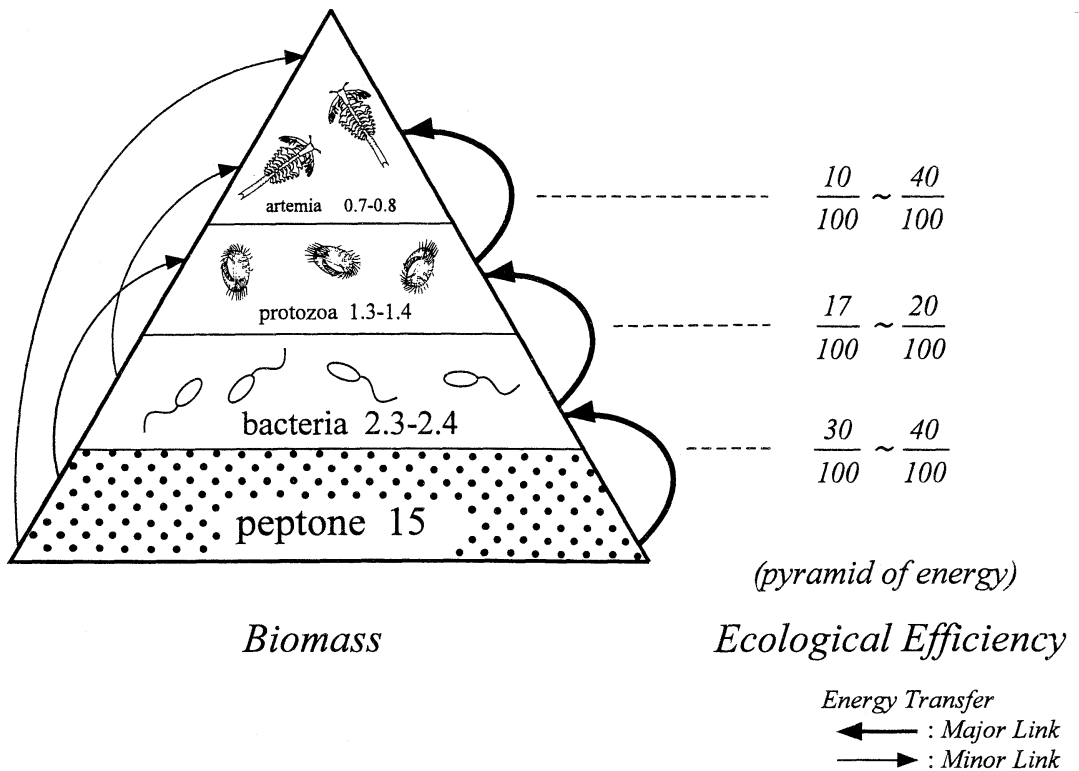


Fig. 1. A continuous culture system for the culture of bacteria, protozoa and brine shrimps. Bacteria and protozoa were isolated from the sea water of Aburatsubo Inlet, Japan (modified from SEKI, 1966)

the hypsometric curve of surface of the earth (WYLLIE, 1976). By comparing the production intensities and distribution areas, the primary production by macrophytes is evaluated as much as up to 40% of that by phytoplankton in the marine ecosystem. In addition to this evaluation, the primary production by floating seaweeds such as *Sargassum* in the surface of open oceans must be taken into account as macrophyte production of the world, because

its production is considerable in such convergence areas as in Shiome (current rip) and the Sargasso Sea.

The process of detritus production from living macrophytes is continuous; *i.e.*, as they grow, leaves or leaf tips die and start to disintegrate. Most grazers on macrophytes are known to be very inefficient, wasting more than they consume and thus contributing to the detritus supply. Once these macrophytes die, the dead



EXPERIMENTAL DETRITUS FOOD CHAIN

Fig. 2. Ecological pyramids based on (1) the biomass of organisms consumed and (2) energy transfer (biological production) from each trophic level of the pyramid of the detritus food chain in the experimental system in Fig. 1

plant materials are covered by bacterial colonies, which support populations of protozoa and other micro-detrivores. Whole microbial communities on a dead macrophyte piece are ingested by fishes and macro-invertebrates as described in DARNELL (1961). These macro-detrivores have been shown to digest only micro-detrivores and bacteria, because their faecal pellets consist almost exclusively of dead macrophytal material (MANN, 1972; SEKI, 1982a). The faecal pellets are recolonized by microbial populations, and the same process is repeated. With every cycle, the particle size of the dead macrophyte piece is reduced. While processes of the detritus food chains proceed, a part of macrophyte production enters into the stock of ocean debris as a dissolved form.

