pituitary remain to be determined. Further work on the functional role of AIP should prove informative in revealing key cellular processes involved in genesis of pituitary adenomas, including potential drug targets.

It has not been previously realized that genetic predisposition to pituitary adenoma, in particular the GH-oversecreting type, can account for a substantial proportion of cases. Our study not only reveals this aspect of the disease but also provides molecular tools for efficient identification of predisposed individuals. Without preexisting risk awareness, the patients are typically diagnosed after years of delay, leading to substantial morbidity. Simple tools for efficient clinical follow-up of predisposed individuals are available, underlining the importance of our findings.

Our results suggest that inherited tumor susceptibility may be more common than previously thought. The identification of the PAP gene indicates that it is possible to identify the causative genetic defects in the low-penetrance conditions even in the absence of a strong family history.

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**Supporting Online Material**

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Materials and Methods
SOM Text
Figs. S1 and S2
Tables S1 to S6
References

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# Strong Top-Down Control in Southern California Kelp Forest Ecosystems

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**Global-scale changes in anthropogenic nutrient input into marine ecosystems via terrestrial runoff, coupled with widespread predator removal via fishing, have created greater urgency for understanding the relative role of top-down versus bottom-up control of food web dynamics. Yet recent large-scale studies of community regulation in marine ecosystems have shown dramatically different results that leave this issue largely unresolved. We combined a multiyear, large-scale data set of species abundances for 46 species in kelp forests from the California Channel Islands with satellite-derived primary production and found that top-down control explains 7- to 10-fold more of the variance in abundance of bottom and mid-trophic levels than does bottom-up control. This top-down control was propagated via a variety of species-level direct and indirect responses to predator abundance. Management of top-down influences such as fishing may be more important in coastal marine ecosystems, particularly in kelp forest systems, than is commonly thought.**

Understanding the relative importance of top-down (consumer-driven) versus bottom-up (resource-driven) control of food webs has long been a focus of ecological studies (*1*–*4*). Anthropogenic nutrient enrichment of the environment through the use of fertilizers has become globally widespread (*5*), with most of these additions being transported to coastal systems via runoff. The abundances of large top-predators have been dramatically reduced in most of the world's oceans (*6*, *7*). How ecosystems respond to changes in the relative strength of top-down and bottom-up forces will affect conservation and restoration efforts aimed at mitigating or reversing these impacts.

Recent studies of large-scale marine ecosystems have drawn contrasting conclusions about the direction of control of community structure, offering strong evidence for either bottom-up control (*8*–*10*) or top-down regulation (*11*, *12*). Kelp forest communities have provided strong evidence of top-down control mediated through trophic cascades (*4*, *13*). However, the likelihood and strength of trophic cascades vary greatly among kelp forest systems (*13*), and there is evidence that kelp distribution and abundance can be controlled from the bottom up by nutrient levels (*14*), which in turn determine the abundance of species belonging to higher trophic levels (*15*). It is in part because kelp (such as *Macrocystis pyrifera*) respond so quickly to nutrients (via growth) or to storm disturbance or grazing (through mortality) that hypotheses of top-down versus bottom-up control are often tested in kelp forest ecosystems; changes in primary production or predator abundance (that in turn affect grazer species) are quickly incorporated into the community and can then be measured.

We used a multiyear data set of species abundances measured at 16 different kelp forest sites around the Channel Islands, California, and combined it with satellite-derived estimates of ocean primary production (from the Sea-Viewing Wide Field-of-View Sensor or SeaWiFS) at each site (*16*) to test whether ecosystem trophic dynamics are driven more by predation or primary production (Fig. 1). The northern Channel Islands lie in the middle of a dynamic oceanographic boundary formed by the convergence and mixing of the cold California Current and the warmer Southern

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California Countercurrent. The strong spatial variability in primary production is driven in large part by the complex bathymetry of the region (*16*), spans the entire range of typical values seen for the northeast Pacific (*9*), and is positively correlated with nutrient levels (*17*). This variability in production in turn generates large variations in community structure and dynamics around the islands (*17–19*). The spatial heterogeneity in productivity in this transition zone and the detailed spatial and temporal scales of the data make it an ideal system for a robust test of the role of top-down versus bottom-up regulation of community structure.

