Marine and Continental Food Webs: Three Paradoxes? [and Discussion]

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Phil. Trans. R. Soc. Lond. B 1994 **343**, 57-69
doi: 10.1098/rstb.1994.0008

Marine and continental food webs: three paradoxes?

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SUMMARY

Carbon stocks and flows give a picture of marine and continental biotas different from that based on food webs.

Measured per unit of volume or per unit of surface area, biomass is thousands to hundreds of thousands of times more dilute in the oceans than on the continents. The number of described species is lower for the oceans than for the continents. One might expect that each species of organism would therefore feed on or be consumed by fewer other species in the oceans than on the continents. Yet in reported food webs, the average oceanic species interacts trophically with more other species than the average terrestrial or aquatic species.

Carbon turnover times imply that the mean adult body length of oceanic organisms is 240 to 730 times shorter than that of continental organisms. By contrast, in reported food webs, marine animal predators are larger than continental animal predators, and marine animal prey are larger than continental animal prey, by as much as one to two orders of magnitude.

Estimates of net primary productivity (NPP) per unit of surface area or per unit of occupied volume indicate that the oceans are several to hundreds of times less productive than the continents, on average. If NPP limited mean chain length in food webs, oceanic food chains should be shorter than continental chains. Yet average chain lengths reported in published food webs are longer in oceans than on land or in fresh water.

In reconciling these unexpected contrasts, the challenge is to determine which (if any) of the many plausible explanations is or are correct.

1. HOW ALIKE, HOW DIFFERENT?

This paper compares and contrasts marine and continental food webs. Continental webs include both terrestrial and aquatic webs. The dichotomy between oceans and continents excludes coastal zones, which some argue deserve equal status with land and the open ocean (Ray 1988). The dichotomy ignores, within the open ocean, the differences among the lighted surface waters, the dark water column, and the ocean floor; on the continents, ignores variation from deserts to rain forests, from brooks and swamps to great lakes. A dichotomy between oceans and continents is a simplified view of reality that may prove useful if interesting generalizations emerge from it.

Elton (1927) assumed that uniform principles operate at sea and on land. He viewed body size as fundamental to the structure of food webs (1927 [1935], pp. 59–60): 'We have already seen how animals form food-chains in which the species become progressively larger in size or, in the case of parasites, smaller in size. A little consideration will show that size is the main reason underlying the existence of these food-chains. . . . We have very little information as to the exact relative sizes of enemies and their prey, but future work will no doubt show that the relation is fairly regular throughout all animal communities.'

I assume that the laws of physics, chemistry and biology are the same in oceans and on continents. Questions to be addressed are: how do the conditions under which these laws operate differ between oceans and continents? How does life in water differ from life on land? Do differing conditions produce substantial differences in ecosystem function and food web structure?

Oceanic and continental biotas will be compared by using two distinct sets of data: global estimates of organic carbon stocks and flows; and food webs of marine and continental habitats. The quality and quantity of both sets of data leave much to be desired.

2. CARBON STOCKS AND FLOWS IN MARINE AND CONTINENTAL BIOTAS

Many estimates of carbon stocks and flows must be rough guesses because the estimates of different authors vary widely. These global totals or global means neglect possible differences in the spatial distribution of carbon stocks and flows between oceans and continents. If the marine distribution of carbon were far more skewed than the continental, for example, then marine carbon could be more concentrated in a few places than the continental, and the comparison of global means between oceans and continents could be misleading. This possibility is often mentioned but little documented. The striking contrasts to be des-

Phil. Trans. R. Soc. Lond. B (1994) **343**, 57–69
Printed in Great Britain

cribed between marine and continental biotas provide further impetus to measure quantitatively the global distributions of marine and continental carbon stocks and flows.

As a preliminary, it is necessary to estimate how much space is occupied by marine and continental life. About 71 percent of the Earth's surface is covered by oceans (table 1). Childress (1983) and Harbison (1992, p. 18) assume that the entire volume of the oceans, with an average depth of 3.8 km, is occupied by life. Then the volume of the marine life zone is 1.4×10^9 km^3. In the North Atlantic, 90 to 95 percent of micronekton and 95 or more percent of plankton in the water column occur within the first 2 km of depth (Angel 1982, p. 10). Setting aside life in the water column below 2 km depth, the volume of the marine life zone is roughly half that just estimated (Ray Beverton, 8 July 1993, personal communication).

Childress (1983) and McFall-Ngai (1990, p. 176) assume that continental life is confined to a zone 50 m deep or 7.5×10^6 km^3 in volume. This zone would exclude high-flying birds, insects and atmospheric microbes. If the depth of the continental life zone were estimated at 500 m, then its volume would be 7.5×10^7 km^3. At the opposite extreme, Ray (1988, p. 37) estimates that terrestrial life occupies only 3×10^6 km^3, implying a 20 m deep life zone over the continents, roughly the level of high forest canopy.

Of the volume occupied by life on Earth, between 90 and 99.8 percent is in the oceans, according to the most extreme estimates. For subsequent calculations, I follow Childress (1983) in supposing that the depth of the marine life zone is 3.8 km and that of the continental, 0.05 km, so that 99.5 percent of the volume occupied by life is in the oceans.

(*a*) *Density of biomass*

According to estimates of Whittaker & Likens (1973) quoted by Harte (1988, p. 257), the living biomass in the Earth's oceans contains about 2×10^{12} kg carbon (C), and that on the continents contains about 560×10^{12} kg C (table 1). Other estimates of oceanic and continental stocks of organic carbon are given by Moore *et al.* (1989*a*) and Post *et al.* (1990).

It follows that the oceans have an average volume-density of living biomass about 1.5 tonnes C km^{-3}; the continents, about 75 000 tonnes C km^{-3} (1 tonne = 1000 kg). The average volume-density of living biomass on the continents is about 50 000 times that in the oceans. The area-density of living biomass in the oceans is about 5.6 tonnes C km^{-2}, that of the continents, about 3700 tonnes C km^{-2}. Measured per unit volume or per unit area, the average continental biomass density is three to five orders of magnitude greater than the marine.

In oceans and on the continents, probably not more than one tenth of the living biomass is in metazoan animals. Estimates of the distribution of biomass among metazoan animals, macrophytes, and microbes range widely. According to classical estimates of Whittaker & Likens (1973) as quoted by Harte (table 1), at least nine tenths of the living biomass resides in plants. Hall (1980, p. 52) estimates that 90 percent of total biomass consists of trees.

The estimate that most biomass is green may need revision. Phototrophs and mixotrophs (mixotrophs are defined in § 3*c*) constitute 15 percent or less of biomass in the top 30 m of a North Atlantic spring bloom, and heterotrophs constitute more than 60 percent (Sieracki *et al.* 1993, p. 222). Phototrophs are likely to constitute a still smaller fraction of biomass in dark or nutrient-poor portions of the ocean. Bacterial and fungal biomass in soils is likely to be significant compared to plant biomass (Fitter *et al.* 1985).

