to 32%, $K_2O \approx 8$ to 9%, and $CO_2 \approx 27$ to 32% (*3–5, 15*). Analyses of fresh samples, which were sealed before complete cooling, indicate that the 1988 lavas were almost water-free. The volatile contents of F (2.5 to 4.5%), Cl (3.5 to 5%), and SO_3 (4 to 5.5%) are higher than reported previously for the 1960 lavas (*15*). Such high volatile concentrations no doubt contributed to the lower solidus temperature of the lava of Oldoinyo Lengai compared with that of the synthetic system studied by Cooper *et al.* (*13*).

The temperature measurements on natural lava flows are in good agreement with experimental melting-temperature determinations carried out on samples from the same flows. The rock powder of the natural lava melted easily at temperatures of 500° to 550°C. The melting temperature at 1 atm was determined by differential thermal analysis (DTA) and differential thermal gravimetry (DTG). A pronounced DTA endotherm, representing the onset of melting, began at 490°C (±5°) and had its maximum at 510° to 520°C. This range (490° to 520°C) is similar to the range of the temperature measurements of the lava flows. Dissociation of CO_2 from the carbonate melt began at 660°C.

The observed temperatures are several hundred degrees lower than the lowest 1-atm temperatures of silicate lavas. Significant cooling must have occurred from temperatures of possible partial melting in the mantle (*6*). Concomitant crystallization can account for the distinctly fractionated composition of natrocarbonatites (*5, 6, 15*).

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Magnification of Secondary Production by Kelp Detritus in Coastal Marine Ecosystems

D. O. DUGGINS, C. A. SIMENSTAD, J. A. ESTES

Kelps are highly productive seaweeds found along most temperate latitude coastlines, but the fate and importance of kelp production to nearshore ecosystems are largely unknown. The trophic role of kelp-derived carbon in a wide range of marine organisms was assessed by a natural experiment. Growth rates of benthic suspension feeders were greatly increased in the presence of organic detritus (particulate and dissolved) originating from large benthic seaweeds (kelps). Stable carbon isotope analysis confirmed that kelp-derived carbon is found throughout the nearshore food web.

ALTHOUGH PHYTOPLANKTON IS UNdoubtedly the primary source of organic carbon in much of the world's oceans, benthic plants are thought to be important contributors to food webs in estuarine and coral reef habitats (*1*). In the early 1970s, Mann and others (*2–4*) showed exceptionally high productivity in benthic macrophytes belonging to the order Laminariales (kelps) and inferred that kelp-derived organic carbon could play a significant role in temperate coastal (nearshore) secondary production. We assessed the significance of kelp-derived organic carbon to secondary production by a natural experiment involving islands in the Aleutian archipelago (Alaska) with and without sea otters, and thus with and without extensive kelp forests (*5*). We show that growth rates of benthic suspension feeders are two to five times as high at kelp-dominated islands as at those without kelp beds. Stable carbon isotope ($\delta^{13}C$) analyses show that kelp-derived carbon contributes significantly to the carbon assimilated by secondary consumers at these islands.

Kelps are a dominant feature of many exposed and semiexposed temperate coastlines, where they frequently form dense stands from the low intertidal zone to depths approaching 40 m. Individual kelps can achieve large biomass and rapid growth even at high density, thus forming one of the world's most productive habitats (*3, 6*). Benthic marine herbivores such as sea urchins (Echinoidea) can retard the growth of kelp populations and occasionally decimate extant populations, but most kelp biomass is not consumed directly (*7*). This has led to speculation that kelp biomass enters the nearshore food web through indirect (detrital) routes. By releasing particulate as well as dissolved organic matter (POM and DOM, respectively) as they grow and senesce, kelps could provide a significant organic carbon source for the diverse and abundant assemblages of nearshore suspension feeders, pelagic as well as benthic. Even the considerable quantity of kelp biomass deposited on beaches adjacent to kelp stands ultimately may reenter the nearshore food web as POM and DOM after decomposition.

