Oikos

OIK-05892

Kimbro, D. L., White, J. W. and Grosholz, E. D. 2018. The dynamics of open populations: integration of top–down, bottom–up and supply-side influences on intertidal oysters. – Oikos doi: 10.1111/oik.05892

Appendix 1

Physical properties and primary production in Tomales Bay

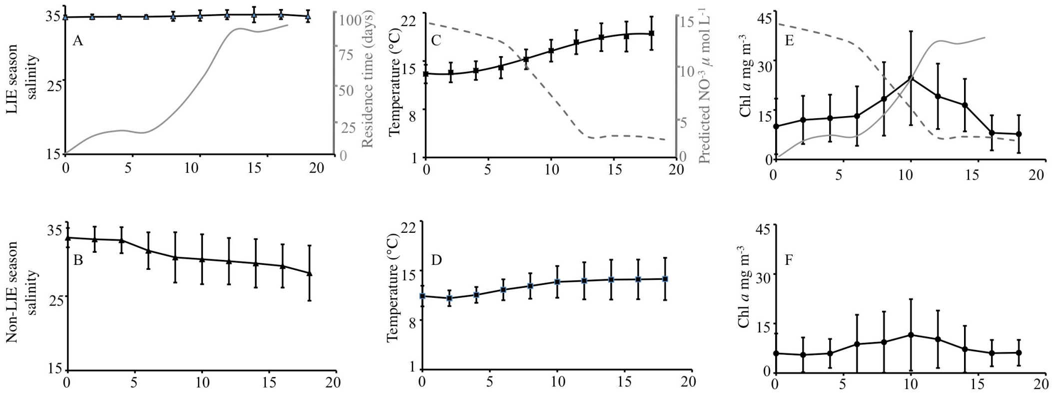

Figure A1. Between 2004–2008, we monitored the spatial structure of physical properties and primary production throughout Tomales Bay. Panels (A, C, E) represent conditions during the dry (i.e. low-inflow estuary; LIE) season and panels (B, D, F) represent conditions during the wet (non-LIE) season. In all panels, the horizontal axis refers to distance (km) from the ocean. Panels (A–) illustrate salinity structure (black triangles, mean + SD) and estimated residence times (grey line); (C–D) temperature (black squares, mean + SD) and estimated nitrate concentration (grey dashed line); and (E–F) phytoplankton biomass (Chl a*,* black circles, mean + SD) across sites. Panel E includes predicted residence times (grey line) and nitrate concentrations (grey dashed line) to illustrate how they interact to influence chlorophyll *a* concentration in the middle of the bay. Reprinted with permission from *Limnology and Oceanography*. In this publication (Kimbro et al. 2000b), there was strong support for the hypothesis that the spatial structure of chlorophyll a controlled the growth of oysters and thus appears to be the bottom-up control in this system.

Appendix 2

Summary of field methods used to quantify the abundance and length of oysters throughout Tomales Bay

We conducted annual intertidal surveys of oyster population density and size structure at eight study sites in Tomales Bay. These surveys occurred from 2004–2006 and in 2009. Because of the strong salinity and residence time gradients in Tomales Bay, the sites consisted of 4 pairs of sites on the east and west sides of the bay, spaced equidistantly along the main (north–south) axis of the bay.

We divided each site into three equally sized sections in the N-S alongshore dimension (i.e. north, center and south). Each of the three sections was then bisected in the E-W, cross-shore dimension to create three high- and three low-intertidal oyster zones per site. In the center of each intertidal zone, a 15 m transect paralleling the waterline was established to sample oysters. To improve dispersion of sampling effort, we further divided each 15 m transect into 7.5 m sub-transects and randomly selected 3 rocks along each sub-transect yielding 6 rocks per transect (6 rocks × 6 transects/site = 36 per site).

For each rock, we centered a 0.10 × 0.10 m quadrat on the top, bottom and side surfaces and then counted and measured all living oysters. Using the three quadrats as sub-samples, we estimated mean density and mean length of living oysters for each rock. These surveys were conducted during the spring of each year so that the population was sampled before the annual summer recruitment (August–October). Thus, these data describe oysters that were ≥ 9 months old.