However, studies of terrestrial and aquatic sites collected by Cyr & Pace (1993) confirm that animals have a small fraction of total biomass. The average herbivore biomasses cluster in the range 0.1–1 g C m^{-2}, and almost all values fall in the range 0.01–10 g C m^{-2}. There do not appear to be systematic differences between terrestrial and aquatic sites in herbivore biomass. If the global average falls in the range 0.1–1 g C m^{-2}, then the global biomass of marine herbivores falls in the range $0.036–0.36 \times 10^{12}$ kg C and that of continental herbivores in the range $0.015–0.15 \times 10^{12}$ kg C. Because other animals are unlikely to have a biomass exceeding one tenth of the herbivore biomass, they are negligible for such rough calculations. Then, because oceanic biomass contains about 2×10^{12} kg carbon (C) and continental biomass contains about 560×10^{12} kg C (table 1), the fraction of oceanic biomass in animals (mainly herbivores) falls in the range from $0.036/2 = 1.8\%$ to $0.36/2 = 18\%$, i.e. around ten percent, and the fraction of continental biomass in animals falls in the range from $0.015/560 = 0.003\%$ to $0.15/560 = 0.03\%$, i.e. around 0.01 percent. If the study sites are biased toward unusually productive habitats (few people choose to study ecology where hardly anything lives), and if the estimates of 2×10^{12} kg C for oceanic biomass and 560×10^{12} kg C for continental biomass are unbiased, then these estimated fractions of biomass in animals are too high.

(*b*) *Net primary productivity*

The NPP of the oceans is estimated at 25 $(\pm 10) \times 10^{12}$ kg Ca^{-1}; that on the continents, at 50 $(\pm 15) \times 10^{12}$ kg Ca^{-1} (Harte 1988, p. 257). Berger's (1989) estimate of $27–30 \times 10^{12}$ kg Ca^{-1} for the NPP of the oceans and recent estimates of 60×10^{12} kg Ca^{-1} for terrestrial NPP (W. H. Schlesinger, 13 March 1993, personal communication) both fall within the ranges quoted by Harte (1988). The NPP of individual ecosystems ranges widely (Pimm 1982, pp. 106–107). Globally, the area-density of NPP in the oceans is about 69 tonnes Ca^{-1} km^{-2}; that on the continents, about 330 tonnes Ca^{-1} km^{-2}. (One tonne Ca^{-1} km^{-2} equals 2.74 mg C d^{-1} m^{-2}.) The volume-density of NPP in the oceans is about 18 tonnes Ca^{-1} km^{-3}; that on the continents, about 6700 tonnes Ca^{-1} km^{-3}. (One tonne Ca^{-1} km^{-3} equals 2.74 µg d^{-1} m^{-3}.) Measured per unit area or per unit volume, the NPP of the continents greatly exceeds that of the oceans.

Table 1. *Biophysics of oceans and continents compared*

estimated quantity/unit	oceans	continents	source
surface area/10^8 km^2	3.6	1.5	Press & Siever (1986, p. 616)
surface area/(% of total Earth)	71	29	Press & Siever (1986, p. 616)
mean depth of life zone/km	3.8	0.05	Press & Siever (1986, p. 616) for oceans, Childress (1983) for continents
volume of life zone/10^9 km^3	1.37	0.0075	product of surface area and mean depth
volume/(% of total)	99.5	0.5	Childress (1983)
living biomass stocks/10^{12} kg carbon	2 (± 1)	560 (+300, −100)	Harte (1988, p. 257); for continents, low-biomass agriculture has replaced high-biomass forests, according to estimates of Olsen *et al.* quoted by Harte
total plant mass/10^{12} kg carbon	1.8	830	Schlesinger (1991, p. 121); the value for continents estimates potential natural vegatation without disturbances, according to Whittaker & Likens as quoted by Schlesinger
living biomass stock per unit of surface/ (10^3 kg carbon km^{-2})	5.6	3700	new estimate
living biomass stock per unit of volume/ (10^3 kg carbon km^{-3})	1.5	75 000	new estimate
dead organic matter/10^{15} kg carbon	2 (± 1)	1.5 (± 1)	Harte (1988, p. 257)
dead organic matter per unit of area/ (10^6 kg carbon km^{-2})	5.5	10	new estimate
NPP[a]/(10^{12} kg carbon a^{-1})	25 (± 10)	50 (± 15)	Harte (1988, p. 257)
NPP/(10^{12} kg carbon a^{-1})	20–44	48	Schlesinger (1991, pp. 121, 267)
NPP per unit of area/ (10^3 kg carbon km^{-2} a^{-1})	69	330	new estimate
NPP per unit of volume/ (10^3 kg carbon km^{-3} a^{-1})	18	6700	new estimate
residence time of carbon in living biomass stock/a	0.08	11.2	Harte (1988, p. 28)
mean adult body mass, relative to oceanic value	1	1.4×10^7	new estimate, assuming residence time $\propto$ mass$^{0.3}$
mean adult body length, relative to oceanic value	1	240	new estimate, assuming residence time $\propto$ mass$^{0.3}$
mean adult body mass, relative to oceanic value	1	3.8×10^8	new estimate, assuming residence time $\propto$ mass$^{0.25}$
mean adult body length, relative to oceanic value	1	730	new estimate, assuming residence time $\propto$ mass$^{0.25}$
body length (at the time of reproduction) of organisms with generation time equal to residence time/m	10^{-3}–10^{-2}	10^{-1}–10	based on Bonner (1965, p. 17)

[a] NPP = net primary productivity.

The conclusion still holds, though less dramatically, under three variations of the estimated quantities. First, because primary production cannot occur deeper than light reaches in the ocean, it might be considered more appropriate to compute the volume-density of NPP in the top tenth of the ocean (to a depth of 0.38 km). Then the volume-density of NPP in the oceans is about 180 tonnes Ca^{-1} km^{-3}. Second, if the continental life zone is 0.5 km deep, the volume-density of NPP on the continents is 670 tonnes Ca^{-1} km^{-3}. Third, if the NPP of the oceans were twice the estimated 25×10^{12} kg Ca^{-1}, the area-density of NPP on the continents would still be more than twice that in the oceans, and the volume-density would still be almost twice.

(*c*) *Generation time and body size*

Dividing the living biomass stock by the NPP gives an estimate of the residence time of organic carbon in the living biomass stock, assuming that the stocks and flows are both near steady state. This calculation ignores gross primary production and respiratory pathways, i.e. production that is consumed for maintenance is omitted from the denominator NPP. Harte (1988, p. 29) argues that 'Using net primary productivity [in the denominator] yields a residence time that bears a closer relation to the lifetimes of typical organisms'. Harte (1988, p. 28) estimates the residence time of carbon in oceanic biomass at 0.08 a and in continental biomass at 11.2 a. The continental residence time of organic carbon is 140 times longer than the oceanic.