The energy transfer in an experimental

system of the detritus food chain (Figs. 1 and 2) was determined firstly by SEKI (1964, 1965, 1966b). Thereafter, efficient bacterial utilization of these abundant organic materials, both from dead phytoplankton and macrophyte, as the production at the primary trophic level of detritus food chains has been shown with both experimental and field studies by many authors (*e.g.*, PARSONS and SEKI, 1970; SEKI, 1969; 1971; 1972; SEKI *et al.*, 1968; 1969; 1972; 1974a; SEKI & YOKOHAMA, 1978).

Difficulty in Classification of The Real Trophic Level of A Species in the Marine Ecological Pyramid

The mythology of the grazing food chains being predominant at the marine ecosystem was also doubted in 1961, since DARNELL (1961)

showed that many animal species do not conform to specific trophic levels, based on the results of a series of detailed investigations obtained in a large estuary of the Louisiana coast.

There are only a few typical carnivorous fish species, such as longnose gar, crevalle jack, bull shark and southern flounder. The really abundant fish and invertebrate species comprise 2 groups: The first includes those omnivorous species which have a rather wide range of food tolerance, such as sea catfish, bay anchovy, spot, Atlantic croaker and blue crab. The second includes those detritivorous species which feed largely upon organic detritus, such as rangia clam, striped mullet, largescale menhaden, white shrimp and hogchoker.

The ontogenetic progression of food habits within a given species frequently involves successive specialization upon different types of foods. This is evidently shown in case of the Atlantic croaker; i.e., the successive shift of its prey proceeds from zooplankton to small benthic animals, then to detritus, and finally to larger crustaceans and fishes.

Hence the study by DARNELL (1961) shows that the ability of a given species to utilize alternative foods has a great buffering action which tends to stabilize population sizes in the complex communities of the marine ecosystem. It was also shown that most of the marine consumer species ingest large quantities of organic debris and some of them are largely dependent upon this material. These conclusions evidently lead also to the importance of the detritus food chains from the predator side of the marine ecosystem.

Stability of the Marine Ecological Pyramid With the Backup System of the Detritus Food Chains

The difficulty of classifying a marine species into a particular trophic level in the marine ecological pyramid is not only seen in the case of predator but also for prey. As has been recently realized (e.g., SIEBURTH *et al.*, 1988), many flagellate species play roles as detritivores as well as primary producers. Their grazing mechanism has been clarified, especially for species in the haptophyta. Food capture and

transport during phagocytosis of these flagellates has been shown clearly using video images for a species *Chrysochromulina hirta* (KAWACHI *et al.*, 1991). Existence of these mixotrophs can stabilize the biomass within the first trophic level of the marine food web towards a very steady state, by efficiently collecting bacterioplankton and the detritus which is released mainly from dead macrophytes and the broken phytoplankton from zooplankton grazing, natural death and virus infection. Thus, constituent members in the first trophic level of marine ecological pyramid comprise these primary producers in the grazing food chains and the detritus food chains; both producers acting as replenishing agents against the loss of organic materials to make the organic debris loss as small as possible. Already by a purely theoretical approach, PARSONS and KESSLER (1986) have predicted this important role of zooflagellates in maintaining an adequate food supply for zooplankton when the phytoplankton has run out of nutrients and collapses.