Appendix 3

Site-specific growth trajectories of oysters in Tomales Bay

In 2005, we tested whether the growth of individual oysters varied among locations within Tomales Bay. For this experiment, we spawned adult oysters under controlled conditions in the Bodega Marine Laboratory (15 km north of Tomales Bay). The resulting larvae were allowed to settle onto sanded PVC tiles (10 × 10 cm) and subsequently out-planted in the field.

Because oysters naturally recruit to adult populations during late summer months (Baker 1995), we randomly assigned and out-planted eight tiles at each of our seven sites (n = 56 total) in August 2005. At each site we deployed tiles within the middle of the oyster's intertidal distribution (–0.2 m MLLW). The tiles were stabilized along transects by fastening them to concrete bricks and by attaching the bricks to 0.5 m steel rebar poles that had been hammered into the ground. The brick-rebar attachment resulted in tile surfaces that were perpendicular to the sediment surface.

Before deploying tiles, we marked five oysters per tile with small numbered tags (Floy Tags Inc., FTF-69 Fingerling Tag-Pennant) and photographed each tile. All tiles were photographed monthly thereafter until August 2006. From August 2006 to December 2007, tiles were photographed every three months. Collectively, these data describe site-specific growth trajectories of oysters over 30 months (Fig. A4).

To represent growth dynamics in the model, we fit von Bertalanffy growth curves to the data from each site, yielding a relationship between age, *a*, and length, *L*:

$$L(a) = L_\infty\left[1 - e^{-k(a-a_0)}\right]$$

with parameters L_∞, the asymptotic maximum length, k, the growth rate, and a_0, the effective age at size zero. Fits were obtained by minimizing the root mean square error using function fmincon in Matlab 9.2. Model fits for each site are shown in Fig. A4, and parameter values are given in Table A4. For fitting purposes, we estimated L_0, the length at age zero, rather than a_0; these are related by the equation $L_0 = L_\infty[1 - e^{-ka_0}]$.

Table A3. Parameters of the von Bertalanffy growth curve fit to data for each study site. CV (coefficient of variation) was estimated directly from the data as the average (over all ages) of the standard deviation of length of replicates at each age divided by the average length at each age; it is dimensionless.

Site	$\boldsymbol{L_\infty}$ (cm)	$\boldsymbol{L_0}$ (cm)	k (year^{-1})	CV
W2	83.28	5.79×10^{-7}	0.68	0.21
W3	65.09	0.13	0.64	0.13
W4	47.70	1.25×10^{-8}	1.26	0.13
E1	75.14	0.20	0.30	0.13
E2	67.11	6.79×10^{-8}	0.97	0.12
E3	52.53	1.85×10^{-7}	1.29	0.13
E4	44.39	0.13	0.91	0.15

