penetrating faults would make lateral fluid flow within upper basement inefficient at removing heat. Circulation would continue within basement locally, redistributing heat or being thermally masked below thick sediments, but heat loss from the crust would be entirely conductive.

This model explains how free convection could be prevented despite very high effective permeabilities, enhancing the efficiency of lateral flow for advecting heat. It does not preclude local thermal homogenization of upper basement[28], either by organized or chaotic flow[29], but local convection could also be channelized. Unlike a homogeneous permeability model for the upper crust, our model is consistent with observed lithostratigraphic, hydrologic, and alteration heterogeneity[5,7,17,30]. There would still be chemically and biologically significant fluid flow within much of the upper crust, but fluid fluxes away from the primary channels would be small relative to those in the channels.

Some important implications for hydrogeology and fluid–rock interaction within oceanic ridge flanks follow from our model. First, most of the fluid flow within the uppermost oceanic crust of ridge flanks would be very strongly guided (perhaps fully constrained) by the permeability distribution. There would be no tendency for hydrothermal convection cells to form with any particular geometry, and flow channelling would reduce the tendency for small-scale convection cells to form, since crustal permeability would be both heterogeneous and highly anisotropic. Second, flow would be much less chaotic than in a homogeneous, isotropic porous system having the same formation-scale permeability. Local flow paths would be strongly influenced by crustal constructional, tectonic and alteration patterns. Third, water–rock ratios would be highly variable over small spatial distances, depending on proximity to primary flow channels, and reaction in surrounding rock would be limited by slower advection and diffusion away from the channels. Borehole permeability estimates from packer testing would indicate the bulk hydrologic properties of most of the upper crust—with decreasing permeability associated with infilling of pores and increasing seismic velocities in young crust—but the flow channels responsible for the ridge–flank heat-flow deficit (Fig. 1e), being spatially rare, would generally not be penetrated by vertical boreholes[8].

Testing of the model we report here can be performed by continuing to map out bulk permeability, apparent water age, and the distribution of lateral and vertical pressure gradients within oceanic crust, over a range of crustal ages. Understanding will also come from measuring permeability at a variety of lateral scales using the same boreholes and the same measurement methods, and by cross-hole testing, in order to establish the spatial dependence of properties. Coupled heat and fluid flow models will continue to provide insight, but should include heterogeneous permeability distributions and anisotropy. ☐

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A highly unsaturated fatty acid predicts carbon transfer between primary producers and consumers

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The factors that regulate energy transfer between primary producers and consumers in aquatic ecosystems have been investigated for more than 50 years (refs 1–3). Among all levels of the food web (plants, herbivores, carnivores), the plant–animal interface is the most variable and least predictable link[4–6]. In hypereutrophic lakes, for example, biomass and energy transfer is often inhibited at the phytoplankton–zooplankton link[4], resulting in an accumulation of phytoplankton biomass instead of sustaining

production at higher trophic levels, such as fish. Accumulation of phytoplankton (especially cyanobacteria) results in severe deterioration of water quality, with detrimental effects on the health of humans and domestic animals, and diminished recreational value of water bodies[7,8]. We show here that low transfer efficiencies between primary producers and consumers during cyanobacteria bloom conditions are related to low relative eicosapentaenoic acid (20:5ω3) content of the primary producer community. Zooplankton growth and egg production were strongly related to the primary producer 20:5ω3 to carbon ratio. This indicates that limitation of zooplankton production by this essential fatty acid is of central importance at the pelagic producer–consumer interface.

During the summer and winter 1997 and the spring of 1998, we performed a series of laboratory experiments in which seston (fine particles in water) collected from hypereutrophic Stonegate pond was fed to the herbivorous zooplankter *Daphnia magna* as a consumer. Trophic transfer was measured as *Daphnia* biomass accrual. The experiments were performed at a constant temperature using standardized animals in a flow-through experimental system. This enabled us to determine directly the effect of phytoplankton elemental and biochemical composition on energy transfer to herbivore biomass, independent of factors such as temperature and predation which can also influence this process[9].

