

gets may provide a means of regulating the size of arbors without affecting their laminar specificity, thereby providing independent control over quantitative and qualitative aspects of connectivity. Because cadherins (10, 11), VVARs (27), and neurotrophins (8, 26) are all expressed in numerous laminated portions of the vertebrate brain, molecular mechanisms elucidated in tectum may regulate connectivity elsewhere as well.

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- The right eye was exposed, and a hole was made with a tungsten needle at a temporal-dorsal position. Dil (Molecular Probes) was then injected through the hole with a microelectrode. One day later, embryos were killed, staged, and fixed in 4% paraformaldehyde. Vibratome sections (90 μm) were counterstained with Hoechst 33342.
- Digital images were analyzed with IP Lab Spectrum, version 2.5.7 (Signal Analysis, Vienna, VA). Laminar boundaries were determined by staining with Hoechst 33342. The increased density in BDNF-treated tecta could reflect either a greater number of retinal axons or a greater degree of arborization. We could not distinguish these alternatives in vivo, but we favor increased arborization on the basis of the in vitro results.
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Stochastic Dynamics and Deterministic Skeletons: Population Behavior of Dungeness Crab

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Ecologists have fiercely debated for many decades whether populations are self-regulated by density-dependent biological mechanisms or are controlled by exogenous environmental forces. Here, a stochastic mechanistic model is used to show that the interaction of these two forces can explain observed large fluctuations in Dungeness crab (*Cancer magister*) numbers. Relatively small environmental perturbations interact with realistic nonlinear (density dependent) biological mechanisms, to produce dynamics that are similar to observations. This finding has implications throughout population biology, suggesting both that the study of deterministic density-dependent models is highly problematic and that stochastic models must include biologically relevant nonlinear mechanisms.

Dungeness crab life-history features are well known (1–4) and have been the basis for many mechanistic models of its population behavior (5–8). Females extrude up to 2 million eggs in the fall. After hatching in winter and pelagic dispersal of larvae in

spring, juvenile crabs settle near shore in late spring and early summer. Reproduction is delayed until crabs reach about 100-mm carapace width (about 2 to 3 years of age). Adults reproduce once per year and may do so repeatedly. Fecundity declines with age and is related to molting, with molting probability dropping precipitously at older ages. Male and female survivorship declines with age. Males become legally vulnerable to harvest at 159-mm carapace width (about 4 years of age). Dungeness crab juveniles are cannibalized by adults and other juveniles.

Data for this study consist of yearly catch records of males (in kilograms), spanning 42 years (1951 to 1992), at eight locations from California, Oregon, and Washington

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(9). These time-series records show large amplitude fluctuations with a cycle period of about 10 years (5, 6, 10). There is gen-