It is reasonable to suppose (but further data are required to show) that the residence time of carbon in living biomass is approximately proportional to the mean generation time. If so, then because generation time scales allometrically with body size, it is possible

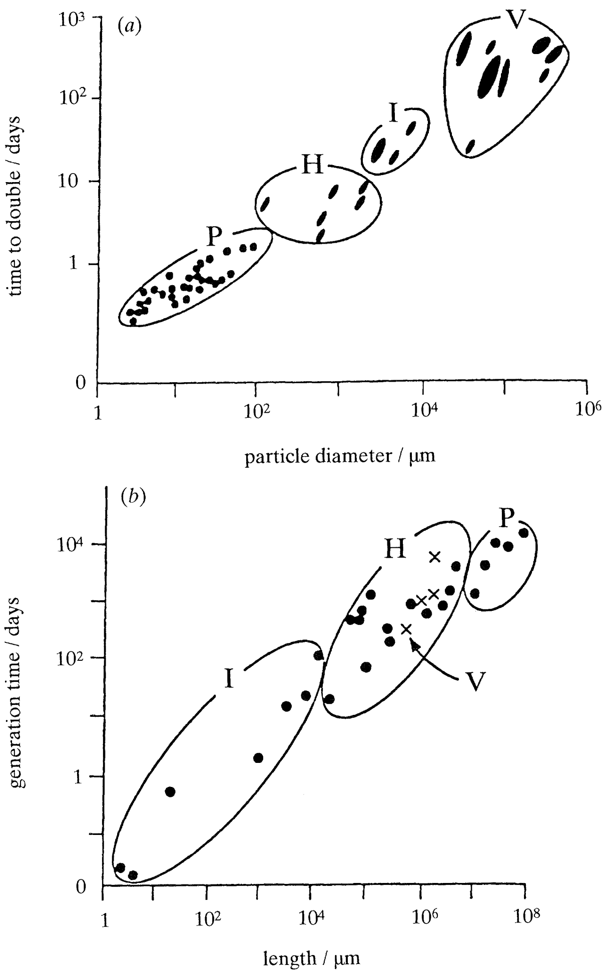

Figure 1. Relation of size to growth for plants (P), herbivores (H), other invertebrates (I) and vertebrates (V). (*a*) From Sheldon *et al.* (1972) for pelagic marine ecosystems. (*b*) From Bonner (1965) using only the terrestrial species. Source: Steele (1991, p. 429).

to compare the mean body sizes of oceanic and continental biota. According to Reiss (1989, p. 44), 'age at maturity, and similarly generation time, are . . . predicted to vary as approximately $W_a^{0.3}$. [W_a denotes adult body mass, and W denotes body mass.] From viruses to giant sequoia trees, generation time and age at maturity scale interspecifically from $W^{0.21}$ to $W^{0.33}$'. If residence time scales as $W_a^{0.3}$, then adult body mass scales as residence time raised to the power 1/0.3. Hence the mean adult body mass of continental organisms is $(140)^{1/0.3} \approx 1.4 \times 10^7$ times larger than that of oceanic organisms. If, as Peters argues (1983, pp. 119, 139), generation time scales $W^{0.25}$ rather than as $W^{0.3}$, and if residence time scales as generation time, then the mean adult body mass of continental organisms is $140^4 \approx 3.8 \times 10^8$ times larger than that of oceanic organisms (table 1). If the allometric relations of mean adult body mass with generation time were estimated using an average of mass over individuals, then the mean adult body masses derived here should be interpreted in the same way, i.e. as an average over individuals.

For many but not all organisms, mass scales as length cubed (Peters 1983, pp. 236–237). Then average continental organisms are from $240 = (1.4 \times 10^7)^{1/3}$ to $730 = (3.8 \times 10^8)^{1/3}$ times longer than average oceanic organisms. (To a zeroth approximation, generation time T scales as body length L because $L \propto W^{1/3} \propto (T^{1/0.3})^{1/3} = T^{1/0.9} \approx T$.) For planktonic crustaceans and algae, mass scales as length to the powers 2.1 and 1.9, respectively (Peters 1983, p. 237). If mass scales as length to the power 2.0, then average continental organisms are from $3.7 \times 10^3 = (1.4 \times 10^7)^{1/2}$ to $1.9 \times 10^4 = (3.8 \times 10^8)^{1/2}$ times longer than average oceanic organisms.

These estimates of relative lengths are consistent with Bonner's (1965, p. 17) famous scatter plot of body length at the time of reproduction as a function of the generation time. Steele's (1991) selection of terrestrial data from this figure and a related figure for oceans appear in figure 1. Organisms with a generation time of one month (0.08 a) range in length from 1 mm to 1 cm, whereas organisms with a generation time of 11.2 a range in length from 0.1 m to tens of meters.

Indirect evidence also indicates that oceanic herbivores are smaller than continental herbivores. In a comparison of 44 aquatic (not necessarily marine) and 67 terrestrial sites, Cyr & Pace (1993) showed that, for any given level of NPP (g Ca^{-1} m^{-2}), herbivores consumed plants at a rate (g Ca^{-1} m^{-2}) that was three times higher in aquatic sites than in terrestrial sites. For a given level of NPP, aquatic and terrestrial sites had similar average herbivore biomasses. Thus the grams of plant carbon eaten per year, per gram of herbivore biomass, were three times higher in aquatic than in terrestrial systems. The mass-specific metabolism of small animals is higher than that of large and scales with mass W as $W^{-0.25}$ (Peters 1983, p. 31). A threefold difference in mass-specific herbivory rates is consistent with aquatic herbivores having average body mass $3^4 = 81$ times smaller than terrestrial herbivores. It would be desirable to distinguish the continental fresh-water, coastal and marine sites among the aquatic sites collected by Cyr & Pace (1993) and then compare continental and marine sites directly.

3. QUALITATIVE COMPARISONS OF MARINE AND CONTINENTAL BIOTAS

In addition to differing in carbon stocks and flows, oceans and continents differ in several other ways that are relevant to the structure of food webs: the temporal variability of the physical environment; the recycling of detritus; trophic adaptations to the differing concentrations of life; plant size; and species diversity (table 2). For further comparisons of aquatic and terrestrial life, see McFall-Ngai & Manahan (1990).

(*a*) *Temporal variability in the physical environment*

The pattern of temporal variability in the physical environment differs between oceans and continents (Steele 1985, p. 355; 1989, p. 187). The variance of deep oceanic temperature decreases very sharply as the period of oscillation decreases from millennia to

Table 2. *Marine versus continental comparisons*

	oceans	continents
Temporal variability of physical environment		
medium (except freshwater bodies on continents)	water	air
heat capacity of medium	high	low
variance of temperature for higher frequency f	$\propto f^{-2}$: 'red'	constant: 'white'
recycling of detritus		
surface where detritus falls	dark	lighted
viscosity of medium	high	low
retention time of detritus	long	short
trophic adaptations to concentration of life		
feeding by filtering and entanglement	common	rare
mixotrophy ('plantimals')	common	rare
plant size and herbivory		
modal plant size	small	large
plants as physical substrate for herbivores	rare	common
plants engulfed by herbivores	common	rare
species diversity		
reported number of species	low	high
reported number of phyla	higher	lower
incompleteness of information	worse	bad

days. To a first approximation, the variance is proportional to (frequency)$^{-2}$. Monin *et al.* (1977, pp. 81–83, especially Fig. 3-3-5) suggest that the variance of temperature is proportional to (frequency)$^{-5/3}$. The difference between the exponents -2 and $-5/3$ is not material here. Because of the heat capacity of water, the ocean damps out short-term fluctuations in temperature relative to major longer-term variations in temperature.

