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Fish in Offshore Kelp Forests Affect Recruitment to Intertidal Barnacle Populations

STEVEN D. GAINES AND JONATHAN ROUGHGARDEN

Kelp forests along the coast of central California harbor juvenile rockfish that prey on the larvae of invertebrates from the rocky intertidal zone. This predation reduces recruitment to barnacle populations to 1/50 of the level in the absence of fish. The dynamics of the intertidal community are thus strongly coupled to the dynamics of the offshore kelp community.

THE EPISODIC RECRUITMENT (THE addition of young to a natural population) of many marine invertebrates (*1*) strongly affects benthic community structure (*2, 3*). The causes of this episodic recruitment are generally unknown, but two components are involved—(i) variation in reproductive output and (ii) variation in the mortality and distribution of larvae while in the water column. This study focuses on the second of these components. We show that substantial numbers of larvae of the intertidal barnacle *Balanus glandula* die as they pass through kelp forests and that yearly variation in the composition of these forests is a major cause of yearly variation in barnacle recruitment.

The giant kelp *Macrocystis pyrifera* is a prominent feature of the Pacific coasts of North and South America (*4*), where it forms continuous beds up to 8 km long and 1 km wide. The extent of these forests and the density of plants within vary greatly in space and time because of storms (*5*), herbivores and their predators (*6*), and major current features (for example, El Niño) (*7*).

A strong negative relation between kelp canopy area and recruitment of *B. glandula* to the rocky intertidal zone was observed during 4 years at Hopkins Marine Station in central California. Annual recruitment to the natural rock substrate varied by two orders of magnitude (*3*); it was high in 1983, low in 1985, and moderate in both 1982 and 1984. Comparable large fluctuations, but of an opposite sign, were seen in the area of the surrounding kelp forest (Fig. 1). The decline in canopy area due to the large winter storms of the 1982–83 El Niño was particularly dramatic. This study examines the potential causal basis for this correlation between kelp area and intertidal recruitment.

Kelp forests interact with the water column and its resident plankton in several ways. (i) The plants exert drag forces that reduce flow velocities and attenuate internal waves (*8*). (ii) They take up nutrients that might be needed for larval growth and survival (*9*). (iii) Kelp forests provide a suitable habitat for larval settlement, thereby depleting larvae from the water before they reach the intertidal habitat (*10*). (iv) Kelp forests harbor invertebrate and piscine planktivores that may further reduce plankton densities (*10, 11*).

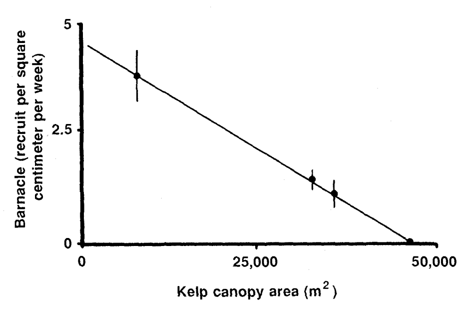

Fig. 1. Correlation of kelp canopy area and *B. glandula* recruitment rates to natural substrate in the rocky intertidal zone. Canopy areas were estimated from infrared aerial photographs provided by ECOSCAN Resource Data of Freedom, California. Recruitment rates were measured from weekly photographs (about 20 per year) of four 35-cm^2 quadrats in the intertidal zone inshore from the kelp forest. Error bars are 95% confidence limits (*22*). Slope = 9.6×10^{-5}; SE = 1.2×10^{-6}.

To examine the effects of kelp beds on the plankton and subsequent inshore recruitment, we collected plankton samples at the inshore and offshore margins of the bed. Three samples (*12*) were collected with a portable pump at fixed stations at approximately weekly intervals beginning in April 1985. *Balanus glandula* releases a nauplius larva. Development proceeds through five additional feeding nauplius stages, terminating in a nonfeeding, cypris larva. Only stage I and stage II nauplii and cyprids were commonly collected close to shore. Both were concentrated in the top meter of the water column (*13*), paralleling their positive phototaxis in laboratory culture (*14*). Therefore, our sampling focused on shallow, surface waters.

Throughout the spring and summer, the plankton samples show steep concentration gradients across the kelp bed (Fig. 2A). *Balanus glandula* cyprids were on average 70 times as abundant in samples collected offshore from the kelp bed as in samples collected inshore. Similarly, a tenfold difference between offshore and inshore concentrations of barnacle nauplii was observed, but the direction of the gradient was opposite to that of cyprids. Comparably steep drops in concentration were consistently found in many other taxa [other barnacle cyprids, copepods, copepod nauplii, gastropod and bivalve veligers, and decapod zoea; Fig. 2A and (*15*)].

