proximately 0.8 kcal/mol for each segment replaced, as indicated by the parallel line drawn through these points. These two parallel relations show that transmembrane segments 1 to 5 of these receptors each contribute approximately 0.8 kcal/mol to the difference in binding energy between PAC and ISO.

In contrast to the progressive change in binding energy preference observed when segments 1 to 5 are exchanged, substitution of transmembrane segment 7 of the α_2-receptor for the corresponding segment of the β_2 receptor causes a dramatic change of 3.7 kcal/mol for a single segment (compare □ and ■ in Fig. 1). The size of this change is independent of the source of transmembrane segments 1 to 5 as illustrated by the parallel lines in Fig. 1. Evidently segment 7 has unique determinants of agonist binding specificity, as concluded by Kobilka *et al.* (*1*).

This quantitative analysis of agonist binding specificity emphasizes the additive contributions of individual transmembrane segments in determining binding energy preference. The use of binding free energy as the measured parameter makes these additive relationships clearer than simple inspection of binding curves and relative K_d values. This approach may prove valuable in similar analyses of chimeras of other members of the family of G-protein–coupled receptors or of other proteins with multiple membrane-spanning segments.

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Response: We are pleased that Catterall's quantitative analysis of our data strengthens the conclusions that we drew about the importance of various transmembrane domains in determining the α- versus β-adrenergic binding specificity of these receptors. Combination of the experimental approaches used in our studies with analytic approaches such as that suggested by Catterall should provide a powerful means of analyzing the structural basis of the function of receptors coupled to guanine nucleotide regulatory proteins.

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Predation on Ocean Krill

In developing the hypothesis that "high-density demersal layers" of krill (*Meganyctiphanes norvegica*) at the bottom of submarine canyons are a major prey of fishes on Georges Bank, Greene *et al.* (*1*) may be missing a major facet of the trophic interactions among these organisms. According to their hypothesis, the fishes make descents into deep water next to the Bank, where, it is suggested, there is advantage in feeding on these vertical migrators when they are in their normal daytime aggregations. But this is not how the interactions proceed in what probably are similar situations elsewhere.

It has been widely reported (*2–4*) that fishes which inhabit relatively shallow banks or shelves feed heavily by day on organisms that, like *M. norvegica*, make extensive diel vertical migrations in adjacent deep water. The reports have come from the continental shelves of North America (*2*) and Australia (*3*), as well as from a central Pacific atoll (*4*); and in addition to various species of krill, the vertically migrating prey have included copepods and myctophid fishes. In the reported cases, however, the predatory fishes do not descend from the shelf or bank into the adjacent depths to take prey from the concentrations that form there by day. Rather, they feed on individuals that, after having been carried by currents (or swimming) over the shelf-bank while in the surface waters at night, are trapped by the relatively shallow shelf-bank when in the morning they descend toward their normal daytime depths. Apparently these organisms are especially vulnerable to predators in this setting, which is very different from their normal daytime habitat.

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Response: In our paper (*1*), we hypothesized that squid and demersal fish production attributed to Georges Bank might be subsidized by the exploitation of krill from the submarine canyons and other deep waters surrounding the Bank. At present, the evidence for such a subsidy is circumstantial; krill are an important but variable dietary component of the Bank's commercially important squid and demersal fish stocks, and many of these stocks seasonally move off the Bank (as defined by the 200-meter isobath) into the surrounding deep waters where the high-density krill demersal layers are found. Unfortunately, little is known about the behavior and diets of these species when they move into deeper water. As we stated, closer examination of the spatial and temporal coupling between predator and prey populations will be essential to determine the validity of our hypothesis.

Hobson (*2*) raises a valid point with regard to the spatio-temporal coupling between predator and prey populations. If krill are the missing link in the Georges Bank food chain, then they must move onto the Bank either through vertical migration and advection by currents (or active swimming), as Hobson suggests, or the squid and fish stocks must descend into deeper water and feed, as we implied. Initially, we favored the mechanism hypothesized by Hobson, since there is ample evidence for such events occurring on other banks (*3*) and seamounts (*4*) around the world. However, extensive zooplankton and micronekton surveys on Georges Bank (*5*) indicate that krill rarely intrude on the shallower portions of the Bank, and thus the circumstantial evidence for Hobson's hypothesis does not appear to exist. On the other hand, fishery surveys on and around Georges Bank (*6*) indicate that many squid and demersal fish stocks move off the Bank seasonally into the deeper waters, where high-density krill demersal layers have been observed. Therefore, we chose to emphasize the latter hypothesized mechanism for the trophic linkage rather than the one Hobson suggests. So little is

known that neither hypothesis should be given preference. A considerable amount of work by oceanographers and fishery scientists must be done before the role of krill in the Georges Bank food chain can be fully appreciated.

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Habitat Compartmentation and Environmental Correlates of Food Chain Length

Briand and Cohen (*1*) conclude that "the dimensionality of the environment influences mean or maximal [food] chain length more than environmental variability" but do not offer an explanation. After examining the first 40 food webs that Briand and Cohen present (*1*), we find 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. Our calculations indicate that the first 40 webs are an adequate sample, as the range and median chain lengths of webs 1 through 40 are similar to those of webs 1 through 113 (Fig. 1).