By contrast with water temperature, the variance of annual fluctuations (apart from seasonal cycles) in atmospheric temperature, which largely determines the temperature experienced by continental biota, is roughly the same as the variance of temperature fluctuations over days or seconds (Steele 1989, p. 187; see Fig. 1*a* of Steele 1985, p. 355). However, atmospheric fluctuations with periods on the order of a decade or longer have a variance that increases with decreasing frequency, as in the oceans.

The difference between oceans and continents in the spectrum of high-frequency temperature fluctuations could have major consequences for the biotas (Steele 1985, pp. 357–358): 'A "terrestrial" system where environmental variability is large at both short- and long-term periods could be expected to develop mechanisms internal to the system which would cope with short-term variability and in so doing, would minimize also the effects of longer-term variations. . . . In "marine" systems, less robust internal processes are needed to handle the smaller amplitude variability at short periods commensurate with the life span of the organisms. The possible absence of such mechanisms, combined with increasing variance with period, can mean that marine populations or ecosystems not only have different ways of dealing with short-term variance but also will respond differently at longer time scales. . . .'

This suggestion can be supported at the levels of the community and the individual. At the community level, theoretical models suggest that differences between oceans and continents in the spectra of environmental disturbances may lead to differences in disturbance-mediated species diversity (Caswell & Cohen 1994).

At the individual level, a hydrothermal vent illustrates a benefit of large body size as a 'terrestrial' type of adaptation to environmental variability over short periods. Contrary to the general deep-sea pattern, in the Rose Garden hydrothermal vent site, temperature and concentrations of silicate, sulphide, and oxygen are highly variable on timescales from days to a few seconds (Johnson *et al.* 1988; Childress & Fisher 1992). 'The fluctuations mean that frequently one or the other of the major nutrients (sulphide and oxygen) will not be present around the animals. One of the primary roles of the animals, with respect to their chemoautotrophic symbionts, must be to smooth these environmental fluctuations so that both oxygen and sulphide are made available simultaneously to the endosymbionts. The large volumes of blood . . . in the clams and tubeworms should allow them . . . to retain [the nutrients] when exposed to water depleted in the various gases' (Johnson *et al.* 1988, p. 1720).

L. R. Pomeroy (31 March 1993, personal communication) suggests that even at the ocean surface 'nutrients, both organic for bacteria and inorganic for phytoplankton, probably have high variances at a frequency of seconds to minutes. Light, as experienced by an individual phytoplankter, has high variance at a range of frequencies: seconds (wave focusing), minutes (clouds), and hours (Langmuir circulation)'. Quantitative comparisons of the spectra of nutrients and illumination in oceans and on continents are needed.

(*b*) *Recycling of detritus*

On continents, detritus collects at the interface of earth and air where photosynthesis and respiration are most active, i.e. dead plants and animals fall to the ground. Nutrients can be retained and biomass stocks can accumulate, and they do so in tropical and temperate terrestrial ecosystems. As always, there are exceptions: in cold climates where litter accumulates as peat, nutrients may not be recycled for very long periods of time.

In the upper ocean, the so-called 'microbial loop' of surface-water phytoplankton, protozoa and bacteria rapidly recycle most dead and fecal organic matter (Pomeroy 1992). By contrast with continental life, some fraction of detritus, particularly larger particles or organisms, falls through the photosynthetic zone, to be stored, eaten or decomposed in the depths. Exchange times between deep and near-surface waters are estimated to range from centuries to millennia (Steele 1985, p. 357). Because nutrients are constantly being lost to the inaccessible depths and are very rapidly consumed in the photic zone at the surface, solar energy is separated from nutrient supplies; oceanic life remains dilute. The falling detritus that decomposes produces carbon dioxide in the dark depths, removing carbon from the atmosphere for long periods of time. The falling detritus that reaches the ocean floor nourishes benthic animals (Smith 1992) or accumulates in sediments.

(*c*) *Trophic adaptations to dilute oceanic life*

Some oceanic organisms display remarkable adaptations to the diluteness of oceanic life. One class of adaptations entangles food. At the microbial level, some marine bacteria produce sticky polymers that increase the bacteria's radius of contact and help them to aggregate food particles. Many marine animals employ extensive systems of tentacles, some loaded with offensive devices, to contact and capture food, alive or dead. Other adaptations filter the water for food. Continental biotas also have filter-feeders, such as spiders that filter the air and caddisfly larvae of the family Hydropsychidae that filter fast-flowing waters (Rossiter 1993), but filter feeding appears much commoner in marine animals.

Through another remarkable adaptation to nutrient scarcity, some marine organisms blur the distinction, sensible in terrestrial ecology, between producers and consumers (Stoecker 1991, 1992). Mixotrophic marine organisms feed on other organisms and also photosynthesize. Reef-building corals are well known to prey on zooplankton with their tentacles while benefiting from the organic carbon produced by photosynthetic algae that live within their tissues. Many tropical radiolarians and foraminiferans, commonly considered consumers, have algal symbionts, and many depend on these symbionts for nutrients when prey are scarce. Some ciliated planktonic protozoans (10–200 μm in size) eat microscopic algae, digest most of the algal cell, and retain the chloroplasts to photosynthesize within the transparent protozoal cell body. According to Stoecker (1992, p. 26), '"green" ciliates are ubiquitous in upper, sunlit ocean layers, from the tropics to polar, ice-covered seas. They have even been found growing in brine-filled pockets at Antarctic sea ice.' Mixotrophy works both ways: some flagellated algal cells ingest bacteria or other small ciliates. In theory, mixotrophy could increase the efficiency with which protozoa convert food to protozoa. Conventional trophic levels (producers, herbivores, carnivores) do not fit well with apparently widespread marine mixotrophy.

(*d*) *Plant size*

On land, most, perhaps as much as 90 percent, of plant biomass occurs in trees, the largest and longest-lived organisms on the continents. Before the industrial revolution, continental plants had an estimated total of 827×10^{12} kg C; of this total, 743×10^{12} kg C occurred in forests, according to Whittaker & Likens (1973) as quoted by Schlesinger (1991, p. 121). (Present continental plant biomass may approximate 560×10^{12} kg C, as shown in table 1.) By contrast, marine photosynthesis occurs in micro-organisms, except for 'coastal seaweeds and floating *Sargassum* (a sprawling brown algae) in the Atlantic Ocean and the Gulf of Mexico' (Pomeroy 1992, p. 28). The longer C residence time of the continents arises because long-lived trees dominate the continental plants and short-lived micro-organisms dominate the oceanic plants.