Stonegate pond is a hypereutrophic (mean total phosphorus, $125 \pm 34\,\mu\mathrm{g\,l^{-1}}$) shallow pond situated in Davis, California, USA. During the summer, cyanobacteria (mainly *Oscillatoria c.f. tenuis*, and *Anabaena c.f. aphanizomenoides*) strongly dominated the phytoplankton community. Although seston carbon was quite high (3.9–$9.4\,\mathrm{mg\,C\,l^{-1}}$), experimentally determined growth rates for *Daphnia* feeding on the summer phytoplankton assemblage were very low: around the threshold for egg production (0–0.5 eggs per clutch). The food quality of seston was poor and the transfer efficiency between primary producers and consumers was low, between 5% and 26% of consumer ingested carbon. During the winter and spring, the phytoplankton community was dominated by diatoms. Although the seston carbon concentration was lower (1.7–$3.8\,\mathrm{mg\,C\,l^{-1}}$) than in the summer, daphnids grew at about their maximal rate at the temperature of our experiments and produced large first clutches (9.1–17.0 eggs per clutch). Conversion of consumed phytoplankton carbon into herbivore biomass was 50–65%. Daphnid growth rates and carbon concentrations were in fact inversely related (Table 1), showing that food quality, rather than quantity, regulated carbon transfer between primary producers and consumers in this system.

We measured a variety of chemical characteristics (chlorophyll *a* (chl *a*) content, elemental and fatty acid composition) of the phytoplankton community, and related these to daphnid growth rates. Regression analyses were performed to determine which of these characteristics best predicted biomass production by these herbivorous zooplankters. The chl-*a*/C ratio was not significantly related to *Daphnia* growth (Fig. 1, Table 1). Chlorophyll *a* is often used as a food parameter because it allows one to infer the relative contributions of phytoplankton and presumably low-quality detritus to the seston C pool. However, our results suggest that the chl-*a*/C ratio may not be a particularly useful food-quality index. The molar elemental P/C ratio was moderately positively (that is, molar C/P was inversely) correlated to daphnid growth in these experiments (Fig. 2, Table 1). However, minimal P/C (maximal C/P) molar ratios observed were higher than 4.7×10^{-3} (less than 210), and most researchers believe phosphorus limitation of *Daphnia* growth will only occur at P/C ratios below 3.3×10^{-3} (C/P ratios above 300)[10,11]. The seston N/P ratio was also correlated to the daphnid growth rates (Table 1), which might well be an indirect effect due to correlation between seston N/P and its 20:5ω3 content ($P = 0.0005$, $r^2 = 65$). Counter-intuitively, the molar N/C ratio was negatively related to daphnid growth rates (Table 1), indicating that growth was negatively related to the nitrogen moiety.

In contrast to these parameters, we obtained a very strong correlation between the seston 20:5ω3 to carbon (20:5ω3/C) ratio and *Daphnia* growth rates (Fig. 3, Table 1) and egg production (Fig. 4). The 20:5ω3/C ratio was clearly the best predictor of *Daphnia* growth of fatty acids measured (Table 1). The fit with other fatty acids was substantially weaker, but still strong (Table 1). However, this is probably due to an inter-correlation with 20:5ω3 (for example, $P = 0.0002$, $r^2 = 0.70$ for 18:4ω3). Variability in phytoplankton 20:5ω3 content could explain the poor predictability of energy transfer at the primary producer–consumer interface. The

Table 1 Regressions with *Daphnia* growth rates

Independent variable	Slope	*Y*-intercept	*P*	r^2
C ($\mathrm{mg\,l^{-1}}$)	–0.05	0.52	0.002	0.55
P/C ($\mathrm{mol\,mol^{-1}}$)	27.11	–0.005	0.0087	0.45
N/P ($\mathrm{mol\,mol^{-1}}$)	–0.013	0.48	0.0031	0.53
N/C ($\mathrm{mol\,mol^{-1}}$)	–4.39	1.04	<0.0001	0.85
Chl-*a*/$\mathrm{C^{-1}}$ ($\mu\mathrm{g\,mg^{-1}}$)	–0.01	0.37	0.445	0.05
18:3ω3/C ($\mu\mathrm{g\,mg^{-1}}$)	–0.02	0.42	0.063	0.26
18:4ω3/C ($\mu\mathrm{g\,mg^{-1}}$)	0.14	0.04	<0.0001	0.80
20:5ω3/C ($\mu\mathrm{g\,mg^{-1}}$)	0.11	0.04	<0.0001	0.95
22:6ω3/C ($\mu\mathrm{g\,mg^{-1}}$)	0.31	0.13	0.008	0.50
Σω3-PUFA/C ($\mu\mathrm{g\,mg^{-1}}$)	3.83	0.11	0.3761	0.07

Chl-*a*, chlorophyll *a*; 18:3ω3, linolenic acid; 18:4ω3, octadecatetraenoic acid; 20:5ω3, eicosapentaenoic acid; 22:6ω3, docosahexaenoic acid; PUFA, polyunsaturated fatty acids.