The major constituent member in the first trophic level of detritus food chains are bacteria which are not only dependent on detrital particles but also on dissolved organic materials. An early study of bacterial production through this process was initiated by PARSONS and STRICKLAND (1962) in order to determine the significant part of photosynthetic production flows via bacteria through the detritus food chains in the marine ecological pyramid. An analysis which greatly contributed to the reliable understanding of the distribution of the organic debris was made by DUURSMA (1960), who determined its approximate biomass as 1 mgC per liter of sea water in the bulk of the ocean. Each organic compound is maintained in a steady-state equilibrium in the order of μg per liter, down to a threshold in the order of ng per liter by bacterial nutrient assimilation in some oligotrophic waters. As much as 5 to 10 times of this concentration occurs within surface waters and throughout the coastal waters, and it is rarely less than 0.5 mgC per liter in deep ocean waters (e.g., SEKI *et al.*, 1974b; 1981a; 1981b). This minimum concentration is the apparent threshold bulk of most

Table 1
Primary production divided into the grazing and
detritus food chains in the world oceans

PRIMARY PRODUCTION(100%)IN THE WORLD OCEANS BY:

PHYTOPLANKTON: 71%	
used for grazing by zooplankton ;	13% ~ 23%
used for generating debris ;	48% ~ 58%
MACROPHYTES: 29%	
used for grazing by benthos;	< 1.5%
used for generating debris;	27% ~ 28%

* Overall energy of the primary production to be used for

- (1) the grazing food chain is between 14% and 24%
(13%~23% used for grazing by zooplankton, and
< 1.5% used for grazing by benthos)
and
(2) the detritus food chain is between 75% and 86%.
(48%~58% used for generating debris, and
27%~28% used for generating debris)

organic compound; more than 0.5 mgC per liter of organic debris are susceptible to dynamic cycling by the bacterial action (SEKI, 1992).

The bacterioplankton production through debris utilization in the world oceans seems to be insignificant because the aquatic humus comprises the major fraction of total organic debris. The annual flux corresponds to 0.20×10^9 tons of carbon in the world oceans, assuming that the total debris amount of 1.3×10^{12} tons of carbon (SKOPINTSEV, 1966) then the resident time of 3740 years (WILLIAMS *et al.*, 1969) is determined by converting 30% into bacterial cells. This amounts to only 0.02% of the maximum primary productivity.

However, when the process is specified within the productive layer of oceans, assuming a value of roughly 0.1 mgC per square meter for the standing crop of bacterioplankton which can utilize highly nutritional organic solute excreted from both living plants and animals (PARSONS and SEKI, 1970; SEKI, 1966a; 1970a; 1970b; SEKI and ZOBELL, 1967), the bacterioplankton production there is as much as 0.5 to 1% of the phytoplankton production (PARSONS and STRICKLAND, 1962). This moderate transfer efficiency is due to rapid cycling of easily metabolizable solutes (*e.g.*, organic acids,

monosaccharides and amino acids) with their resident time as short as several tens of days (SEKI, 1992). This contribution of bacterioplankton is still extremely small, when compared with that of attached bacteria on the dead macrophytes and the faecal pellets of dead phytoplankton (SEKI, 1970a; SEKI *et al.*, 1972; HONJO, 1978).

As mentioned before, the grazing efficiency of phytoplankton by zooplankton in the oceans varies from 50 to 90% even if there is an ideal prey-predator relationship without the grazing loss. As such an ideal period for grazing has been observed to be only less than 3 months a year in the world oceans (HEINRICH, 1962), less than 25% of the annual primary production can be used for the grazing food chains of marine ecological pyramid. The approximate calculations, thus, lead to the definite conclusion that the detritus food chains are dominant over the grazing food chains in the marine ecosystem, just the same as in the terrestrial ecosystems (Table 1).