The reestablishment of sea otters in the Aleutians after their near extinction in the 19th century and the subsequent resurgence of otter predation upon sea urchins allow us to compare secondary production between areas that differ greatly in kelp biomass but are otherwise similar. Oceanographic data indicate that the pervasive influence of the westward-flowing Alaskan Stream accounts for relatively uniform physical conditions among the central and western Aleutian Islands (*8*). Neither the few prior studies nor our surveys provide evidence for significant differences in species composition (including phytoplankton) along this segment of the archipelago (*9*).

The mid- and low-intertidal zones throughout the Aleutian Islands are dominated by kelps belonging to the genera

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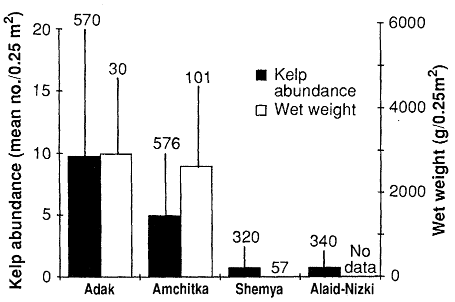

Fig. 1. Kelp abundance and wet weight (means and 1 SD of quadrat counts and sample weights) from islands with sea otters (Adak and Amchitka) and without otters (Shemya and Alaid-Nizki). Biomass at Shemya = 0. Sample size is given above each error bar.

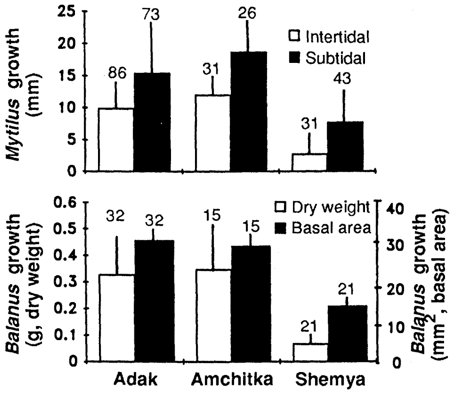

Fig. 2. Results of translocation experiments; means and 1 SD of growth in length (mussels, *Mytilus*) or dry weight and basal area (barnacles, *Balanus*). Sample size is given above each error bar.

Laminaria and *Alaria*, which exist in a refuge above the foraging range of sea urchins. Rocky subtidal habitats at islands with sea otters are characterized by low urchin biomass and large stands of both understory and surface canopy kelps; however, islands where sea otters have not become reestablished are characterized by large urchin biomasses and few kelps (*5*). This nearshore community variation allowed us to assess (by comparison) the importance of kelp carbon to the production of nearshore consumers. Between 1985 and 1987 we conducted benthic surveys, experiments, and δ^{13}C analyses at Adak and Amchitka Islands (sea otters abundant) and at Shemya and Alaid-Nizki Islands (no sea otters) to determine whether growth (as an indicator of production) and δ^{13}C of consumer organisms were related positively to kelp biomass.

Systematic benthic surveys verified differences in kelp abundance and biomass between islands. At each island, transects were established at 16 to 30 randomly selected sites along the 6-m contour. All sites were on the Bering Sea side of each island and were judged subjectively to be of similar wave exposure. Along each transect, 20 randomly selected 0.25-m^2 quadrats were censused by divers for kelp abundance. The resulting data (Fig. 1) show orders of magnitude differences in subtidal kelp abundance and biomass between islands with and without sea otters. Although abundance and biomass are not synonymous with production, research on similar kelp assemblages indicates that benthic production should be vastly different among these islands (*2, 10*).

If kelp-derived organic carbon is available to nearshore suspension feeders, detritivores, and (indirectly) their predators, and if phytoplankton alone is a limiting resource (*11*), then secondary production should be significantly different between island groups. We used two analyses to determine whether suspension-feeding organisms grow faster in kelp-dominated than in urchin-dominated environments. First, we translocated two species of suspension feeders (the mussel *Mytilus edulis* and the barnacle *Balanus glandula*) from a common source (Puget Sound, Washington) into cages at six intertidal and six subtidal sites at Adak, Amchitka, and Shemya islands. Mussels were translocated in 1985 and 1986 and barnacles in 1986. Mussels were individually tagged and measured (maximum valve length) (*12*); barnacles were allowed to settle on fiberglass plates, thinned to minimize competition, and measured in four dimensions (length and width of operculum and base). Barnacle locations were mapped for individual identification and the plates were placed in the same cages with the mussels. All animals were remeasured after 1 year. Mussel valve elongation, barnacle final dry weight (*13*), and change in barnacle basal plate area were the parameters used to compare growth among islands.