The much larger average size of continental plants could be an adaptation to mitigate the relatively greater magnitude of high-frequency physical fluctuations on continents (Steele 1985, 1989, 1991). Alternatively, Colinvaux (1978, pp. 86–87) observes that large marine plants occur wherever they can avoid dispersal by ocean currents, as in coastal zones and the Sargasso Sea, and suggests 'that large plants are excluded from [all other parts of the open ocean] . . . by the restless motion of the waters that would sweep them all away never to return' to the limited areas where nutrients are concentrated.

Microscopic oceanic plants provide no mechanical substrate for their consumers; pelagic marine consumers must engulf their food. Trees provide a stationary mechanical substrate for their consumers, and through their bulk average over some of the short-term physical fluctuations of the terrestrial environment. Their consumers, particularly insects, can be smaller than the plants they consume. Such arguments (e.g. Smith 1975, p. 4) may help to explain the differing positions of plants and herbivores in the terrestrial and oceanic panels of figure 1.

(*e*) *Species diversity*

Angel (1993) and May (this symposium) compare marine and continental species diversity. Fewer oceanic than continental species have been described (perhaps in part because people live on land), but about twice as many oceanic phyla as terrestrial phyla have been described (Ray 1988, pp. 38–39; Wilson 1992, p. 136). Grassle & Maciolek (1992, p. 336) estimate that as more of the deep sea is sampled, 'the number of species will certainly be greater than 1 million and may exceed 10 million'. Methods now being developed will give refined information about the diversity of marine species, especially microbial (Powers *et al.* 1990; DeLong & Ward 1992).

4. FOOD WEBS OF MARINE AND CONTINENTAL BIOTAS

Food webs provide alternative approaches to comparing marine and continental biotas. A food web is the pattern of flows of energy and materials among organisms that result when some organisms eat or consume other living organisms or their parts (Cohen *et al.* 1993*a*). A web sometimes incorporates flows between organisms and the abiotic or dead biotic environment, including decomposers and detritus. Food webs have been described and analysed in diverse ways (e.g. Cohen 1978; Pimm 1982; Cohen *et al.* 1990; DeAngelis 1992).

Cohen (1968, 1978), Briand (1983), and Briand & Cohen (1987) collected 113 community food webs of natural communities from 89 published and two unpublished studies. The webs are available in print (Cohen *et al.* 1990) and machine-readable form (Cohen 1989*a*). They include 55 continental (23 terrestrial and 32 aquatic), 45 coastal, and 13 oceanic webs, ranging from arctic to antarctic regions. Other documented collections of webs do not cover the same range of habitats, food sources, or organisms (see Schoenly *et al.* 1991; Havens 1992).

In the common representation of food webs by boxes (sets of organisms) joined by arrows (feeding relations, or trophic links), a trophic species refers to the largest set of organisms that can accurately be represented by a single box, given the available information about feeding. Formally, a trophic species is defined as a maximal set of organisms that eat the same kinds of foods and are consumed by the same kinds of consumers. The following analyses are restricted to the 97 webs in Cohen *et al.* (1990) with ten or more trophic species (table 3).

An apothegm applies here: a person with one watch knows what time it is; a person with two watches is never sure. Those who espouse solely the approach based on carbon stocks and flows, or solely the approach based on food webs, can confidently contrast marine and continental biotas. Those who consider both approaches have grounds for further thought.

(*a*) *Trophic interactions*

If life is more dilute in the oceans and if there are fewer presently described species there, one might expect the average species to interact trophically with fewer species in the oceans than on the continents. The number of other species that the average species interacts with trophically (feeding or being fed upon) is twice the ratio of links to species, because each link has both a head and a tail. (To convince yourself, consider a hypothetical web with one link joining two species.) Contrary to expectation, the average oceanic species is reported to interact trophically with $5.4 = 2 \times 2.7$ species, while the average aquatic species interacts with 4.2 species and the average terrestrial species with 3.4 species (table 3). Under the assumption (necessary for statistics, but doubtful in fact) that the webs from each habitat are independent random samples, the excess in the links:species ratio of oceanic over terrestrial webs has a probability between 0.025 and 0.01 of occurring by chance alone, according to a one-tailed *t*-test with possibly heterogeneous variances and Satterthwaite's approximation for degrees of freedom (Snedecor & Cochran 1980, p. 97); more succinctly, $0.01 < p < 0.025$.

Possible explanations

The larger number of trophic interactions per trophic species in oceans than on continents, in spite of the fewer described species and lower density of life in the oceans, can be explained in several different ways, none of which excludes the others.

One possibility is that, because of the greater role of filter feeding in oceans, oceanic consumers may eat a greater fraction of the species that come within reach than do continental consumers.

A second possibility is that the mixing of oceanic water brings a larger absolute number of species within reach of an average marine consumer species than passive dispersal and animal mobility bring continental species into contact with one another, even if marine and continental species eat the same fraction of the species within reach, and even if there are fewer described marine species in total.

A third possibility is that marine webs are spatially more variable than continental webs. It could be that, in an average cubic meter of space occupied by life, the average number of trophic interactions per species is the same for marine and continental species, but that with each additional cubic meter of life space, the trophic interactions (not the species involved, but the feeding relations among them) change more in the oceans than on the continents. Statistically speaking, perhaps marine web structure shows lower spatial autocorrelation than that of continental webs. A marine web that cumulates trophic interactions over a thousand cubic meters would then show more trophic interactions per species than does a continental web cumulated over the same volume.

A fourth possibility is that the size differences between phytoplankton and zooplankton in the oceans, compared with the size differences between trees and insects on land, could contribute to the difference between sea and land in links per species. If a typical phytoplankton is 15 μm long and a typical zooplankton is 800 μm long (Rothschild 1990, p. 69), then an individual zooplankter must eat many different individual phytoplankters in the course of its life, and could sample many different prey species. On land, a typical insect is a tiny fraction of the size of a tree, shrub or even grass that it feeds on. The insect could pass its entire adult life on a single individual or on just a few individual plants. Many insects specialize on a single species of host plant. Because insects are a large fraction of all terrestrial animals, if they had a smaller average number of links, they could contribute significantly to the difference in links per species between oceans and continents (R. M. May, 8 July 1993, personal communication).

A fifth possibility is that marine consumers change their prey more in the course of time or ontogeny than do continental consumers (Isaacs 1972). For example, if the diets or consumers of organisms change as the organisms develop, one might expect more changes per unit of time for smaller marine organisms than for larger continental organisms, as the smaller organisms would grow faster. If marine feeding links change faster per unit of time than do continental, then marine webs cumulated over some interval, say a year or a century, would show more trophic interactions per species than a continental web cumulated over the same interval. The temporal scale of observation could make a difference: temporal cumulation can dramatically affect some characteristics of web structure (Schoenly & Cohen 1991). The observation that atmospheric temperatures fluctuate relatively more at short periods than do marine temperatures (Steele 1985, 1989, 1991) argues against the possibility that feeding links change because of short-term physical fluctuations, because then continental webs should have more links per species than marine.