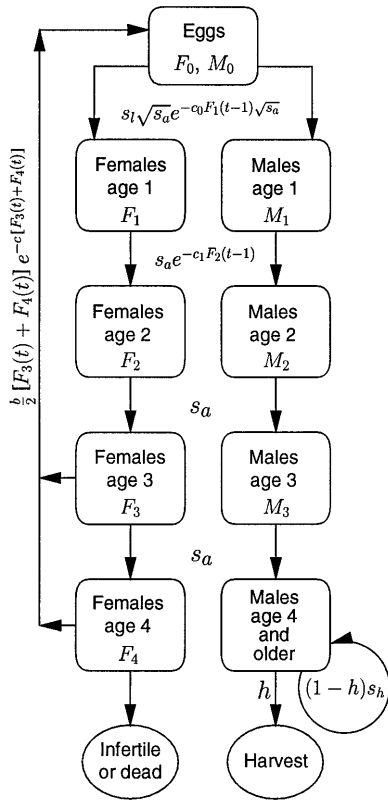


Fig. 1. Deterministic model skeleton for Dungeness crab. The model clock starts in December (many models in the literature start in May) with the production of male and female eggs, $M_0(t)$ and $F_0(t)$. We assume that density-dependent production of eggs by 3- and 4-year-old females, numbered n , is given by the Ricker formulation (34), bne^{-cn} (Eq. 6). Density-independent fecundity, b , is fixed at 2 million eggs, the largest biologically reasonable value (35), and c controls the intensity of density dependence. We assume a planktonic larval phase (survival, s) and a young-of-the-year phase during the first year (survival, $\sqrt{s_a}$). Survival of young-of-the-year depends on the density of 1-year-olds (cannibalism coefficient, c_0), $e^{-c_0F_1(t-1)\sqrt{s_a}}$ (Eq. 5). Survival of 1-year-olds depends on the density of 2-year-olds (cannibalism coefficient, c_1), $e^{-c_1F_2(t-1)}$ (Eq. 4). The cannibalism terms are general and can represent any process where the survival of one class is dependent on the density of another class. Density-independent survival of 1-, 2-, and 3-year-olds is s_a . Before age 4 there is no difference in male and female numbers. One-, 2-, and 3-year-old males are denoted $M_1(t)$, $M_2(t)$, and $M_3(t)$. One-, 2-, 3-, and 4-year-old females are denoted $F_1(t)$, $F_2(t)$, $F_3(t)$, and $F_4(t)$. Reproduction begins at age 3, and females beyond age 4 are excluded from the model because of their sharply reduced fecundity (4). Male vulnerability to harvest begins at age 4 (on the basis of the conventional clock in other studies, males are vulnerable to harvest at age 3.5), and males remain vulnerable to harvest [harvest rate, h (36)] and natural mortality forever (survival, s_h).

eral agreement that these fluctuations in catch records reflect actual changes in abundance of Dungeness crab and not just changes in fishing effort (1, 3, 11).

The potential for exogenous influences on this system has been studied. Wind-driven surface currents (3, 12) and ocean temperature (3, 13) are the environmental variables best correlated with catch. Field studies have shown that in some locations year-to-year variability in settlement of larvae depends on the number of relaxations in upwelling winds each year (14). In addition, laboratory culture of eggs at higher temperatures increases egg mortality (14).

Population models may be mechanistic

(15, 16) or statistical (17) or intermediate (18). We use biological knowledge and assumptions about multivariate noise structure to construct a mechanistic model (Fig. 1). Although this is a spatially extended population (19) connected by pelagic dispersal of larvae, we assume that dynamics are local and may be modeled by a density-dependent age-structured model (15, 16) with stochastic forcing to include the impact of random environmental processes (15-17, 20, 21).

The approach we use (15, 16) incorporates the possibility that the effect of exogenous environmental forces is similar for different age classes (22). With this assump-