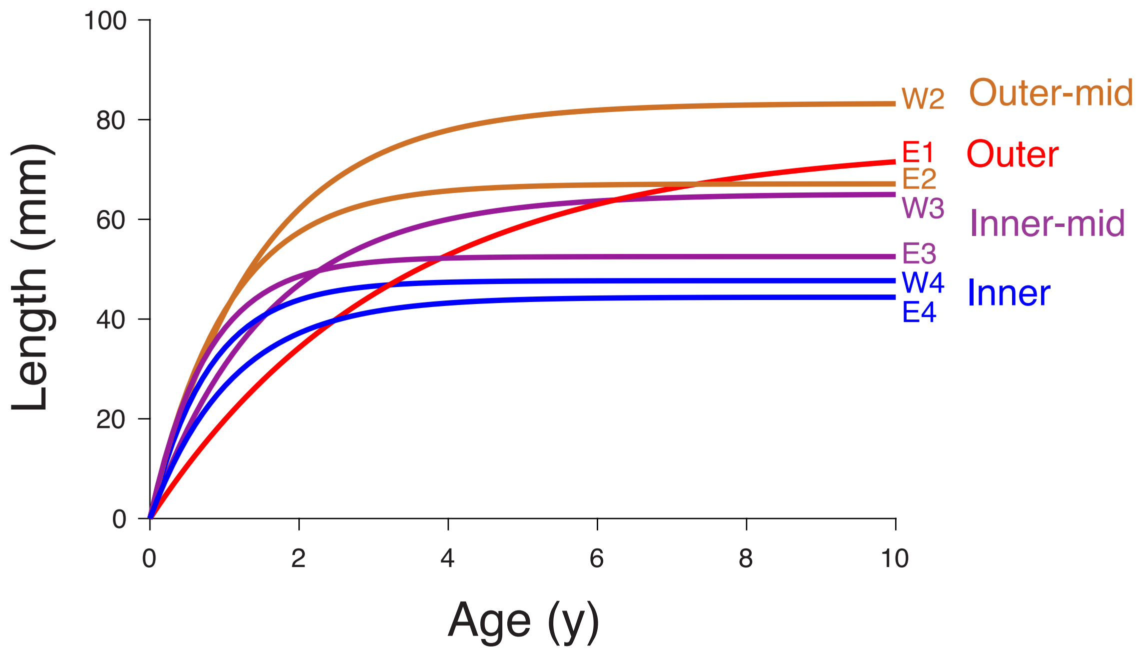

Figure A3. von Bertalanffy growth curve fits for each site. Curves are labelled with the corresponding site name, and colors indicate spatial position within Tomales Bay.

Appendix 4

State-space integral projection model description

The state-space integral projection model (SSIPM) consists of a process model and an observation model. We describe each of those, plus the Markov chain – Monte Carlo model-fitting approach, in turn.

Process model

The process model is a linear model in discrete time, with a time step of one year, which is intended to match the annual schedule of population surveys in Tomales Bay. The process model describes the abundance of oysters of size x at time $t + 1$ and site i, $N_i(x,i,t+1)$, as a function of survival, larval recruitment, and random variability (process error):

$$N(x,i,t+1) = \int_{\Omega} K(x,y,i,t)N(y,i,t+1)\,dy + R(i,t)\rho(x) + v(x,i,t). \quad \text{(E1)}$$

The first term on the right-hand side (RHS) of this equation is the typical IPM formulation. The 'kernel', $K(x,y,i,t)$, describes the probability density of an oyster of size y in time t surviving and growing to size x in one time step (unlike other IPM formulations, there were no terms for reproduction in K, as all recruitment to a site was assumed to be externally forced). Both K and N are continuous distributions, and their product is integrated with respect to size over the entire range of possible oyster sizes, Ω. The second term on the RHS describes larval recruitment as the product of the total number of recruits $R(i,t)$ and the recruit size distribution $\rho(x)$. This corresponds to an annual input of recruits from an external source. Finally, the third term on the RHS represents process error affecting the abundance of oysters of size x.

The probability density $K(x,y,i,t)$ is the product of the probability density of growth from y to x in one time step, multiplied by the probability of survival of an individual of size y during one time step. The growth probability density was modeled as a normal probability distribution with mean given by the value $L_\infty - (L_\infty - L_y)e^{-k}$, which is the expected size of an individual at time t+1 for an individual that is size y at time t; the parameters k and L_∞ were taken from the von Bertalanffy relationship estimated from field data (Supplementary material Appendix 4). In model scenarios with spatially variable growth, we used the von Bertalanffy relationship specific to site i; in the constant growth scenarios we used a von Bertalanffy relationship averaged across all seven sites. The standard deviation of the normal distribution was the mean multiplied by the coefficient of variation in growth (Supplementary material Appendix 4).

The survival probability was modeled as $e^{-M_{y,i,t}}$, where the instantaneous mortality rate M could vary across time t or space i and was different for adult and juvenile sizes. The adult/juvenile size threshold was modeled as a cumulative normal probability distribution with respect to size,

$\pi(y)$, with mean and standard deviation chosen as the mean size of six-month-old oyster recruits and two times the standard deviation of size of recruits of that age, respectively (both values from Supplementary material Appendix 4). This was intended to ensure that new age-0 oysters observed in the spring census (which would have settled from the plankton the previous fall) would experience the juvenile mortality rate. In the kernel, the value of $\pi(y)$ determined the relative exposure to juvenile and adult mortality rates for individuals of size y:

$$M_{y,i,t} = \pi(y)M_{A,i,t} + [1 - \pi(y)]M_{A,i,t}$$

where $M_{A,i,t}$ and $M_{J,i,t}$ are the adult and juvenile mortality rates at site i, time t, respectively. The parameters of $\pi(y)$ were either constant over space or varied by site, depending on whether the model included spatial variability in growth.