A sixth possibility is that oceanic and continental webs are sampled differently. Even if oceanic and continental webs had measurably identical structures locally and identical spatial and temporal autocorrelations, it could be that the technology of sampling oceanic webs (typically, ship transects) captures a greater volume and therefore a greater diversity of trophic relations than the technology of sampling continental webs (typically, captures by a few field workers).

If marine sampling effort were enough greater than continental sampling effort to outweigh the lesser species diversity of marine biotas, oceanic webs might contain more trophic species than continental webs. In fact, marine webs have slightly fewer trophic species than terrestrial (18 versus 21 on average; $0.025 < p < 0.05$ by a one-tailed test) and about the same number as aquatic and coastal webs (18 and 17, respectively). Table 3 shows that, between any pair of oceanic, fresh-water, terrestrial, and coastal habitats, the mean numbers of trophic species do not differ as much as a single standard deviation. In all cases, the reported numbers of trophic species are probably a very small fraction of the numbers of distinct species present, but roughly equal numbers of species appear to have been sampled in different habitats. There is no independent reason to believe that links are more finely described in marine than in continental samples. Differences in sampling effort probably do not explain the observed difference in the links:species ratio.

A seventh possibility is that the difference is an artifact of the use of trophic species, instead of biological species, together with poor resolution of planktonic species (e.g. Schoenly *et al.* 1991, p. 609). In some of the taxonomically best resolved pelagic webs, for example webs of Pacific upwelling areas (Vinogradov & Shushkina 1978; web 42 of Cohen *et al.* 1990) or tropical Pacific plankton communities

Table 3. *Food webs of oceans and continents compared*

estimated quantity	ocean[a]	fresh water[b]	land[c]	coast[d]	source
number of webs with ⩾10 trophic species	11	29	21	36	Cohen *et al.* (1990)
trophic species (mean ± standard deviation)	18 ± 3.6	18 ± 6.8	21 ± 9.9	17 ± 6.1	new estimate from data in Cohen *et al.* (1990)
trophic links per trophic species (mean ± standard deviation)	2.7 ± 1.3	2.1 ± 0.70	1.7 ± 0.54	1.7 ± 0.36	new estimate from data in Cohen *et al.* (1990)
mean chain length (links) (mean ± standard deviation)	3.8 ± 1.4	3.0 ± 0.88	2.6 ± 0.67	2.7 ± 0.56	new estimate from data in Cohen *et al.* (1990)
predicted mean chain length (links) (mean ± standard deviation)	4.2 ± 1.5	3.5 ± 1.0	3.1 ± 0.90	3.0 ± 0.55	new estimate from data in Cohen *et al.* (1990)
maximal chain length (links) (mean ± standard deviation)	5.8 ± 2.4	4.3 ± 1.4	4.0 ± 1.3	3.9 ± 1.0	new estimate from data in Cohen *et al.* (1990)
number of trophic links with known masses of prey and predators	57	140	48	109	Cohen *et al.* (1993*b*, table 2)
body mass of animal prey (geometric mean g)	13	0.0072	1.2	3.4	Cohen *et al.* (1993*b*, table 2)
body mass of animal predators (geometric mean g)	4700	20	140	190	Cohen *et al.* (1993*b*, table 2)

Food web serial numbers in Cohen *et al.* (1990):

[a] Ocean: 20, 29, 30, 31, 32, 37, 41, 42, 43, 86, 103.

[b] Fresh water: 19, 33, 34, 35, 38, 39, 45, 46, 47, 63, 64, 65, 66, 67, 68, 71, 72, 73, 76, 77, 78, 79, 80, 82, 83, 84, 85, 88, 89.

[c] Land: 22, 23, 24, 25, 26, 27, 28, 40, 58, 59, 60, 62, 90, 91, 92, 93, 95, 97, 98, 99, 100.

[d] Coast: 2, 3, 4, 6, 7, 8, 16, 17, 18, 36, 44, 48, 49, 50, 51, 52, 53, 54, 55, 56, 69, 70, 74, 81, 87, 94, 104, 105, 106, 107, 108, 109, 110, 111, 112, 113.

(Petipa 1979; web 103 of Cohen *et al.* 1990), species are described simply as small phytoplankton, medium phytoplankton, large phytoplankton, bacteria, and zooflagellates. Other marine webs treat the plankton even more crudely. In general, combining biological species into trophic species can increase or lower the links:species ratio. It is unknown whether lumping could explain quantitatively the higher links:species ratio in marine webs.

In summary, there are at least seven possible explanations of why the average species interacts trophically with more species in the oceans than on the continents, though fewer oceanic than continental species have been described. The first five possible explanations remain viable, present evidence is against the next, and the last is uncertain.

(*b*) *Chain lengths*

If the oceans have much smaller NPP than the continents, and if chain lengths are constrained by the energy available from NPP, one might expect oceanic chains to be shorter than continental chains. To test this expectation, I first computed the average length of all chains within each web, then averaged that mean over webs, weighting each web equally. Oceanic webs have an average chain length of 3.8 links. Contrary to expectation, that is greater than the average chain length in aquatic webs (3.0 links), terrestrial webs (2.6 links), and coastal webs (2.7 links). The greater average chain length of oceanic compared to terrestrial webs is probably not due to chance alone ($0.005 < p < 0.01$). Similarly, the average (over webs) of the maximal chain length is greater in oceanic webs (5.8 links) than in aquatic webs (4.3 links), terrestrial webs (4.0 links), or coastal webs (3.9 links). The greater maximal chain length of oceanic compared to terrestrial webs is probably not due to chance alone ($0.01 < p < 0.025$). Marine chain lengths, measured by the mean or the maximum, are consistently larger than those of other habitats (table 3). Using a different classification of webs, Schoener (1989, pp. 1567–1572) found longer maximum chain lengths in marine pelagic webs than in any other class of webs.

Possible explanations

First, the greater average and greater maximal chain length of oceanic webs is at least partially a consequence of the greater links:species ratio of oceanic webs. If the observed numbers of trophic species and links of each real web are used to calculate the average chain length predicted by the cascade model (Cohen *et al.* 1990, p. 153, second formula from top), the predicted means (over webs in each habitat) vary from habitat to habitat much as the observed means do (table 3), though the predicted mean chain lengths are longer than the observed by an average of 0.3–0.5 links.

Second, Whitehead & Walde (1992) suggested a mechanistic explanation of a greater chain length of webs in solid, compared to flat, environments. They were prompted by empirical observations of such a difference by Briand & Cohen (1987). Under specific behavioral assumptions, if searching predators who live in a three-dimensional world are confined to a slab thinner than twice their range of perception, and if prey are not very abundant, then the predators must travel further between prey items. If travel costs energy, the extra travel imposed by a flattened habitat could diminish the size of a predator population, and ultimately that predator's viability. Hence a given level of productivity should support shorter chains in flat habitats than in solid habitats. This ingenious proposal does not consider the much smaller average NPP of the oceans, which could potentially outweigh the advantage of three-dimensionality. Related biophysical analyses of predator-prey contacts are developed by Rothschild & Osborn (1988, 1990) and Evans (1989).