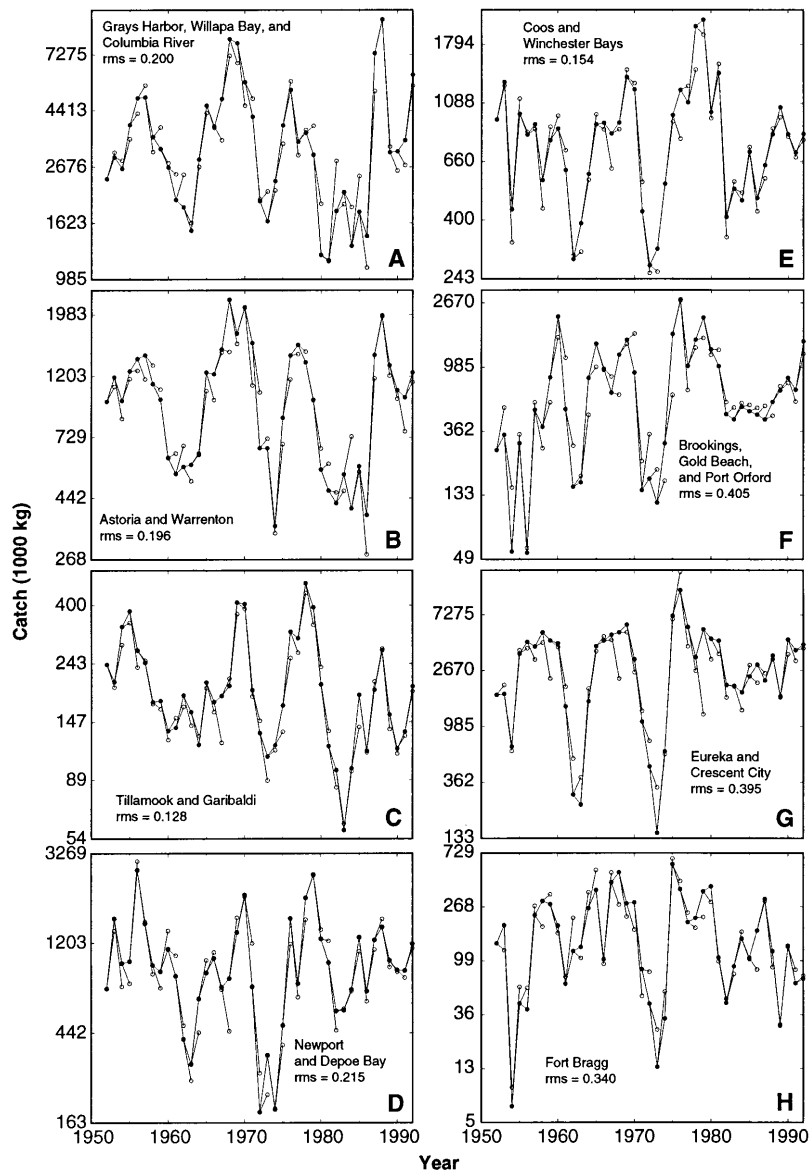


Fig. 2. One-year-ahead model predictions (○) and Dungeness crab catch data (●) for ports in Washington, Oregon, and California (ports run north to south) (A to H). Differences between model prediction and catch provide estimates of environmental perturbations. Estimated environmental perturbations are much smaller than the amplitude of fluctuations in crab catch. Initial conditions for model dynamics will be provided by the authors upon request.

tion, relative perturbations on each age class are treated as free parameters, ρ_1 , ρ_2 , ρ_3 , and ρ_4 , for age classes 1 to 4, respectively

(23). Stochasticity is assumed to be additive on a logarithmic scale that corresponds to environmental fluctuations (24). This leads

to the stochastic model,

$$\sigma(t) = \ln[\text{catch}(t)] - \ln \left\{ h \left[M_3(t-1)s_a + \frac{\text{catch}(t-1)}{h} (1-h)s_h \right] \right\} \quad (1)$$

$$F_4(t) = F_3(t-1)s_a e^{\sigma(t)} \quad (2)$$

$$M_3(t) = F_3(t) = F_2(t-1)s_a e^{\sigma(t)\frac{\rho_3}{\rho_4}} \quad (3)$$

$$M_2(t) = F_2(t) = F_1(t-1)s_a e^{-c_1 F_2(t-1) + \sigma(t)\frac{\rho_2}{\rho_4}} \quad (4)$$

$$M_1(t) = F_1(t)$$

$$= F_0(t-1)s_l \sqrt{s_a} e^{-c_0 F_1(t-1)} \sqrt{s_a + \sigma(t)\frac{\rho_1}{\rho_4}} \quad (5)$$

$$M_0(t) = F_0(t)$$

$$= b/2 [F_3(t) + F_4(t)] e^{-c[F_3(t) + F_4(t)]} \quad (6)$$

Environmental perturbations, $\sigma(t)$, are estimated by comparing the predicted catch, $h[M_3(t-1)s_a + (\text{catch}(t-1)/h)(1-h)s_h]$, with the observed catch, $\text{catch}(t)$, in year t (Eq. 1). The deterministic model skeleton (25) (Eqs. 2 to 6 without stochasticity) is defined in Fig. 1. We fit the model to 42 years of highly variable (26) time-series data from eight locations (Fig. 2) by minimizing the square root of the mean square perturbation, rms (27). Model residuals are assumed to be due to environmental stochasticity (15, 16, 20), and the measurement error is assumed small enough that it can be ignored.