Spatial variation in mortality followed three different forms: constant, linear gradient, and quadratic gradient; the latter two a function of d_i, the distance of site i from the mouth of Tomales Bay (in km). The functional forms for adult mortality were

$$M_{A,y,i,t} = \exp[m_{A,t}] \qquad \text{[constant]}$$

$$M_{A,y,i,t} = \exp[m_{\text{Int},A,t} + m_{\text{grad},A} d_i] \qquad \text{[linear gradient]}$$

$$M_{A,y,i,t} = \exp\left[m_{\text{Int},A,t} + m_{\text{unim},A}\left(d_i - m_{\text{offset},A}\right)^2\right] \qquad \text{[quadratic gradient]}$$

where the m terms are fitted parameters. The value of $m_{\text{offset},A}$ corresponds to the distance at which M_A reaches a maximum or minimum. Using the exponential function essentially allowed us to have the m parameters have a normal posterior distribution without creating biologically impossible negative mortality rates, which simplified parameter estimation.

Temporal variation in M_A was achieved by estimating different values of M_A for each model year (and thus different values of $m_{A,t}$, which serves as a baseline mortality rate). In models without temporal variation, m_A is constant over time.

Juvenile mortality, $M_{J,i,t}$, was modeled in the same was as adult mortality, substituting J for A subscripts in all of the preceding equations.

Recruitment variability (i.e. $R(i,t)$) was modeled using the same approach as for mortality, with the same three functions of spatial variability (constant, linear, quadratic) and either annual variability or not. Like M, $R(i,t)$ was also modeled as an exponential function to ensure it was always positive. The recruit size function ρ was modeled as a normal probability distribution with mean and standard deviation equivalent to the mean and standard deviation of six-month-old recruits at each site (if there was growth variability) or across all sites (if no growth variability). This is based on the same logic used to create $\pi(y)$.

Finally, the process error term $v(x,i,t)$ represents variations in population variability due to random chance or other unaccounted-for factors. $v(x,i,t)$ is normally distributed with mean 0 and standard deviation σ_v and is assumed to represent small variations about the mean survival of oysters of each size from year to year.

Observation model and particle filter

The basic premise of a state-space model is that there is an underlying process model representing the true dynamics of the system, $\boldsymbol{N}(t)$, but that the true state is hidden and only observed imperfectly as data, $\boldsymbol{X}(t)$, (t = 1, 2, … T). The hidden state evolves over time as a Markov process, with the value at t, $\boldsymbol{N}(t)$, depending on the state at t–1 and a process error term, ν(t): $\boldsymbol{N}(t) = G(\boldsymbol{N}(t-1), \nu(t-1))$. Similarly, the observed data at t depends on the hidden state at that time and a measurement error term, ε(t): $\boldsymbol{X}(t) = H(\boldsymbol{N}(t), \varepsilon(t))$. A state-space model uses a filter to estimate the true hidden states $\boldsymbol{N}(t)$ given the observations $\boldsymbol{X}(t)$, and possibly also to estimate unknown parameters of the functions G and H.

In our case $\boldsymbol{N}(t)$ is the true abundance and size structure of oysters at t and $\boldsymbol{X}(t)$ are the visual census observations. The function G is the IPM, including process error, as described in the previous section.