Approximately equal concentrations of organisms have shown to occur at every particle size group within the range from phytoplankton to whales in Antarctic waters or from phytoplankton to tuna in the equatorial Pacific

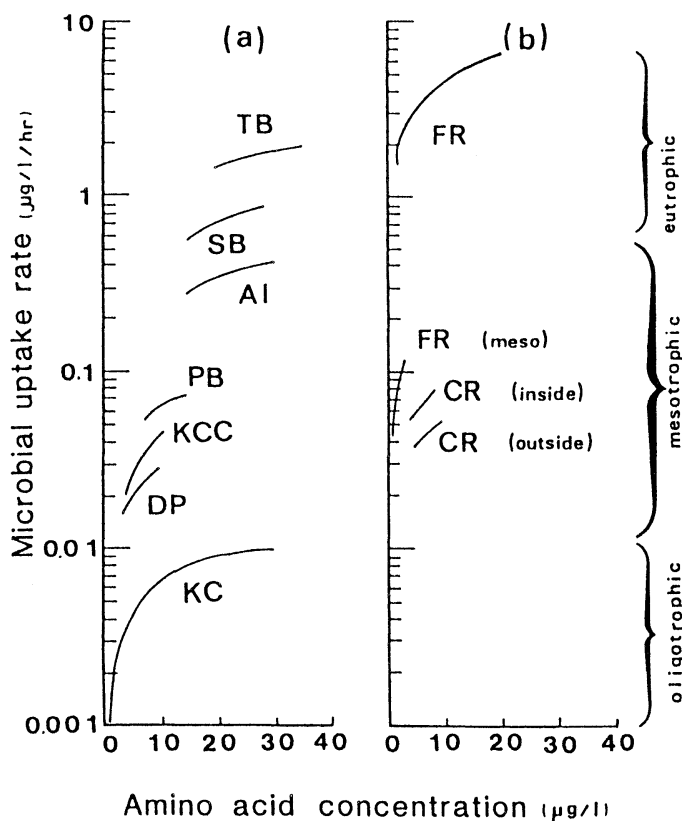


Fig. 3. Assimilation of amino acids by natural microbial communities (95% confidence limits) at Kuroshio Current (KC), Kuroshio Counter Current (KCC), Shimoda Bay (SB), Tokyo Bay (TB), Discovery Passage (DP), Patricia Bay (PB), Alberni Inlet (AI) in the Pacific coast (a); and at Campbell River Estuary (CR) and Fraser River Estuary (FR) in the Canadian estuaries (b) (reproduced from SEKI, 1992)

Ocean (SHELDON *et al.*, 1972). The same biomass structure is kept even with the addition of the bacterial size group into the scheme (SEKI, 1982a). In the structure, some decrease of standing stock actually determined in the oceans may occur as particle size increases, so the pyramid of biomass has a slightly upright shape. However, concentrations in the bacterial and phytoplankton size ranges should be reduced by a factor of at least two to eliminate living organisms only. The zooplankton concentrations are approximately correct, as it is unlikely that many nonliving particles are present in that size range. The estimated concentrations of tuna and whales represent minimums for particles of these sizes due to tech-

nical problems in estimation. When these corrections are performed to estimate standing stocks of living particles, the constant concentrations represent the possible spectrum of living particles in the Antarctic and equatorial Pacific Oceans. The pattern of standing stocks are similar in each of the two oceans, although the absolute values differ by approximately a factor of ten. This could be reasonably expected because of differences in the productivity of each region.

The arithmetic distribution of biomass in any ocean must be a column shape. Then the pattern of this standing stock can be maintained only if the rate of production varies inversely with particle size, in order that the