Many of the webs presented by Briand and Cohen are truncated. In the first 40 webs, 17% of the 138 "producers" are actually consumers. For example, the Aspen parkland community food web (*2*) producers include primary producers, but also consumers, for example, coots, ducks, mice, and ants. Because in all cases these consumers have no resource identified below them and only a single link above them, the mean and maximum food chain lengths are underestimated. Moreover, the intermediate and top predators of many web descriptions are missing. In the New Zealand salt-meadow (*3*) the low mean chain length (1.96) results from single-link chains that portray organisms such as weevil larvae, Hemiptera, harpacticoids, staphylinids, dipterous larvae, haplotaxid worms, oribatid mites, bumblebees, adult Hymenoptera, and redpolls as top predators. Jones (*4*) described a web for the River Clydach that included predatory fish, but Briand and Cohen and others (*5, 6*) use a simplified web for this system, in which predatory fish and some intermediate consumers are deleted. Numerous webs are missing predatory birds and insects and primary decomposers (bacteria and saprophytic fungi) or do not have phytoplankton distinguished from zooplankton.

We find that the concept of habitat dimensionality lacks sufficient rigor to be used in a standardized manner. In the study by Briand and Cohen, three-dimensional (solid) habitats include lakes, oceans, and forests (including kelp beds), whereas two dimensional (flat) habitats include creeks, rivers, intertidal zones, marshes, grasslands, deserts and tundra. Habitats with both two- and three-dimensional aspects are considered to have mixed dimensions. Habitats may appear to us as solid or flat; however, we question whether organisms within the habitats make this distinction. For example, the Long Island salt-marsh (estuary) includes an air column for birds, a water column large enough to support pelagic organisms and plankton, and a flat bottom for molluscs and water plants; yet this is classified by Briand and Cohen as a two-dimensional habitat. The Marshall Island coral reef is considered a three-dimensional habitat even though it contains only two of the three strata of the Long Island salt-marsh (no air column).

We do not mean to criticize the original food web studies, since their objectives did not include having the webs subjected to structural analyses; however, the completeness of Briand and Cohen's descriptions of the food webs is confounded with the webs' dimensions. In the three-dimensional habitats of Briand and Cohen, phytoplankton are differentiated from zooplankton and generally include top predators [see webs 17, 19–21, 24, 25, 27, 29–32, and 40 (*1, 5*)], whereas the two-dimensional habitats [webs 3, 10–13, 23, 34, and 35 (*1, 5*)] do not have plankton differentiated and lack top predators (birds, fish, and mammals). We consulted some of the investigators of the original studies, outside experts on the habitats included in the studies, or the original publications and corrected biases in the descriptions by differentiating plankton, conservatively adding top predators where they were obviously missing [for example, gulls and other predators feed on shellfish in the rocky intertidal—webs 10–13 (*6, 7*)]. We then recalculated the mean chain lengths. Differentiating plankton accounted for 20 to 30% of the difference in the median chain length between two-dimensional and three-dimensional webs reported by Briand and Cohen (*1*), while 60 to 70% could be explained by the differentiating plankton and missing top predators (Fig. 1).

The difference in mean chain length between the two-dimensional and three-dimensional webs appears to be a function of how closely their descriptions depict the real food web. If the top predator(s) resided in the same habitat or medium as their prey, the original investigator(s) included them in the description (for example, large mammals, sharks, and boney fish for food web descriptions of open seas). If the top predator(s) of a web spent much time in a habitat or medium other than their prey, however, the investigator(s) did not generally include them (for example, birds and mammals for food web descriptions of the rocky intertidal, streams, and some terrestrial habitats). Of the 12 three-dimensional webs included in our analysis, the four with the lowest mean

Fig. 1 (facing page). Box plots of the frequency distributions of mean chain lengths calculated after Briand and Cohen (*1*). In Group I (A) represents the two-dimensional webs presented by Briand and Cohen (*1*), (B) the subset of two-dimensional webs from the first 40 webs (*1*), and (C) the subset of two-dimensional webs with web 12 corrected to reflect the mean chain length of the food web presented by Briand (*5*) [mean chain length was 2.25 (*1*); it is now 2.32] and small frogs separated from large frogs in web 23. Group II (D, E) are the two-dimensional webs (3 and 10–13) with phtyoplankton and zooplankton separated. Method D assumes that phytoplankton are only consumed by zooplankton, while Method E additionally assumes that phytoplankton are consumed by predators of zooplankton. Group III (F, G) consists of the two-dimensional webs (3, 10–13, 23, and 34) with predators added. Method F adds missing top predators to the Method D webs, and Method G adds top predators to the Method E webs. In Group IV Method H represents the subset of three-dimensional webs from the first 40 webs, (I) the complete set of three-dimensional webs presented by Briand and Cohen, and (J) the subset of three-dimensional webs with predators added (24, 25, and 40) (*1*). Q1 is the 25th percentile, Q2 the 50th percentile, and Q3 the 75th percentile. For each box plot, the upper asterisk represents the largest observation less than Q3 + (Q3 − Q1), and the lower asterisk represents the smallest observation greater than Q1 − (Q3 − Q1).