A common approach to approximating $\boldsymbol{N}(t)$ given the observations $\boldsymbol{X}(t)$ is the Kalman filter (Kalman 1960, Meinhold and Singpurwalla 1983, Dennis et al. 2006), which provides an exact solution to the state-space problem for the special case of a linear model and normally distributed error terms. We used the alternative, less restrictive approach of a particle filter (Gordon et al. 1993, Knape and de Valpine 2012). Knape and de Valpine (2012) provide a thorough description of the particle filter procedure, but the basic approach is as follows: 1) For t = 1, simulate q independent random vectors $\boldsymbol{N}(t)_i$ (i = 1, 2, 3, …. q) from a distribution around $\boldsymbol{N}(t)$. This set of vectors $\boldsymbol{N}(t)_i$ is the particles, and they represent the distribution of possible true hidden states. We generated this distribution by adding q different realizations of the process error, ν, added to the population. 2) Calculate weights $w_{t,i}$ for each particle that indicate how well each particle matches the corresponding observed data $\boldsymbol{X}(t)$. The weight is essentially a likelihood: $w_{i,t} = L(\boldsymbol{X}(t)|\boldsymbol{N}(t))$. 3) Resample the particles with replacement according to their relative weights $w_{t,i}/\sum_{i=1}^{q} w_{t,i}$. 4) Advance the model to obtain a new set of particles: $\boldsymbol{N}(t+1)_i = G(\boldsymbol{N}(t)_i, \nu(t))$. Steps 1-4 are then repeated for each step of the time series. At each step, the resampled particles, $\boldsymbol{N}(t)_i'$, represent the approximate distribution of the hidden state at t given the observations up to that point, $\boldsymbol{X}(1{:}t)$, and the mean of those resampled particles can be taken as a representation of $\boldsymbol{N}(t)$. Helpfully, the weights also approximate the likelihood of the data given the current parameter values, θ:

$$L(X(1{:}T)|\theta) = \prod_{t=1}^{T} 1/q \sum_{i=1}^{q} w_{t,i}$$

In order to start the filter algorithm, it is necessary to specify the true state at $t = 1$. One option is to simply use the stationary distribution of the process model (i.e. the stable size distribution of the deterministic IPM) as a starting point (de Valpine and Hastings 2002). We took this approach, and simulated the initial particles $\boldsymbol{N}(1)_i$ by adding process noise ν to the initial distribution $\boldsymbol{N}(1)$.

The calculation of the particle weights $w_{i,t}$ requires an expression for the likelihood $L(\boldsymbol{X}(t)|\boldsymbol{N}(t))$. The form of the likelihood largely depends on the form of the observational data. Because the survey data were integer count data of individual organisms, they should follow a Poisson distribution. Therefore we modeled a Poisson likelihood expectation $\langle X(x,t)\rangle = \int_{x-h/2}^{x+h/2} H(N(x,t))dx$ for each width-h interval of the integration mesh. No explicit observation uncertainty term is required because the variance equals the mean in the Poisson distribution. To obtain a reliable sample of the empirical size distribution, we pooled all of the quadrats sampled in a given year at a site into a single set of observations. Because the number of quadrats varied from year to year, we let the model population represent the density in a single quadrat, and multiplied the model expectation by the number of quadrats in a sample in order to calculate the likelihood for that date.

In general the accuracy and precision of the particle filter method (i.e. its ability to consistently reproduce correct results) improves if more particles are used. This is because a larger number of particles will provide a better representation of the hidden process state $\boldsymbol{N}(t)$. However, there are diminishing returns and the computational demand increases linearly with the number of particles. We determined the optimal number of particles to simulate by calculating the coefficient of variation (CV) of the likelihood for 100 independent simulations of the IPM for each of a range of values of the number of particles, q (White et al. 2016). The logic of this is that once there are sufficiently many particles, the IPM produces a consistent estimate of the likelihood for the same set of parameter values, which is thus suitable for likelihood-based parameter estimation. Based on this analysis we used $q = 100$ particles in our model.

Parameter estimation using MCMC

Given the high dimensionality of the unknown parameter space and the possibility of a multi-modal likelihood surface, the only practical choice for parameter estimation in our implementation was Markov chain – Monte Carlo (MCMC; as in Knape and de Valpine 2012) using a delayed-rejection one-at-a-time Metropolis–Hastings algorithm (Chib and Greenberg 1995, Green and Mira 2001).