Abundance data were available for 4 algal, 27 invertebrate, and 15 fish species; each of the 46 species was classified as predators (12 fishes and 4 invertebrates), herbivores (1 fish and 9 invertebrates), planktivores (2 fishes and 14 invertebrates), or algae (4 species). Details on how these data were processed before analyses are provided in Halpern and Cottenie (*18*) and are summarized in the supporting online material (also see the species listed in table S1). We used variation decomposition based on redundancy analysis to isolate the effect of predator abundance versus primary production variables on the abundance of herbivore, planktivore, or algal trophic levels within the kelp forest community. This technique is the multivariate extension of linear regression (with corresponding $R^2$) that measures the amount of variation (computed as the percentage of the total variation in the community matrix) that can be attributed exclusively to either top-down or bottom-up variables, after eliminating confounding spatial and temporal variables (*20*, *21*). In particular, we included and controlled for spatial, temporal, and environmental variables to account for (and therefore remove) the effect of inherent small-scale differences in populations and communities, population cycles, El Niño events, and biophysical drivers of species and community dynamics such as temperature [see (*18*) for specific variables and their treatment]. We tested all direct food web paths (Fig. 2) with secondary and primary predators as separate and summed explanatory variables, because there were only two secondary predator species. We also conducted analyses with herbivores and planktivores treated as the same trophic level. A forward selection procedure was used to isolate which predator species and primary production variables were the most important for driving the results. To further test whether differences in primary production drove variation in abundance across sites, we used linear regression analysis with annual or winter monthly average primary production as the independent variable and the summed abundances of predators or entire communities as the dependent variable.

Despite the strong spatial (Fig. 1) and temporal gradient in primary production across the waters surrounding the islands, we found little evidence of bottom-up control and a 7- to 10-fold larger influence of top-down relative to bottom-up regulation of kelp forest community structure (Fig. 3). When controlling for spatial, temporal, and environmental variables, overall predator abundance had a significant effect on algal, herbivore, and planktivore abundances, explaining 11 to 20% of abundance patterns of autotroph and primary consumer trophic levels, whereas local primary production had no significant effect (<2% explained in all cases; Fig. 3 and table S2). Top-down effects were nearly twice as strong for algae as for herbivores or planktivores. These overall results were largely driven by the abundance of primary predators, because these predators alone also explained a significant, although slightly smaller, amount of the variation in the abundance of other trophic levels, although secondary predators alone did not explain a significant amount of the variation in the abundance of the other trophic levels. Neither predator abundance nor entire community abundance was significantly correlated with annual or winter local primary production ($P > 0.50$ in all cases). Forward selection models isolated two key predator species that drove the top-down effects on algae, herbivores, and planktivores. For all trophic paths in the food web, spiny lobster (*Panulirus interruptus*) and Kellet's whelk (*Kelletia kelletii*) were significantly important species, likely due to their strong impacts on key grazers of kelp (urchins) and algae (limpets and snails). Kelp rockfish (*Sebastes atrovirens*) and striped seaperch (*Embiotoca lateralis*) also explained a significant amount of the variation in algal abundance. Both fishes eat a variety of small invertebrates that are not major consumers of algae, and so the mechanism of control on algal abundance is not clear. This top-down control is much stronger for algae as compared to that of mid-level trophic levels; in other words, the trophic cascade is accentuated rather than attenuated. The top-down control was largely mediated through these few key species, an effect that would have been missed had all species' abundances been lumped into trophic levels, as in past studies of community regulation.

Our results suggest that, regardless of local patterns of primary production, the

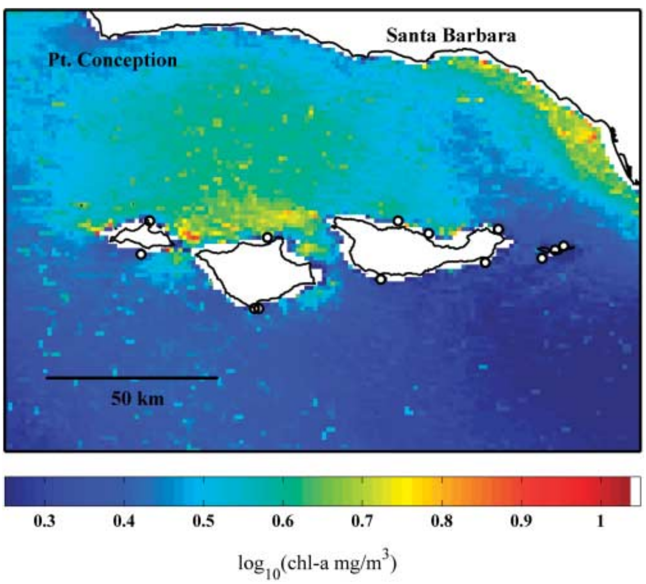


**Fig. 1.** Map of the northern Channel Islands and location of the Kelp Forest Monitoring Program (KFMP) sites (open circles) and the long-term mean SeaWiFS chlorophyll a concentration across the region.