Growth rates were significantly different (*14*) among islands. Mussels in kelp-dominated habitats (Adak and Amchitka) grew approximately two (subtidal) to four (intertidal) times as fast as mussels in urchin-dominated habitats (Fig. 2). Likewise, barnacles (intertidal) grew up to five times as fast in kelp-dominated environments (Fig. 2) (barnacles from subtidal cages did not survive).

As a second, independent verification of the translocation data, age-size relations were analyzed for intertidal mussels collected from six sites at each of four islands (*15*). Mussel valves were sectioned and age determined by the methods of Lutz (*16*). For year classes 2 to 5, mussels were significantly larger at islands with substantial subtidal kelp forests (Fig. 3) (*17*).

Our results do not exclude the possibility that a carbon source other than that derived from kelps accounted for differences in mussel and barnacle growth among islands. We employed δ^{13}C analyses to determine the extent to which consumers were using kelp-derived organic carbon and if such use differed among islands as predicted (*18*). The Aleutian nearshore food web lends itself well to such analyses for several reasons. Unlike other habitats such as estuaries where diverse autotrophs (phytoplankton, benthic algae, and marine and terrestrial angiosperms), each with a distinctive δ^{13}C signature, contribute POM and DOM to nearshore waters, the Aleutians have only two principal sources of organic carbon: benthic algae and phytoplankton (*19*). Furthermore, at high latitudes, phytoplankton is more deplete in ^{13}C than at low latitudes (*20*) and thus the difference in signatures between kelps and phytoplankton is large, leading to less ambiguous interpretation of the origins of organic carbon in nearshore consumers. In addition, because islands differ greatly in the potential input of kelp carbon, we could incorporate the measured consumer δ^{13}C enrichment at kelp-dominated islands in a simple mixing model to assess quantitatively the magnitude of kelp carbon input to the nearshore food web.

To characterize predominant carbon sources, δ^{13}C was determined from samples of the dominant kelps (*Laminaria groenlandica*, *L. longipes*, and *Alaria fistulosa*) collected at Adak and Amchitka islands. Six suspension feeders, two detritivores, and three

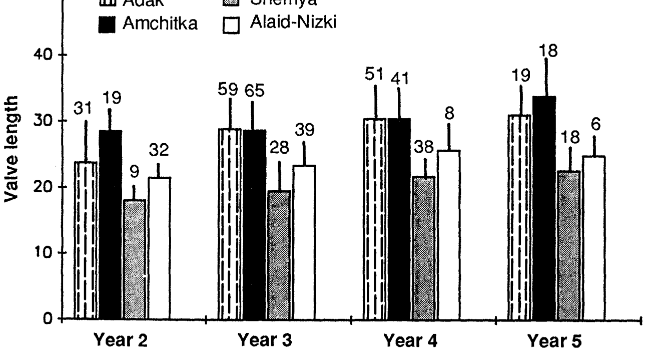

Fig. 3. Age-size relations for *Mytilus edulis* at four Aleutian Islands; means and 1 SD of valve length. Sample size is given above each error bar.

predator taxa were collected at each island as indicators of the islands' nearshore consumers (*21*). Phytoplankton isotopic values were derived from cultures incubated on board the R.V. *Alpha Helix*. Cultures inoculated from ambient seawater were used rather than net tow samples because of the inevitable problem of contamination by non-phytoplankton carbon in plankton net tows. These cultures were made up primarily of *Chaetoceros* and *Thalassiosira*, which were the dominant genera in net tows at all islands as well as the most common genera reported for the region (*9*). The mean phytoplankton isotopic value (−24.0 per mil ± 1.0 SD, $n = 5$) corresponds with published values (−22.9 to −24.4 per mil) for this region and surface water temperatures. Kelps were considerably enriched in ^{13}C relative to phytoplankton, and values were relatively consistent among taxa and islands (overall mean of −17.7 per mil ± 2.3 SD, $n = 162$).