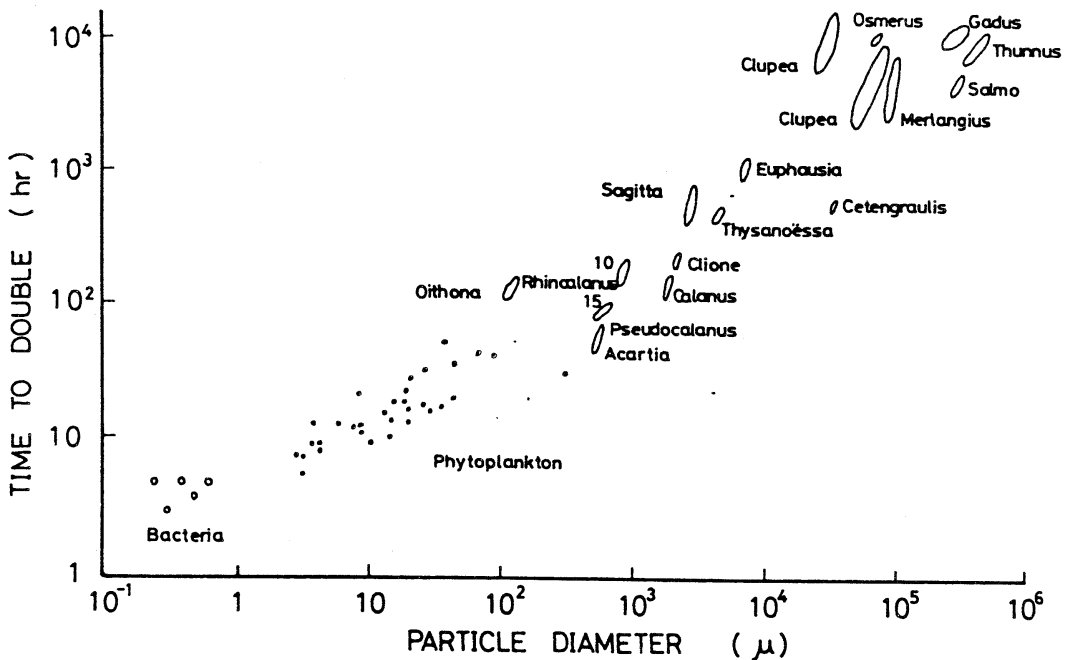


Fig. 4. The relationship between production rate and particle size (modified from SHELDON *et al.*, 1972)

pyramid of energy can reasonably take a true upright pyramid shape. This is evident in Figure 4 which shows the relationship between production rates and particle sizes of all groups of marine organisms including bacteria. A striking characteristic of bacteria and other nanoplankters is their rapid rates of reproduction, accomplished by vegetative cell division. Their biomass formation can be extremely rapid since the increase is by geometric progression. The rate of bacterial division is as frequent as once every few hours in the production layer, where bacterioplankton acts as a replenishing agent against the loss of organic materials from phytoplankton to make the organic debris losses from the marine ecological pyramid as minimal as possible. The growth rate and size of a multi-cellular organism vary significantly during its life-time, whereas a single-celled microbe is less variable. Growth rate of marine microorganisms varies greatly with temperature and other environmental factors in usual laboratory experiments, but this effect has been determined to be relatively small with prompt biological

reactions such as the species succession and other phenomena in the natural environment of oceans (SEKI, 1982b).

When organisms in both grazing food chains and detritus food chains at each trophic level of the marine ecological pyramid are related as whole (size ranges; 10^{-1} to $10^2 \mu\text{m}$ for the first trophic level, 10^2 to $10^4 \mu\text{m}$ for the second trophic level, 10^4 to $10^6 \mu\text{m}$ for the third trophic level), production rates between prey and predators vary by roughly one order of magnitude (Fig. 5). Although experimental results represent higher efficiencies almost exclusively due to the predator's assimilation, those efficiencies in Nature must include also energy loss of finding and accessing the prey by predator. Therefore, some experimental results have shown that the energy transferred from one trophic level to another can be more efficient than 30% (STEELE *et al.*, 1970), but the standing stocks of every trophic level is kept similar with the ecological efficiency of about 10% in the oceans.