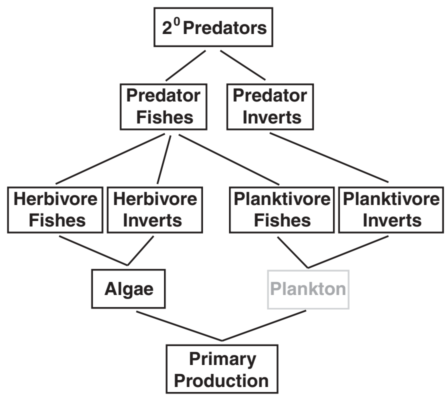


**Fig. 2.** Schematic of the kelp forest food web analyzed. Lines indicate paths of trophic interactions, as determined by the feeding habits of species included in analyses. Primary production was measured by concentrations of chlorophyll a. Plankton abundances are shaded gray because no measurements were available for phytoplankton or zooplankton.

abundance of top predators is markedly influencing the structure of this benthic ecosystem. We focused here on determining which variables explained the variation of species' abundances across space and time, because biomass data were not available, and so we were unable to calculate the effect size per se of top-down control. Previous experimental studies of rocky intertidal ecosystems have found similarly strong top-down regulation (*22*, *23*), suggesting that such control may be typical for coastal ecosystems. Although the range of primary production values in our study included a broad range of typical values, it did not include some of the more extreme possible values, in particular those that occur during strong El Niño years; indeed, benthic communities in coastal ecosystems have been shown to be influenced by nutrient input in these cases (*24*). Coastal ecosystems are heavily fished, highly variable in natural productivity, and subject to high levels of anthropogenic nutrient input, and so it is particularly important to understand how such coastal systems are regulated.

Almost all ecosystem-scale tests of the direction of community control have only been able to look for correlations at a single (albeit large) site, given the challenges of conducting repeated sampling over large scales. A notable exception (*9*) found bottom-up control of top trophic levels at the oceanwide and regional (and replicated) scales. Our study is well replicated at a spatial scale relevant to most community and ecosystem dynamics, while still spanning a similar (although narrower) range of productivity seen across the entire northeast Pacific. Our results suggest that the importance of bottom-up control in coastal ecosystems may often be overestimated.

Top-down regulation was the dominant and only significant factor controlling algal abundance, in contrast to past work showing the sensitivity of giant kelp to nutrient levels and local-scale disturbance regimes (*14*). Our study had a relatively large spatial scale and broad taxonomic coverage, which likely explains these differences in results. Given that kelp is a foundation species for the ecosystem, this top-down regulation of kelp dynamics is likely to have community-wide consequences (*25*). For the midlevel trophic groups, top-down control is still highly significant, but explains less of the variation than that for the indirect control of algae. We have shown elsewhere that these differences in community structure are driven primarily by site-based variables (such as habitat or recruitment) and not by climate variables (such as local temperature, regional disturbance regimes, or El Niño–Southern Oscillation events) (*18*). In fact, the combination of spatial, temporal, and environmental variables included in our analyses also explained a significant amount of variation in community structure for mid-level trophic groups but not for algae (table S2). We anticipate that local-scale recruitment dynamics may be driving the differences in community structure not explained by top-down control, because recruitment limitation has been noted in other studies of kelp forest and intertidal communities in the region of our study (*19*, *26*). If local-scale predator abundance and recruitment dynamics are indeed the driving forces for the community dynamics of coastal ecosystems, then the difference in the scales of community regulation may be a fundamental reason for the different results among different systems, in particular between pelagic and benthic ecosystems.

Future efforts to manage and protect coastal ecosystems will be challenging, given all of the threats that these systems face. Our results suggest that efforts to control activities that affect higher trophic levels (such as fishing) will have far larger impacts on community dynamics than efforts to control, for example, nutrient input, except when these inputs are so great as to create anoxic zones (i.e., dead zones). In fact, as predators return to systems in response to conservation and restoration efforts, top-down regulation should become even more important than we found in our study, although the role of any particular species in this control of community dynamics may decrease. In contrast, if humans continue to "fish down" coastal food webs, essentially removing the agents of community control, large ecosystems by default become controlled by bottom-up rather than top-down factors, making these systems even more sensitive to future nutrient inputs.

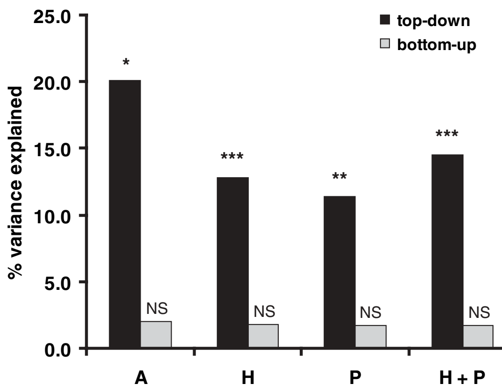


**Fig. 3.** Percent variance in community structure explained by bottom-up versus top-down variables for different trophic levels. A, algae; P, planktivores; H, herbivores. Significance values are indicated for variance decomposition analyses testing whether the abundance of that trophic level is explained by predator abundance (black bars) or primary production (gray bars). *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$; NS, not significant.

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Materials and Methods
Tables S1 and S2
References

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