The large concentration gradients translate directly into an equally steep gradient in larval recruitment. During July and August of 1985, recruitment was monitored at each of the plankton pumping stations on settling plates affixed to the marker buoys just below the surface (samples, $n = 4$ at each site). On average, recruitment rates by *B. glandula* to these plates were 54 (95% confidence inter-

Hopkins Marine Station, Stanford University, Pacific Grove, CA 93950.

Table 1. Yearly comparisons of kelp canopy area, juvenile rockfish recruitment (*23*), and barnacle recruitment rates. No quantitative records of rockfish recruitment are available for 1982 although qualitative records suggest densities were comparable to 1984 (*23*). Values in parentheses are standard errors.

Year	Kelp canopy area in August (m^2)	Rockfish density (number per minute of diver observation)	*Balanus glandula* recruitment (recruits per square centimeter per week)
1982	36,000		1.1 (0.1)
1983	8,500	0.7 (0.3)	3.7 (0.3)
1984	33,000	7.2 (2.0)	1.4 (0.1)
1985	46,500	236.2 (24.6)	0.05 (0.01)

val ± 14.3) times higher offshore from the kelp bed than inshore, closely paralleling the 70-fold (±20.8) difference in cyprid concentrations. An even larger recruitment gradient was seen for the low intertidal barnacle *Megabalanus californicus* on the plates.

In the autumn and winter, however, all

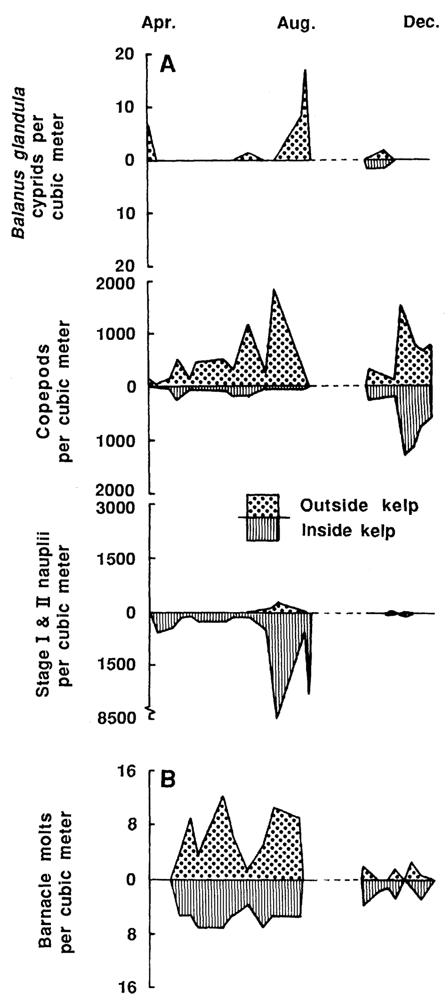

Fig. 2. (**A**) Concentrations of plankton taxa from three samples taken on a weekly basis in 1985 from inshore and offshore margins of the kelp bed. Values above the horizontal axis are from offshore samples, values below are from inshore samples. No samples were collected during September. (**B**) Concentrations of intertidal barnacle molts for the same pump samples. Molts are buoyant.

concentration gradients either disappeared or were markedly reduced (Fig. 2A). This dramatic seasonal change in plankton concentration gradients did not correspond to changes in the area of the kelp bed canopy, which was actually 2% larger in late November 1985 than in August. The breakdown of the concentration gradients coincided with reductions in the density of planktivorous juvenile rockfish (*Sebastes* spp.), thereby implicating predation on larvae by these fish as the main cause of the concentration gradients.

Kelp forests harbor many kinds of invertebrate and fish planktivores. Because of their abundance, feeding rates, food (as judged by stomach contents), feeding preferences in the laboratory, and position in the water column, fish are the most important predator on zooplankton in the size range of barnacle larvae [150 to 1000 μm (*16*)]. During 1985 the most abundant planktivorous kelp bed fishes were juvenile *Sebastes* (over ten species). Adults are mostly benthic predators occurring in many habitats. Juveniles of many species, however, live in the kelp forest (*17*) where they can be exceedingly abundant, often with over 100 individuals per cubic meter near the margins of the kelp forest.