Third, in 34 of the first 40 webs in the Briand–Cohen collection, Yodzis (1984) found that, at any fixed 'trophic height' above the primary producers, energetically more efficient animals (e.g. invertebrate ectotherms) were more likely to be the sole food source of some consumer than energetically less efficient animals (e.g. vertebrate endotherms). He defined the 'trophic height' of a species as a rough estimate of the proportion of NPP lost through the shortest food chain leading to that species; the more energy estimated to be lost, the greater the species' trophic height. His conclusion was that energy availability could explain variations in chain length. Yodzis's (1984) analysis assumes equal NPP at the base of chains in different webs, contrary to the gross observed difference in NPP between marine and continental webs. His conclusions about single-resource consumers of animals of particular metabolic types are not necessarily in conflict with the above crude comparisons of average and maximal chain lengths for webs from regions as different in NPP as oceans and continents, but tend qualitatively to predict a difference opposite from the observed.

The greater chain lengths of oceanic webs are not necessarily due to differences in life histories between oceanic and continental species. For example, both fishes and insects (e.g. butterflies and caterpillars, or flies and maggots) have independently feeding larval stages with diets and consumers different from those of the adults. In such examples, a single genetic species might represent two trophic species.

Fourth, if primary production in the ocean is very unevenly distributed in space and time, for example, as a result of local upwellings, turbulence, rings or eddies, then organisms and food webs may occur only where NPP is high, and the oceanic average NPP may not measure the relevant levels of NPP (Steele 1980, p. 96). A classic illustration is the luxuriant life concentrated in a narrow strip in the open ocean along the confluence of two warm, westwardly flowing currents southwest of Panama, vividly described by Beebe (1926). Upwellings cover only 0.1% of the ocean surface, and productive coastal zones about 10% (Ryther 1969; Colinvaux 1978, p. 92). The global average NPP may not pertain to the reported food webs. However, food resources are also not uniform on continents, and continental animals can also concentrate where food and other resources are rich. Whether variability in food resources differs quantitatively on continents and in the oceans is not clear.

Fifth, could the apparent differences between oceanic and continental food webs be artifactual? Attacking the data of Briand & Cohen (1987), Moore *et al.* (1989*b*, p. 238) argued that 'most of the difference in chain length between habitats of different dimensions appears to be an artifact of the completeness of the web descriptions'. Compared with the three-dimensional webs (many of them marine), they argued, the two-dimensional webs (many of them terrestrial) selectively omit top predators as well as the trophic link from phytoplankton to zooplankton. Briand & Cohen (1989, p. 239) confirmed that 'intertidal ecologists generally do not report the phytoplankton-zooplankton linkage' whereas oceanic ecologists rarely lump phytoplankton and their zooplankton grazers. However, Briand & Cohen (1989) argued that not all the difference between two- and three-dimensional webs is an artifact of incomplete description, and that it is not generally justified to 'complete' reported two-dimensional webs by adding a phytoplankton–zooplankton link and top predators. Only the collection of better data in the future can exclude artifactual differences (Cohen *et al.* 1993*a*).

Sixth, the greater chain length of oceanic webs is consistent with Schoener's (1989) productive-space hypothesis. This hypothesis states that food-chain lengths are limited by the area or volume of a habitat times its NPP. 'More precise testing will necessitate the difficult task of measuring areas or volumes that particular food webs occupy' (Schoener 1989, p. 1571).

In summary, the greater average and greater maximal chain length of oceanic webs may be partly, but not entirely, explained by each of the six explanations above except the third. The first and fifth probably do not account for the quantitative difference observed; it remains to be determined whether the others might.

(*c*) *Animal body sizes*

If oceanic organisms have much shorter average generation times and much smaller body sizes than continental organisms, one might expect animal body sizes to be smaller in oceanic than in continental webs.

Cohen *et al.* (1993*b*) analysed the adult body masses of animal predators and animal prey in 18 of the first 40 webs in the Briand–Cohen collection. The geometric mean mass (table 3) of adult animal prey (counting each species once, not weighted by biomass or abundance) is 13 g in marine webs, 0.0072 g in aquatic webs, 1.2 g in terrestrial webs and 3.4 g in coastal webs. Using $\log_{10}$(mass) to measure body size, the marine versus terrestrial contrast is not likely to have occurred by chance alone ($0.025 < p < 0.05$). The geometric mean masses of adult animal predators have the identical ordering by habitat (the marine versus terrestrial contrast has $p < 0.0005$). Cohen *et al.* (1993*b*, their table 2) give the uncertainties of these estimates as the standard deviation of $\log_{10}$(mass). Contrary to expectation, the masses of both animal predators and animal prey are larger in marine than in coastal, terrestrial, or aquatic webs.

Possible explanations

If oceanic organisms have much smaller body sizes than continental organisms, why are adult animal predators and animal prey reported to be larger in marine food webs than in continental webs? The many possible explanations are not all mutually exclusive.

One possibility (pointed out by W. M. Post, 30 March 1993, personal communication) is that, because most living biomass resides in microbes and plants, the derivation of body sizes from turnover times applies mainly to microbes and plants rather than to animals. This possibility does not explain the difference between marine and continental animal body sizes, but merely weakens the expectation that marine animals should be smaller than continental.

A second possibility is that marine animals depend mainly on very small plants and micro-organisms, whereas continental animals depend mainly on larger plants, including trees, which are large enough to buffer environmental fluctuations. Lacking relatively large plants to support them, marine animals could be selected to buffer environmental fluctuations with their own bodies and hence be larger. The presence of trees on continents may be selected by the greater variability at short time scales of continental climate. However, W. M. Post (30 March 1993, personal communication) pointed out a problem with this explanation: if marine phytoplankton are small because they do not need to buffer high-frequency variability in temperature, why cannot most marine animals be small also?

A third possibility (suggested by M. Pascual, 28 March 1993, personal communication) is that a concentrated oceanic food resource could support larger animals than the marine average would suggest. It is not known whether the variability in food resources differs quantitatively on continents and in the oceans.

A fourth possibility is that oceanic organisms do not really have much smaller body sizes than continental organisms; the apparent difference may be an artefact because global estimates of terrestrial turnover omit the microbial loop in the soil (e.g. Fitter *et al.* 1985, p. 349). The apparent difference in body sizes between oceans and continents may diminish when microbial loops in both habitats are considered.

A fifth possibility (suggested by Daniel Weihs, 15 July 1993, personal communication) is that the much greater density and viscosity of water compared with air select for greater muscle in marine animals compared with terrestrial animals. For animals with a characteristic length L, muscular mass and power scale roughly as $L^{2+\varepsilon}$ with $0 < \varepsilon \leqslant 1$, whereas drag scales roughly as L^2. The advantage in muscular power of greater body mass outweighs the disadvantage due to increased drag.

A sixth possibility (also suggested by Daniel Weihs, 15 July 1993, personal communication) is that the greater average dilution of potential food in the oceans compared to the continents selects for animals with greater reserves to sustain them between meals.