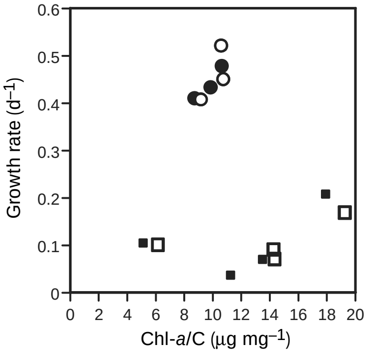

Figure 1 The relationship between the seston chlorophyl *a* to carbon ratio and daphnid growth rates. Squares denote the cyanobacteria-dominated summer assemblages, and circles denote the diatom- and cryptophyte-dominated winter/spring assemblages. Open symbols represent the seston fraction less than 30 µm, and closed symbols the total seston.

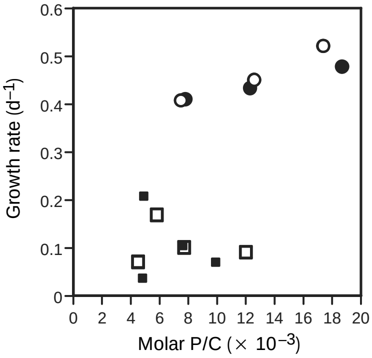

Figure 2 The relationship between the seston molar phosphorus to carbon ratio and daphnid growth rates. Symbols as in Fig. 1.

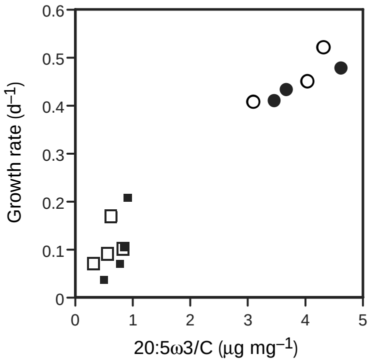

Figure 3 The relationship between the seston 20:5ω3 to carbon ratio and daphnid growth rates. Growth rate $= 0.74\,[1 - \exp(-0.25x + 0.01)]$, where x is the ratio 20:5ω3/C, $r^2 = 0.96$; for linear regression see Table 1. Symbols as in Fig. 1.

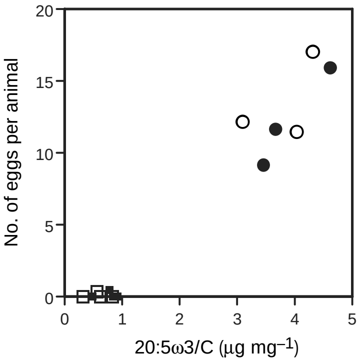

Figure 4 The relationship between the seston 20:5ω3 to carbon ratio and mean number of eggs produced by daphnids (mean clutch size). No of eggs per animal $= 4.0x - 2.5$, where x is the ratio 20:5ω3/C; $P < 0.00001$; $r^2 = 0.96$. Symbols as in Fig. 1.

phytoplankton's relative content of this highly unsaturated fatty acid was a strong predictor of zooplankton carbon conversion (that is, secondary production) in this hypereutrophic system. In contrast to the present results, the absolute concentration of 20:5ω3 (that is, 10:5ω3 per litre) was found to be the best predictor of *Daphnia* growth when fed seston from a mesotrophic lake (Schöhsee, Germany)[12]. Unlike mesotrophic Schöhsee, where food carbon concentrations were below saturating *Daphnia* growth, seston concentrations in Stonegate pond were well above the growth saturation level. Thus, 20:5ω3 seems to be of general importance for the trophic transfer of energy and elements within the aquatic food web[13], both in an absolute sense at low food concentrations and in a relative sense at high seston concentrations.

In Stonegate pond, the 20:5ω3 was diluted by the vast amount of carbon present during summer cyanobacteria dominance. Prokaryotic cyanobacteria have a fatty-acid pattern distinct from eukaryotes and generally do not contain highly unsaturated fatty acids like 20:5ω3 (refs 14–16). In contrast, cryptophytes and especially diatoms contain high amounts of 20:5ω3 (refs 14–16). The source of 20:5ω3 under cyanobacteria-dominated conditions was probably cryptophytes, which are often present in low numbers during cyanobacteria blooms. Although relatively rare, 20:5ω3-rich algal taxa might be of prime importance for trophic transfer at the producer–consumer interface during cyanobacteria-dominated conditions.