Extremely good model fits to the Dungeness crab time-series data (Fig. 2) indicate that the assumed biological mechanisms are able to produce dynamics consistent with empirical observations. Estimated parameter values (Table 1) are all biologically reasonable and consistent across locations, which provides further support for the model. In contrast, the exogenous forcing, the process errors as determined by the fitting process, do vary from site to site. Estimated harvest rates are uniformly high for all fits, consistent with the broad consensus that harvest in this fishery is intense (1–3, 6, 7, 28). Furthermore, the model is able to pro-

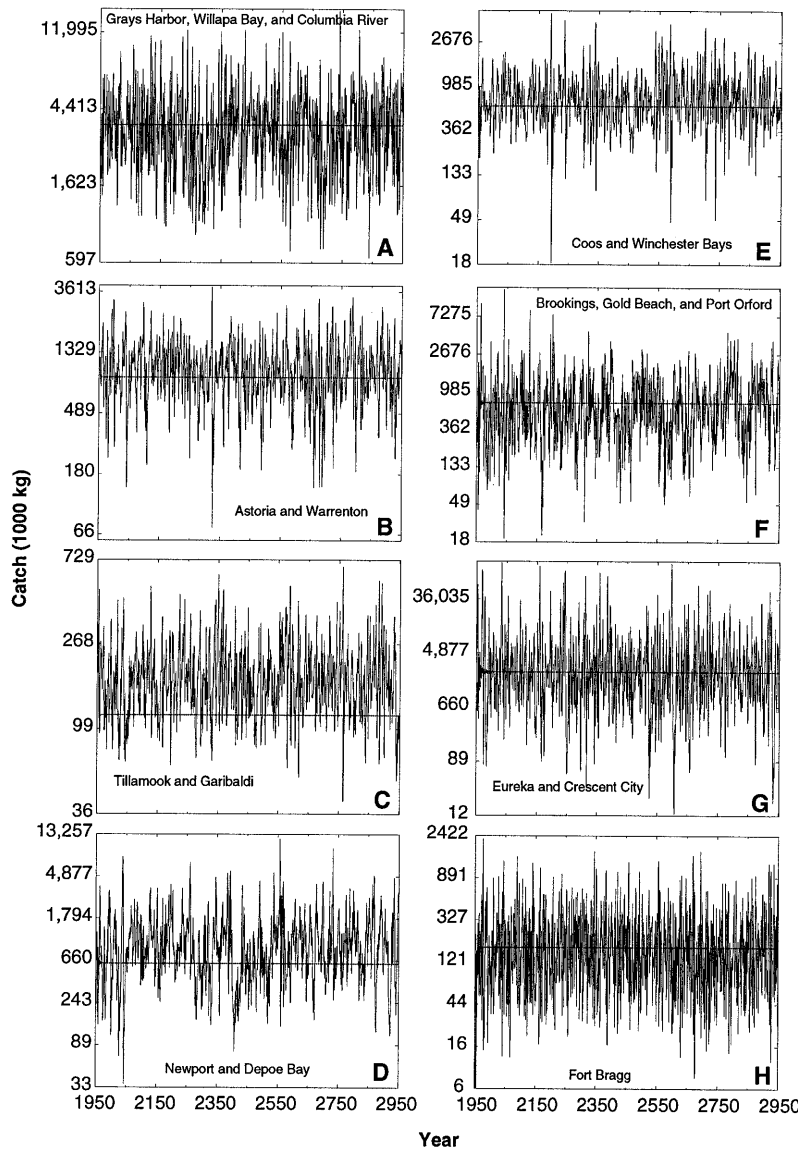


Fig. 3. Simulated stochastic model dynamics for 1000 years. Simulations use parameter values that provided the best fit to observations and resampled perturbations from the estimated distribution of environmental perturbations, $\sigma(t)$. In all cases, the stochastic dynamics are highly variable. The heavy black line represents the deterministic model dynamics (equilibrium). Both the deterministic and stochastic dynamics start from the same initial conditions.