Differences in consumer $\delta^{13}C$ between kelp-dominated islands and urchin-dominated islands support the hypothesis that carbon fixed by kelp is found throughout the nearshore food web and may even be consequential at islands with comparatively low kelp abundance. For each of 11 consumers tested, with the single exception of *Mytilus edulis* (*22*), mean $\delta^{13}C$ values for animals from kelp-dominated islands (Adak and Amchitka pooled) were more enriched than mean values for animals from islands without kelps (Shemya and Alaid-Nizki pooled) (*23*). On the basis of a simple mixing model (*24*), primary consumers at kelp-dominated islands average, conservatively, 58.3% kelp-derived carbon (Fig. 4), whereas at urchin-dominated islands they average only 32.0%. This was the case despite all consumers being collected in midsummer during periods of peak phytoplankton abundance, when $\delta^{13}C$ values should be indicative of maximum phytoplankton influence. The moderate percentage of kelp-derived carbon in consumers at urchin-dominated islands is probably the result of input from intertidal kelps and kelps existing in subtidal refuges from urchin grazing. The relatively consistent enrichment of consumers at Adak and Amchitka, regardless of feeding type or trophic level, argues for the pervasive occurrence throughout the nearshore food web of organic carbon originally derived from kelp photosynthesis.

Both the transplant translocation experiments and age-size analysis show that suspension feeders grew at a significantly higher rate at islands with extensive subtidal kelp forests than at those without. The $\delta^{13}C$ data indicate that this difference in growth rate most likely results from the use of organic carbon photosynthesized by kelps, rather than from differences among islands in phytoplankton production or some other variable. Isotopically enriched signatures of organisms such as mysids, rock greenling, and pelagic cormorants at kelp-dominated islands further indicate that use of kelp-derived organic carbon is not restricted to benthic organisms.

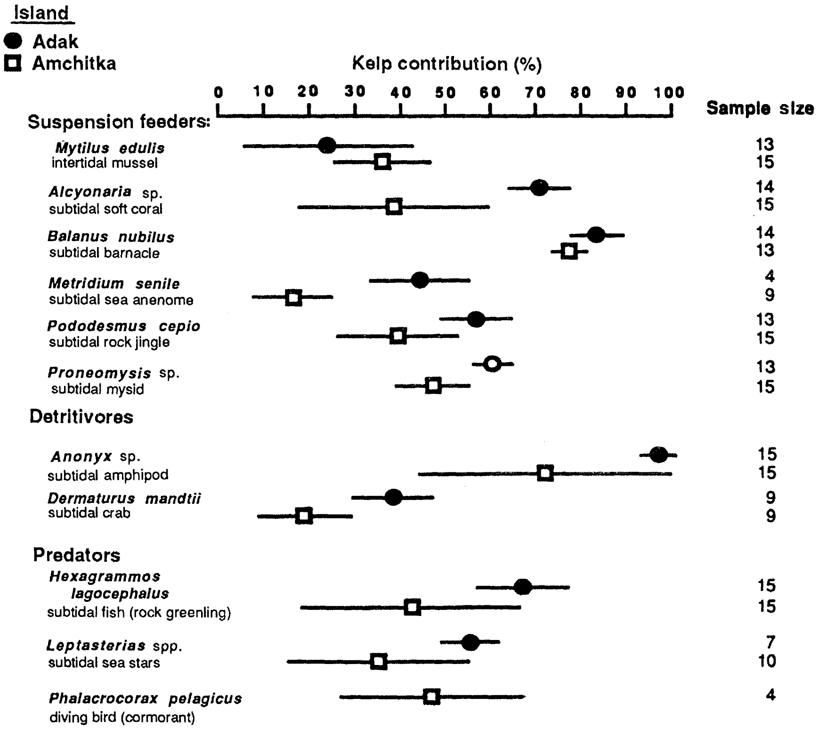

Fig. 4. Percentage of carbon photosynthesized by kelps found in tissues of consumers at islands with extensive subtidal kelp beds. Values are means and 1 SD. Three to five samples were collected and analyzed from each of three sites at each island.