Cyanobacteria have long been known to be of poor quality for herbivorous zooplankton[17–19], but the causes of this low food quality are still poorly understood: mechanical interference, toxocity and nutritional inadequacy have been suggested[7,8,17–20]. Although experimental evidence is contradictory, mechanical interference of the filtering process is often thought to be the main reason for poor food quality of filamentous cyanobacteria, allowing them to build up nuisance blooms in nutrient-enriched lakes. Despite the fact that filamentous cyanobacteria dominated the phytoplankton assemblage during the summer, daphnid growth rates in the total seston fraction were not significantly depressed relative to the less than 30-μm size seston fraction ($F_{1,9} = 2.37$, $P = 0.1638$, analysis of covariance), although large interfering cyanobacteria filaments were more prevalent in the total seston fraction. In contrast to the prevailing view of mechanical interference, our results show that the lack of 20:5ω3 in cyanobacteria could itself be responsible for the poor quality of seston dominated by cyanobacteria. The lack of 20:5ω3 in cyanobacteria appears to be the main reason for the decoupling between primary and secondary production. This is a well known problem when trying to biomanipulate the food web with the aim of reducing phytoplankton biomass by altering higher trophic levels[7]. Our findings may therefore be relevant to lake restoration measures that utilize biomanipulation approaches. ☐

Methods

Experiments

We performed seven laboratory growth experiments with two treatments (total seston, $<$30-μm seston) run in duplicate. Growth rates were determined as $g = (\ln W_t - \ln W_0)/t$ where W is the mean body weight of the experimental animals ($n = 8$) at the beginning (W_0) and end (W_t) of the experimental duration of $t = 4$ (±0.1 d, resulting from 2 h required to process the animals). The carbon transfer efficiency was calculated as the ratio of daphnid carbon accrual to carbon ingested. Daphnid carbon was assumed to be 40% of the dry weight of the animals, as determined from a sub-sample of the experimental animals. Hourly ingestion rates were assumed to be 3.2% of the carbon weight of the daphnids[21]. Daphnids were grown in a flow-through system[22] which minimized the influence of grazing and sedimentation on food (seston) concentrations. This ensured that seston was maintained constant at the ambient level. The entire flow-through system was maintained at 20 ± 0.1 °C in a temperature-controlled water bath in a temperature-controlled room. The water was pumped from continuously stirred reservoirs by a multichannel peristaltic pump (Watson-Marlow) to individual 250-ml chambers at the rate of 1.61 per day per chamber. Fresh water from Stonegate pond was collected daily, and ambient large zooplankton were removed before feeding if necessary. *Daphnia magna* used in these experiments originated from a single clone, and were raised under standardized conditions. At the start of each experiment, eight 3-day-old daphnids were pipetted into each chamber. Juveniles were selected randomly from offspring released over 8 h and raised with *Scenedesmus acutus* for 3 d until the start of the experiment. At the end of each experiment, all 7-day-old animals were collected, examined for body length and clutch size under a dissecting microscope, dried and weighed.

Analyses

Particulate matter was collected in duplicate. Total seston was filtered directly onto precombusted (24 h at 450 °C) glass-fibre filters (Whatman GF/C). Seston for the $<$30-μm fraction was screened three times through a 30-μm mesh and then filtered as above. Seston carbon and nitrogen content was determined with a CHN analyser (Perkin-Elmer Model 2400). Particulate phosphorus was calculated by subtracting soluble reactive phosphorus (SRP) from total phosphorus (TP). Water for SRP analyses was filtered through a glass-fibre filter and then measured colorimetrically[23]. TP was analysed in unfiltered water by colorimetric means after autoclaving[23]. Chl-*a* concentrations were determined using a fluorometric method with acid correction for degradation products[24]. Fatty acids were analysed, after extraction and methylation[25], with a gas chromatograph (HP 6890) equipped with a programmable temperature vaporizer-injector, a fused silica DB-WAX (J&W Scientific) capillary column and a flame ionization detector.