Barnacle larvae were found in the stomachs of several rockfish species feeding near the surface at the offshore margin of the kelp forest. *Balanus glandula* cyprids constituted approximately 10% (by number of items) of the diet of the most abundant species (blue rockfish, *S. mystinus*), occurring in over 40% of all individuals sampled (n = 30). Moreover, the diets of the rockfish themselves parallel the gradient in cyprid concentrations across the kelp bed; individuals feeding near the inside margin of the kelp forest contained no barnacle cyprids whereas those feeding near the outside did. In fact, *S. mystinus* feeding inshore of the kelp bed switched to herbivory, feeding on ephemeral red algae.

Most rockfish juveniles enter the kelp bed in late winter or early spring and reach peak abundances by midsummer (*18*) when the gradient in plankton concentrations is steepest (Fig. 2A). By early autumn, however, many species move to their adult habitats, often outside the kelp bed, and the plankton concentration gradient disappears. The few species that remain as plankton feeders (for example, *S. mystinus*) decline in abundance and switch diets to larger planktonic organisms (*19*).

The loss of the concentration gradients throughout the autumn without changes in canopy area implies that the impact of kelp forests on water flow is not the cause of the gradients. As further evidence, molts from adult barnacles, which are released inshore but probably are not eaten by anything in the water column, showed no significant differences in concentration across the kelp bed at any time of the year (Fig. 2B). Finally, settlement of barnacle larvae within the kelp bed does not explain the gradient in barnacle larvae concentrations, because the same patterns occur in taxa that are strictly planktonic (copepods, for example, do not settle). Moreover, there is no hard substrate available near the surface, and *B. glandula* does not settle on kelp blades.

The strong negative relation among years for barnacle recruitment in the intertidal zone and kelp canopy area actually combines two causal factors (Fig. 1). The mortality of barnacle larvae in transit across the kelp bed depends on the total stock of rockfish, which is a function of both the size of the kelp forest and the density of rockfish within it (*20*). Table 1 shows a close parallel between the fluctuations in kelp canopy area and juvenile rockfish density (*21*); 1983, a banner year for *B. glandula* recruitment, had nearly complete recruitment failure for rockfish associated with the kelp bed. In contrast, the virtual absence of *B. glandula* recruits in 1985 coincided with excellent rockfish recruitment success. Intermediate numbers of both barnacles and rockfish arrived in 1984, and more qualitative records from 1982 suggest a similar pattern.

This study shows the dynamics of two traditionally distinct communities—the offshore kelp forest and the intertidal community—to be strongly coupled. Subtidal kelp communities and the processes affecting them [for example, El Niño (*7*) and sea otters (*6*)] affect intertidal communities through their impact on recruitment to the intertidal zone.

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14. Late stage II nauplii eventually exhibit weak negative phototaxis.
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16. Early stage barnacle nauplii may be the exception because laboratory studies suggest nauplii are more readily eaten by several invertebrates resident in the kelp canopy (for example, caprellid amphipods, mysids). Their concentrations may also be affected by changes in phototaxis with development (*14*).
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20. The rockfish are concentrated primarily at the perimeter of the bed (*11*), and yearly variation in fish density is probably more important than yearly variation in kelp canopy area per se. A more definitive test awaits years in which rockfish recruitment success is decoupled from yearly fluctuations in kelp canopy area.
21. The cause of the relation is under further study. It is unlikely, however, that the observed variation in rockfish density was a direct response to changes in kelp bed area since parallel annual fluctuations were seen throughout the central California coast including rockfish species that do not recruit to kelp beds (unpublished data from E. Hobson). Moreover, preliminary data from 1986 show that rockfish recruitment rates are low despite a large kelp canopy comparable to that of 1985.
22. The error bars pertain to observation error inherent in measuring recruitment rates from several quadrats; the error does not represent the sample variance in recruitment from different years in which the canopy area was the same. Therefore, the differences in confidence interval size are largely irrelevant to the assumption of homoscedasticity.
23. Unpublished data from E. Hobson for the Mendocino coast. Less extensive records and qualitative reports from the California Department of Fish and Game suggest comparable patterns for Monterey Bay. Counts are number of fish seen per minute of water column observation time during the peak abundance periods of July and August. Totals of 45, 67, and 277 minutes of observation are included for 1983, 1984, and 1985, respectively. This density estimate probably has a conservative bias at high fish densities.
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Mapping Human Brain Monoamine Oxidase A and B with ^{11}C-Labeled Suicide Inactivators and PET