The ecological role of kelps in the nearshore region is multifaceted. Strong evidence exists that they provide habitat (substratum and canopy) for a wide range of benthic, epibenthic, and pelagic organisms and alter the hydrodynamic environment of the nearshore region (*25*). Here we report a strong trophic link between kelps and a wide range of organisms of varied feeding strategies and trophic levels, extending beyond the obvious kelp-grazer-predator food chain. The common occurrence of extensive, highly productive kelp forests along most temperate to subpolar coastlines suggests that our results are not specific to the Aleutian Islands. The relative trophic contributions of kelp detritus and phytoplankton may vary with latitude, habitat, or season, particularly given the punctuated nature of phytoplankton production. The role of kelp production may actually be greatest in winter, when phytoplankton production is at a minimum, and kelp standing stock is either senescing (annual species) or being physically degraded during storms (annual and perennial species).

Our data support quantitatively the suggestions of Mann (*2, 3*) and others that kelps contribute significantly to coastal secondary production, perhaps ultimately establishing limits to the abundances of food-limited populations. Factors affecting kelp occurrence and production such as the recolonization or extinction of sea otters, sea urchin disease, catastrophic storms, nutrient depletion during El Niño events, or oil spills and other pollution are thus likely to have wide-ranging and often long-lasting influences on the productivity of coastal ecosystems.

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11. Phytoplankton production in the Aleutians is comparatively low (38 to 243 mg of carbon per square meter per day) concentrated during a relatively short growing season and probably restricted to bays (rather than the exposed coast) with vertical water stability (*9*).
12. Mussels were initially of equal size and were assigned to cages randomly. We could not replicate the "no kelp" treatment of this experiment because we were unable to visit Alaid-Nizki Island until the summer of 1987.
13. All barnacles recruited to the settling plates within a span of several weeks and were of similar size. Barnacle physical dimensions were measured within 48 hours of placement in cages; at that time there was no statistically significant difference in mean basal plate area among islands ($n = 4$) for those individuals that survived to the experiment's conclusion (Kruskal-Wallis, $P > 0.1$). Final dry weight was measured on animals removed from the plates and dried at 50°C for 24 hours.
14. Kruskal-Wallis ANOVA on mean growth of individuals at a site (cage) were mussel intertidal, $\chi^2(2) = 19.3$, $P < 0.0001$; mussel subtidal, $\chi^2(2) = 17.2$, $P < 0.0002$; barnacle dry weight, $\chi^2(2) = 6.4$, $P < 0.05$; barnacle basal plate area, $\chi^2(2) = 6.2$, $P < 0.05$.
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18. See B. Fry and E. B. Sherr [*Contrib. Mar. Sci.* **27**, 15 (1984)] for comprehensive discussion and critique of the application of δ^{13}C techniques to ecological studies. The ratio of ^{13}C to ^{12}C is fixed at the time (and according to the pathway) of photosynthesis. With minor modification (+0.5 to 1.5 per mil per trophic level), this ratio is maintained through consumer trophic levels. Thus consumer signatures reflect those of key primary producers.
19. Terrestrial input of organic matter to nearshore coastal waters was presumed to be insignificant primarily because most terrestrial vegetation is maritime tundra of grasses and lichens, which degrade in situ; there is no woody vegetation that would produce large amounts of exportable detrital matter.
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21. Five whole (above holdfast) kelp specimens per species were collected at each of three randomly selected sites at each island and subsampled systematically by taking a number of plugs uniformly along the length of the blade. Three to five specimens of each consumer taxon were collected at the same sites as the kelps and were used whole (mysid, amphipod, sea anemone) or subsampled (muscle tissue of others).
22. The single exception to the pattern of greater consumer enrichment at islands with kelps was *Mytilus edulis*, which was the only consumer we collected from the intertidal zone, where kelps are abundant at all four islands. *Mytilus* δ^{13}C values showed no pattern between kelp and no kelp islands.
23. Differences between kelp and no kelp islands were significant in a random-block ANOVA (with species as blocks, thus allowing analysis of all species simultaneously) considering all subtidal consumers pooled [$F(1,27) = 7.96$, $P < 0.0001$] or only suspension feeders [$F(1,14) = 11.64$, $P < 0.005$].
24. A simple mixing model based upon that of T. McConnaughey and C. P. McRoy [*Mar. Biol.* **53**, 263 (1979)] was possible because of the two-carbon source system. Percentage contribution from kelp is calculated as [δ^{13}C sample − δ^{13}C phytoplankton − I]/ [δ^{13}C kelp − δ^{13}C phytoplankton] × 100, where I represents a post-photosynthetic isotope fractionation and was empirically derived for each species by calculating the difference in δ^{13}C between the most deplete sample of that species ("pure" phytoplankton diet) and the mean phytoplankton value (−24.0). In cases where the most δ^{13}C deplete value for a species was less than our phytoplankton value, the mean of our measured enrichment values (2.5 per mil per trophic level) was used. This method makes our model conservative in favor of phytoplankton (reducing the percentage of carbon from kelp) in that our calculations indicate that even the most isotopically deplete consumers incorporate some kelp-derived carbon.
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26. Supported by NSF grant DPP-8421362. We sincerely appreciate the discussions and comments of our colleagues M. Dethier, B. Fry, T. Michaels, and G. VanBlaricom, and the assistance provided by a small army of divers plus the U.S. Coast Guard (17th District), the U.S. Navy (Adak Naval Station), the U.S. Air Force (Shemya Air Force Base), and the U.S. Fish and Wildlife Service (Alaska Maritime Refuge), during our surveys, collections, and experiments in the Aleutians. We thank P. Hassett, L. Johnson, A. Sewell, and J. Watson who were particularly helpful in the field or laboratory.