A seventh possibility suggested by Thomas W. Schoener (21 June 1993, personal communication) is that the carbon-flux data weight species by abundance, unlike the food-web data, and that small species are relatively more abundant in oceans than on continents.

An eighth possibility also suggested by Thomas W. Schoener (21 June 1993, personal communication) is that food-web data disproportionately neglect very small organisms. This bias against small organisms could affect pelagic more than terrestrial systems (Schoener 1989, p. 1569, col. 2).

In summary, the first two proposals are not satisfactory explanations. Whether the remaining proposals are satisfactory remains to be determined.

5. SIMILARITIES BETWEEN MARINE AND CONTINENTAL FOOD WEBS

I have reviewed apparent differences between oceanic and continental food webs. However, some generalizations govern oceanic and continental food webs alike.

(*a*) *Animal body sizes and feeding relations*

Cohen *et al.* (1993*b*) analysed data on the adult body sizes of animals in community food webs. Relations between body size and food web structure were uniform across oceans and continents. This uniformity supports Elton's confident prediction that 'future work will no doubt show that the relation [between the sizes of consumers and their prey] is fairly regular throughout all animal communities'.

In about nine-tenths of the feeding links among the animal species with known sizes, a larger predator consumes a smaller prey. This empirical finding provides strong, but not perfect, support for Platt & Denman (1978, p. 62): 'we assume that in all of the significant trophic interactions, large organisms eat small ones, and not the opposite.' Larger predators eat prey with a wider range of body sizes than do smaller predators. The geometric mean predator size increases with the size of prey. The increase in geometric mean predator size is less than proportional to the increase in prey size, i.e. has slope less than one on log–log co-ordinates. Invertebrates are commonly eaten by vertebrate ectotherms, and both invertebrates and vertebrate ecotherms are commonly eaten by vertebrate endotherms, but it is very rare for any of these relations to be reversed. Obviously parasitism played little role in these data. Mean sizes of prey increase as the metabolic type of prey changes from invertebrate to vertebrate ectotherm to vertebrate endotherm, but the same does not hold true for predators.

Prey and predator sizes are positively correlated in links from invertebrate prey to invertebrate predators. In links with other combinations of prey and predator metabolic types, the correlation between prey and predator body sizes is rarely large when it is positive, and in some cases is even negative.

Species' body sizes are roughly lognormally distributed. When body size is taken as the physical interpretation of the ordering assumed in the cascade model (Cohen *et al.* 1990), as was first suggested in print by Warren & Lawton (1987), and when the body sizes of different animal species are taken as lognormally distributed, many of the empirical findings can be explained by the cascade model.

(*b*) *Topological structure of community food webs*

Community food webs assemble trophic links in a stochastically consistent way (Cohen 1988, 1989*b*; for technical details, see Cohen *et al.* (1990)). An analogy may help explain what this means. In population biology and demography, though it is very difficult to predict the length of life of a single organism, the fraction of individuals who survive from birth to any given age is often predictable. Similarly, though every two real food webs differ in detailed structure in ways that remain difficult to predict, some consistent patterns have been discovered in ensembles of food webs. The empirical patterns cross the boundaries between oceans and continents.

The empirical patterns are not all logically independent. Simple stochastic models reduce the number of independent assumptions required to explain the patterns. For example, as pointed out above, if the ratio of links to species in one web is larger than the ratio in another, then according to the cascade model the mean chain length in the first should exceed that in the second in a predictable way. The stochastic models also cross the boundaries between oceans and continents.

One empirical pattern has become clearer as more and better webs have become available. The increase in the number of trophic links L with increasing numbers of trophic species S was originally described by Briand (1983) as a power law $L = cS^{\alpha}$ with α slightly greater than one. While recognizing that the relation could be nonlinear, Cohen & Briand (1984) approximated it linearly as $L = cS$ because the data then available did not require $\alpha > 1$. It is now clear that, while $L = cS$ describes webs with 50 trophic species or fewer, the power law with $1.3 < \alpha < 1.5$ is required to describe webs with larger numbers of species. Many, although not all, of the remaining empirical generalizations have proved robust (Schoener *et al.* 1989; Sugihara *et al.* 1989; Schoenly *et al.* 1991; Havens 1992) in spite of legitimate criticism. Doubtless present generalizations and models are not the last word.

6. CONCLUDING REMARKS

Carbon stocks and flows give a picture of marine and continental biotas that differs from that based on food webs. Little evidence is available to discriminate among the many possible explanations for the differences. The food web data are inadequate in quality and quantity (Cohen *et al.* 1993*a*). The data on the productivity and carbon stocks of the oceans are also limited. For example, in a compilation of 8000 measurements of oceanic productivity made from 1944 through 1985, the number of determinations per 10° square of longitude by latitude varied from 150 to zero (Berger 1989, pp. 441–442). In some southern portions of the major oceans, no one knows what productivity is. Berger (1989, p. 442) put it clearly: 'Guesswork is unavoidable in producing a global productivity map, given the amount and quality of existing information.' Better data on both food webs and carbon stocks and flows will determine whether the contrasts reported here are real and, if they are real, will provide clues to reconciling them.

J.E.C. thanks Martin V. Angel, Ray Beverton, John T. Bonner, Hal Caswell, James J. Childress, Adam E. Cohen, Kevin J. Gaston, John Harte, Claudia M. Jacobi, Robert M. May, Mercedes Pascual, Robert H. Peters, Stuart L. Pimm, Lawrence R. Pomeroy (with Paul Hendrix), W. Mac Post, William H. Schlesinger, Thomas W. Schoener, Kenneth Schoenly, John H. Steele, Diane K. Stoecker and Daniel Weihs for scientific help, the U.S. National Science Foundation for grant BSR92-07293, and Mr and Mrs William T. Golden for hospitality during this work.

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Discussion

T. Fenchel (*Marine Biological Laboratory, University of Copenhagen, Denmark.*) Your conclusions depend on including the huge amounts of structural plant materials (cellulose, lignin, etc.) of trees in the inventory of living reduced carbon of terrestrial ecosystems. Is it reasonable to include this as living biomass? It would seem that if only living plant tissue is included the 'paradoxes' (regarding average body sizes) in the comparison between marine and terrestrial ecosystems might disappear.

J. E. Cohen. I cannot find a quantitative estimate of the fraction of structural plant materials in the biomass carbon of terrestrial ecosystems, but I can estimate the fraction required so that marine and continental ecosystems would have equal carbon turnover times. Excluding structural plant materials would not alter the estimates of net primary productivity (NPP) in marine and continental ecosystems. The aggregate NPP per year of the continents would remain roughly twice (that is $(50 \pm 15)/(25 \pm 10)$) as large as the aggregate NPP per year of the oceans. For biomass carbon to have equal turnover times in marine and continental ecosystems, the continental biomass stock of carbon would have to be roughly twice the marine biomass stock of carbon. The oceans have roughly 2 million million kg C, the continents 560 million million kg C (table 1). The structural plant materials would have to account for 556 million million kg C (99.3% of continental biomass carbon) to reduce the amount of 'active' continental biomass carbon to twice the marine biomass stock of carbon.