J. S. Fowler, R. R. MacGregor, A. P. Wolf, C. D. Arnett, S. L. Dewey, D. Schlyer, D. Christman, J. Logan, M. Smith, H. Sachs, S. M. Aquilonius, P. Bjurling, C. Halldin, P. Hartvig, K. L. Leenders, H. Lundqvist, L. Oreland, C.-G. Stålnacke, B. Långström

The regional distributions of monoamine oxidase (MAO) types A and B have been identified in human brain in vivo with intravenously injected ^{11}C-labeled suicide enzyme inactivators, clorgyline and L-deprenyl, and positron emission tomography. The rapid brain uptake and retention of radioactivity for both ^{11}C tracers indicated irreversible trapping. The anatomical distribution of ^{11}C paralleled the distribution of MAO A and MAO B in human brain in autopsy material. The corpus striatum, thalamus, and brainstem contained high MAO activity. The magnitudes of uptake of both [^{11}C]clorgyline and L-[^{11}C]deprenyl were markedly reduced in one subject treated with the antidepressant MAO inhibitor phenelzine. A comparison of the brain uptake and retention of the ^{11}C-labeled inactive (D-) and active (L-) enantiomers of deprenyl showed rapid clearance of the inactive enantiomer and retention of the active enantiomer within MAO B–rich brain structures, in agreement with the known stereoselectivity of MAO B for L-deprenyl. Prior treatment with unlabeled L-deprenyl prevented retention of L-[^{11}C]deprenyl. Thus, suicide enzyme inactivators labeled with positron emitters can be used to quantitate the distribution and kinetic characteristics of MAO in human brain structures.

MONOAMINE OXIDASE (MAO) (E.C. 1.4.3.4) is responsible for the oxidative deamination of endogenous neurotransmitter amines as well as amines from exogenous sources. It exists in two forms, MAO A and MAO B, which are identified by their inhibitor sensitivity and by their substrate selectivity (*1*). Both forms may be important for neurotransmitter regulation, and fluctuations in functional MAO activity may be associated with human diseases such as Parkinson's disease, depression, and certain psychiatric disorders (*2*). A number of MAO inhibitors are used as antidepressant drugs (*3*); L-deprenyl, an inhibitor of MAO B, is used to treat Parkinson's disease (*4*), and brain MAO B plays a key role in 1-methyl-4-phenyl-1,2,3,6-tetrahydropyridine (MPTP)–induced parkinsonism (*5*). Speculation as to the relation of MAO activity to human disease has been based on the measurement of platelet MAO activity or on the analysis of postmortem human brain samples. However, platelet MAO is only MAO B (*6*), and, although the platelet enzyme is probably a genetic marker for serotonergic mechanisms in the brain (*7*), direct attempts to correlate platelet and brain MAO B have failed (*8*). Furthermore, even the process of isolation of MAO from its native environment within a tissue for measurement in vitro may change some properties of the enzyme (*9, 10*).

A major milestone in the study of MAO has been the design and synthesis of the highly selective, mechanism-based inhibitors clorgyline (*N*-[3-(2,4-dichlorophenoxy)propyl]-*N*-methyl-2-propynylamine) (*11*) and L-deprenyl [(−)-*N*,α-dimethyl-*N*-2-propynylphenethylamine] (*12*), which irreversibly inhibit MAO A and MAO B, respectively, by binding covalently to the enzyme itself (*13*), a process frequently referred to as "suicide enzyme inactivation" (*14*).

We have explored the feasibility of using ^{11}C-labeled clorgyline and L-deprenyl for mapping functional MAO in brain directly and noninvasively by using the covalent bond formation between labeled inhibitor and enzyme to label the enzyme in a selective and irreversible manner. The regional

J. S. Fowler, R. R. MacGregor, A. P. Wolf, C. D. Arnett, S. L. Dewey, D. Schlyer, D. Christman, J. Logan, M. Smith, H. Sachs, Brookhaven National Laboratory, Upton, NY 11973.
S. M. Aquilonius, P. Bjurling, C. Halldin, P. Hartvig, K. L. Leenders, H. Lundqvist, L. Oreland, C.-G. Stålnacke, B. Långström, University of Uppsala, Uppsala, Sweden.