Table 1. Statistics for Dungeness crab model. s_l , larval survival rate; s_a , juvenile and adult survival rate; s_h , harvestable male survival rate; c , coefficient of density-dependent fecundity; c_0 and c_1 , cannibalism coefficients; ρ_1/ρ_4 , ρ_2/ρ_4 , and ρ_3/ρ_4 , relative perturbations (compared to age 4) on age classes 1, 2, and 3; and h , harvest rate. Goodness of model fit is measured by rms.

Location	$\ln(s_l)$	s_a	s_h	$\ln(c)$	$\ln(c_0)$	$\ln(c_1)$	ρ_1/ρ_4	ρ_2/ρ_4	ρ_3/ρ_4	h	rms
Grays Harbor, Willapa Bay, and Columbia River	-13.3	0.95	0.46	-16.6	-18.9	-24.4	-0.82	1.01	2.02	0.91	0.200
Astoria and Warrenton	-11.4	0.50	0.81	-15.6	-25.6	-30.4	-0.032	3.26	1.01	0.75	0.196
Tillamook and Garibaldi	-12.7	0.71	0.68	-13.8	-17.8	-16.1	1.48	1.07	0.54	0.61	0.128
Newport and Depoe Bay	-12.9	0.70	0.31	-16.3	-19.6	-16.5	1.32	0.94	1.29	0.78	0.215
Coos and Winchester Bays	-11.4	0.48	0.64	-15.3	-19.2	-20.5	1.12	1.09	1.46	0.95	0.154
Brookings, Gold Beach, and Port Orford	-12.9	0.90	0.37	-16.0	-15.3	-16.1	-0.17	1.08	1.42	0.92	0.405
Eureka and Crescent City	-12.0	0.96	0.63	-15.9	-17.9	-18.3	-4.71	-0.23	2.59	0.43	0.395
Fort Bragg	-12.2	0.60	0.32	-14.2	-17.2	-21.9	-0.95	-0.33	0.46	0.85	0.340

duce dynamics consistent with the highly variable data at eight different locations, spread over 1000 km of coast, which suggests the model structure is robustly capturing essential population mechanisms (29). In contrast, in all cases the best fitting parameter values for the underlying deterministic skeleton produce equilibrium in the absence of environmental perturbations. That such erratic time-series data (26) are generated by density-dependent mechanisms that not only are not chaotic, but in almost all cases produce a strongly stable equilibrium in the absence of exogenous stochasticity, is surprising. Additionally, even though the stochastic version of the model produces highly variable dynamics, the dynamics are not chaotic (30).

In six of the eight time series of residuals, some oscillatory structure remained (31). To determine whether the highly variable model dynamics were an artifact of a particular sequence of random perturbations, we simulated model dynamics by resampling from the estimated distribution of perturbations, $\sigma(t)$ (Fig. 3), and found no difference in dynamics as measured by the variability of the dynamics or by examining the fourier transform of the dynamics. Simulations with decreased variance in $\sigma(t)$ produced the same qualitative behavior (that is, highly variable dynamics). Larger values for the residuals (measured by rms in Table 1) at southern locations are consistent with the observed increase in oceanographic variability at these southern locations. To determine whether the highly variable model behavior is an artifact of particular parameter values, we simulated model dynamics by resampling in a neighborhood of s_l and s_a (32). In all cases, model dynamics had coefficients of variation comparable to or larger than those obtained with parameter values providing the best fit.

We have shown that relatively small environmental perturbations can markedly alter the dynamics of deterministic biological mechanisms, producing very large fluctuations in crab numbers (Fig. 2). These results imply that Dungeness crab population dynamics are produced by inexorably intertwined endogenous and exogenous forces. This conclusion has consequences throughout population biology and shows both that the study of deterministic density-dependent models is highly problematic and that stochastic models must include biologically relevant nonlinear mechanisms.

Traditional linear statistical approaches seek correlations between random environmental variables (for example, sea surface temperature and upwelling) and subsequent population numbers. Such statistical correlations for Dungeness crab

have detected possible forcing variables (1, 12, 13) that have been further scrutinized by examining both potential nonlinear effects of the environmental variables and density-dependent recruitment (8). With the nonlinear methods of this study, we have shown that relatively small random perturbations, uncorrelated from year to year, may lead to large fluctuations with a multiyear period, which calls into question the value of using linear correlation analysis alone to understand population dynamics. That random perturbations can have a marked effect on persistence has been previously noted (33) without discussion of the effects on dynamics.