Finally, the bacterial production processes are less susceptible to seasonal and other

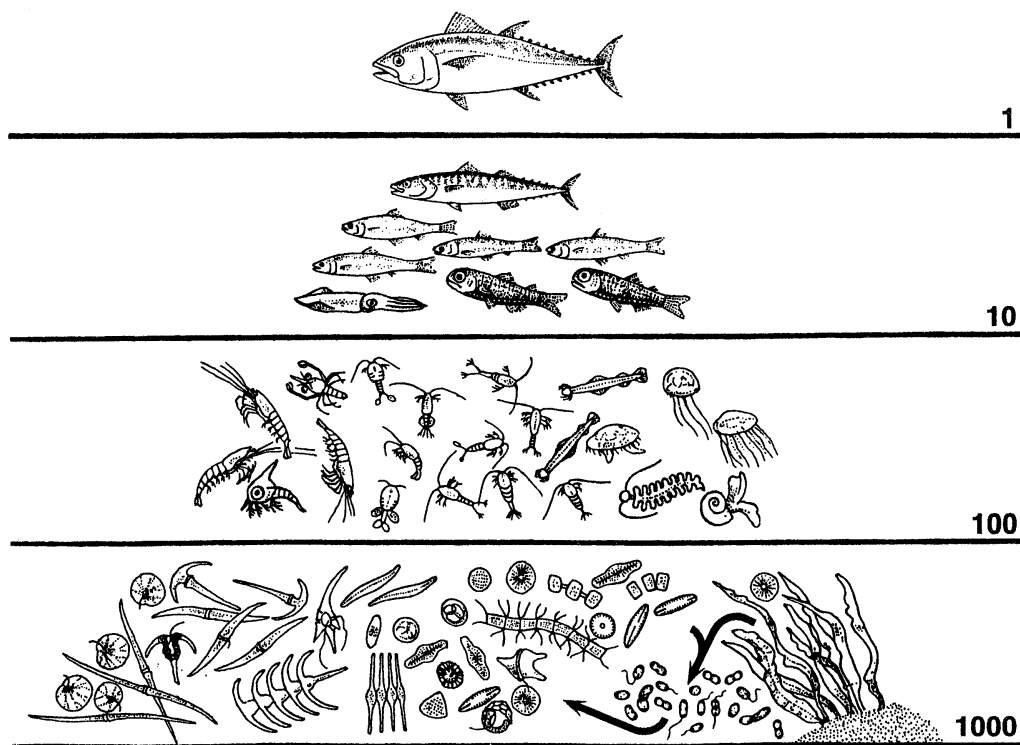


Fig. 5. Pyramid of energy in the marine ecosystem, based on the marine food web with the grazing food chains and the detritus food chains

variable factors of the marine ecosystem. This characteristic has a favourable function for the constant supply of biomass to the second trophic level of the ecological pyramid, by backing up the unstable supply of phytoplankton, and eventually contributing to the stability of marine ecosystem.

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「海洋食物網における腐食連鎖の卓越性に関する主導的研究」

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要旨：生物圏を構成しているすべての生態系では、被食者と捕食者との関係における繋がりは、生態系の機能から生きている生物を直接に食う連鎖である生食連鎖と、死骸または生体の破片や排出物を食う連鎖である腐食連鎖によって構成されている。

この両者の関係において、著者(SEKI, 1964; 1965; 1966; SEKI *et al.*, 1968)は、「海洋においては生産層でも分解層でも腐食連鎖が卓越して、その結果として海洋全体としても腐食連鎖が卓越すること」を先駆的に実験生態学的に実証した。その後、多くの海洋生態学者が種々な角度から研究を重ねて、大同小異の結果を得ている。それらの研究結果の共通した結論から、海洋食物網における腐食連鎖の卓越性は、現在では海洋生態学上の常識となっている。

このように「海洋において腐食連鎖が卓越すること」が海洋生態系の安定性をもたらすことを、(1)食物網を構成する海洋動物の食性と(2)全海洋の生物群集におけるエネルギー流の視点から、明らかにしてきた主導的な研究を簡潔に総説する。

前者の視点に関しては、多くの海洋動物種が食物連鎖の特定な栄養段階に分別されることなく、環境変化に応じて食物種を自在に変更することによって、複雑な海洋生態系構成生物群にあって個体群サイズを安定させていることから、解明されるに至っている。

後者の視点に関しては、全海洋における基礎生産に利用可能な太陽エネルギー量や、全海洋において観測された基礎生産量、そしてFAOなどの全海洋における水産統計から生態学的に算定される基礎生産量を突き合わせることで、明白な現象と認識されている。