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A 48-Million-Year-Old Aphid–Host Plant Association and Complex Life Cycle: Biogeographic Evidence

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Biogeographical and paleobotanical evidence suggests that the aphid subtribe Melaphidina has been associated with its sumac host plant since the early Eocene when these plants were continuously distributed across the Bering land bridge. Transfer experiments indicate that the American species, *Melaphis rhois*, shows an unusual complex life cycle, similar to that known in Chinese melaphidines, with some generations feeding on mosses as alternate host plants. As with the association with sumac, this complex life cycle may have been established in the melaphidine lineage before the southward retreat of sumac from Alaska 48 million years ago. This example suggests that the interactions and life histories shown by modern populations may be determined, in large part, by evolutionary commitments made in the distant past.

DESPITE THE LARGE AMOUNT OF attention paid to possible coevolutionary interactions between herbivorous insects and their host plants, the ages of interactions between specific insect and plant lineages have been estimated in only a few cases (*1, 2*). These ages are difficult to obtain from fossils of damaged plant tissues since the damage must be distinctive enough to be definitely associated with a modern insect group. The ages of life cycle phenomena observed in modern animal species are even more difficult to establish, because these are rarely documented by any fossil evidence. I have used biogeographic evidence to establish the antiquity of an association between an aphid and a plant lineage and of a peculiar complex life cycle.

The aphid subtribe Melaphidina (Homoptera: Aphididae: Pemphiginae: Fordini) consists of four Asian genera and a monospecific American genus (*3, 4*). All known species form galls on sumac species [Anacardiaceae, *Rhus* L., subgenus *Rhus* (*3, 4*)]. These galls are induced by aphid feeding and are inhabited by three generations of parthenogenetic females. Galls are closed, sac-like structures with a structure and composition very different from leaves from which they are derived (*5*). Eclosion of the final winged emigrant generation is synchronized with opening of gall exit slits. Although this level of intricacy suggests that a sumac-Melaphidina association is ancient, more definite evidence concerning the age of the interaction is provided by biogeographic considerations.

The current distribution of the Melaphidina implies that use of sumac was established before the geographic separation of the ancestors of modern hosts in Asia and America. The occurrence of the subgenus *Rhus* in both the Old and New Worlds is attributed to dispersal across the Bering land bridge during or before the early Eocene, an explanation strongly supported by fossil evidence (*6*) (Fig. 1). The vicariance between Asian and American plant lineages resulted when climatic changes pushed plant distributions southward during the Tertiary (*7*). For sumac, this occurred about 48 million years ago, as judged by the distribution of leaf fossils in Alaskan Tertiary floras (*6, 8*). The sumac-Melaphidina association must be

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