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The Santa Barbara Basin is a symbiosis oasis

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It is generally agreed that the origin and initial diversification of Eucarya occurred in the late Archaean or Proterozoic Eons when atmospheric oxygen levels were low[1] and the risk of DNA damage due to ultraviolet radiation was high[2]. Because deep water provides refuge against ultraviolet radiation[3] and early eukaryotes may have been aerotolerant anaerobes[1,4,5], deep-water dysoxic environments are likely settings for primeval eukaryotic diversification. Fossil evidence shows that deep-sea microbial mats, possibly of sulphur bacteria similar to *Beggiatoa*, existed during that time[6]. Here we report on the eukaryotic community of a modern analogue, the Santa Barbara Basin (California, USA). The *Beggiatoa* mats of these severely dysoxic and sulphidic sediments support a surprisingly abundant protistan and metazoan meiofaunal community, most members of which harbour prokaryotic symbionts. Many of these taxa are new to science, and both microaerophilic and anaerobic taxa appear to be represented. Compared with nearby aerated sites, the Santa Barbara Basin is a 'symbiosis oasis' offering a new source of organisms for testing symbiosis hypotheses of eukaryogenesis.

Table 1 SBB eukaryotic taxa/morphotypes

Taxa/Morphotype	Method	Ectobionts	Endobionts
Protista			
Foraminifera			
Allogromid sp. 1	DAPI	No	Yes
Allogromid sp. 2	TEM	No	No
Buliminella tenuata	TEM	No	Yes
Chilostomella ovoidea	TEM	No	No
Fursenkoina rotundata	Autofluorescence	No	Yes*†
Nonionella stella	TEM	No	Yes‡
Euglenozoan Flagellates			
Calkinsia aureus	DAPI/SEM	Yes	No
Notosolenus ostium	DAPI/SEM	No	No
Postgaardi mariagerensis	DAPI/SEM	Yes	No
Sphenomonas sp.	DAPI	No	No
Euglenoid sp.	DAPI/SEM/TEM	Yes	No
Flagellate sp. 1	DAPI	No	Yes
Flagellate sp. 2	DAPI	Yes	No
Ciliophora			
Frontonia? sp.	DAPI	No	No
Litonotus duplostriatus?	DAPI	No	No
Metopus halophila	DAPI	Yes	Yes
Metopus verrucosus	TEM/DAPI	Yes	No
Parablepharisma collare?	DAPI	Yes	No
Parablepharisma sp.	DAPI	Yes	Yes
Ciliate sp. 1	DAPI	No	Yes
Ciliate sp. 2	DAPI	Yes	No
Ciliate sp. 3	DAPI	Yes	No
Ciliate sp. 4	DAPI	Yes	No
Ciliate sp. 5	DAPI	Yes	No
Ciliate sp. 6	DAPI	Yes	No
Ciliate sp. 7	DAPI	No	Yes
Ciliate sp. 8	DAPI	No	Yes
Ciliate sp. 9	DAPI	Yes	No
Metazoa			
Nematoda			
Desmodora masira	TEM/DAPI	Yes	No
Daptonema sp.	TEM/DAPI	No	No
Gastrotricha			
Urodasys sp.	DAPI/SEM	No	No†
Polychaeta			
Meganerilla? sp.	TEM/SEM	Yes	No
Gastropoda			
Astryx permodesta	TEM	No	No†§

* Cyanobacteria?
† Preliminary examination; TEM studies pending.
‡ Chloroplasts.
§ Absent in most severely dysoxic samples.
We omit three species of foraminifera (*Bolivina tumida*, *Spiroplectammina earlandi*, *Suggrunda eckisi*) because they have not yet been examined with TEM. Also omitted are single or rare occurrences of a given flagellate or ciliate morphotype. Yes, present; No, absent. DAPI, 4,6-diamidino-2-phenylindole; TEM, transmission electron microscopy; SEM, scanning electron microscopy.

The Santa Barbara Basin (SBB), which is a depression between the California mainland and the northern Channel Islands (34° 15′ N, 120° 02′ W; maximum depth ~600 m, sill depth ~475 m), has dysoxic bottom waters owing to local bathymetry, circulation and a well-developed Oxygen Minimum Zone. The surface sediments of the central SBB are even more oxygen-depleted ($[O_2] \leqslant 1\ \mu M$ within the top 2–3 mm; ref. 7) and sulphide concentrations in the surface centimetre can be more than 0.1 μM (ref. 8). These conditions support a mat of the filamentous sulphide-oxidizing bacterium *Beggiatoa*[9] but are toxic to mega- and macrofauna except the surface-dwelling gastropod *Astryx permodesta*. Although much is known regarding shallow-water anaerobic and microaerophilic eukaryotes and their symbionts[10–14], little is known about comparable deep-water organisms. Furthermore, previous studies of meiofaunal eukaryotes from shallow-water or bathyal oxygen-depleted sediments have not methodically assessed symbioses on a community scale, including all protistan and metazoan groups.