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22. Potentially each age class is affected by environmental perturbations that do not affect other age classes and by environmental perturbations that affect all age classes. Because we have only univariate observations (catch records for legal size Dungeness crab males), we can estimate the perturbations on the observed (harvested) class of crabs and the relative perturbations on other age

classes—perturbations to all age classes are exactly correlated, but of varying intensities. To estimate perturbations unique to other classes would require multivariate observations.

23. To prevent arbitrarily large perturbations on unobserved age classes (because we observe only one class), we use the following conditions, $\rho_1^2 + \rho_2^2 + \rho_3^2 + \rho_4^2 = 1$ and $-1 \leq \rho_i \leq 1$, $i = 1$ to 4. Because of these constraints there are only three independent ρ 's.
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26. Catch records for Dungeness crab do not vary smoothly and show extreme year-to-year variation. From north to south, the coefficients of variation are 0.61, 0.49, 0.47, 0.57, 0.52, 0.85, 0.66, and 0.77 for the eight time series. The most variable time series change over almost two orders of magnitude [see (10) for details].
- 27.

$$\text{rms} = \sqrt{\frac{\sum_{t=2}^{42} \sigma(t)^2}{41}}$$

A very complex bifurcation structure for models of this type (10) leads to a difficult fitting (optimization) problem, which we have solved with a novel approach. Our method of negotiating the goodness of fit surface is based on a hybrid of simulated annealing [W. L. Goffe, G. D. Ferrier, J. Rogers, *J. Econometrics* **60**, 65 (1994)], Powell's direction method [W. H. Press, S. A. Teukolsky, W. T. Vetterling, B. P. Flannery, *Numerical Recipes in C: the Art of Scientific Computing* (Cambridge Univ. Press, Cambridge, ed. 2, 1992)], and a sophisticated step-size adjuster that we designed.

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29. We cannot test all alternative models, which is a drawback of nonlinear versus linear modeling. We do strongly suspect that the model framework is not critical to the main result.
30. We calculated largest Lyapunov exponents for the stochastic model dynamics on the basis of expansion and contraction of an arbitrary perturbation vector using a Jacobian method. At successive locations on the stochastic attractor, the Jacobian was applied to the same renormalized perturbation vector. Chaotic attractors have a direction along which this vector grows (that is, a positive largest Lyapunov exponent). The largest Lyapunov exponents for the best-fitting model at each location are as follows: -0.43, Grays Harbor, Willapa Bay, and Columbia River; -0.39, Astoria and Warrenton; -0.43, Tillamook and Garibaldi; -0.31, Newport and Depoe Bay; -0.36, Coos and Winchester Bays; -0.26, Brookings, Gold Beach, and Port Orford; -0.057, Eureka and Crescent City; -0.30, Fort Bragg.
31. Oceanographic variables in this system exhibit a pronounced correlation structure (that is, El Niño). Assuming that oceanographic variables (for example, sea temperature) that impact biological processes (for example, development) are correlated, a model based only on biology should not be able to remove all of the determinism from the data. In fact, if the model left behind pure white noise, this would imply that biological mechanisms were accounting for the correlation structure of physical variables.
32. For each location we characterized simulated model dynamics with the coefficient of variation over the range of estimated values for s_l and s_a . For example, in Table 1, s_a ranges between 0.48 and 0.96 over the eight locations. In this range for s_a , all models had simulated dynamics with very high variability. True confidence intervals (by bootstrapping) for this 10-parameter highly nonlinear model would require thousands of days of computer time, which is clearly not feasible. So we confirmed the qualitative behavior over a reasonable range of a

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35. b and s_j are displayed separately for biological clarity, but b could be absorbed into s_j without consequence.
36. We assume harvest rate, h , is a simple proportion of the legally harvestable males. More realistic would be some functional form for h that depends on the density of harvestable males. Effort data were not used because there does not seem to be any reliable way to deal with long-term changes in effort.
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