The details of implementing Metropolis-Hastings MCMC are described extensively elsewhere (Brooks et al. 2011). In our implementation, we followed Knape and de Valpine (2012) in using the particle-filter approximation of the likelihood $L(X(1:T)|\theta)$ for the Metropolis–

Hastings step. We updated the candidate parameters $m_{1\text{-}3}$, $R_{t,i}$, and σ_v one at a time. For each parameter the proposal distribution was a normal distributions (except σ_v) centered at the current state of the Markov chain and with a coefficient of variation that decreased geometrically during the delayed-rejection process. For σ_v, we used an inverse gamma proposal distribution with a mean equal to the current parameter state and a shape parameter that decreased geometrically during delayed rejection. MCMC runs were made with 10^4 steps (this number is relatively small because the delayed-rejection procedure allowed rapid mixing of the chain), with the first half of the chain discarded as burn-in. We simulated three chains for each model and checked chains for convergence using the scale reduction factor diagnostic (Gelman and Shirley 2011), then pooled chains to estimate the posterior distribution of each parameter. We used relatively flat, uninformative priors for each parameter.

Model simulations

All model simulations were initialized by starting the population at arbitrary density $\boldsymbol{N}$ and iterate the IPM for 50 time steps with time-invariant recruitment and mortality to obtain the starting size distribution in the year 2000. The model was then iterated in state-space mode from 2000 to 2009, including time-varying parameters if appropriate. For model years in which no data were available (2000–2003 and 2007–2008), it was not possible to calculate weights for the particles in the filter, so all particles were assigned weight $1/q$. This allowed process error to enter the model in those years, but the error was not filtered based on observed data.

References

Brooks, S. A. et al. (eds) 2011. Handbook of Markov chain Monte Carlo. – Taylor and Francis.

Chib, S. and Greenberg, E. 1995. Understanding the Metropolis–Hastings algorithm. – Am. Stat. 49: 22.

de Valpine, P. and Hastings, A. 2002. Fitting population models incorporating process noise and observation error. – Ecol. Monogr. 72: 57–76.

Dennis, B. et al. 2006. Estimating density dependence, process noise and observation error. – Ecol. Monogr. 76: 323–341.

Gelman, A. and Shirley, K. 2011. Inference from simulations and monitoring convergence. – In: Brooks, S. et al., (eds) Handbook of Markov chain Monte Carlo. – Taylor and Francis, pp. 163–174.

Gordon, N. J. et al. 1993. Novel approach to nonlinear/non-Gaussian Bayesian state estimation. – IEE Proc. F 140: 107–113.

Green, P. J. and Mira, A. 2001. Delayed rejection in reversible jump Metropolis–Hastings. –

Biometrika 88: 1035–1053.

Kalman, R. E. 1960. A new approach to linear filtering and prediction problems. – J. Basic Eng. 82: 35–45.

Knape, J. and de Valpine, P. 2012. Fitting complex population models by combining particle filters with Markov chain Monte Carlo. – Ecology 93: 256–263.

Meinhold, R. J. and Singpurwalla, N. D. 1983. Understanding the Kalman filter. – Am. Stat. 37: 123–127.

White, J. W. et al. 2016. Models for adaptive management: methods for fitting state–space integral projection models to time series data. – Ecol. Appl. 26: 2675–2692

Appendix 5

Summary of candidate SSIPM models and model selection results

Contents:

Table 5A: Summary of models and model selection

Table 5B: Summary of most parsimonious model

Figures 5A-5D: Fits of SSIPM to field data for each site and year

Table 5A. Summary of model selection. Each model is described in terms of the type of variability in each of the demographic parameters. Temporal variability in recruitment and mortality and spatial variability in growth could either be constant (‘Con’) or variable (‘Var’). Spatial variability in recruitment and mortality could be constant (‘Con’), a linear gradient (‘Grad’), or a unimodal quadratic function (‘Unim’).

Abbreviations: $\overline{L}$: mean log-likelihood over all post-burn-in MCMC iterations. P_d: effective number of parameters estimated for DIC calculation. ΔDIC: difference in deviation information criterion (DIC) between model *i* and the model with the lowest DIC value. *w*: DIC weight

Model parameters

Model no.	Recruitment		Adult mortality		Juvenile mortality		Growth	$\overline{L}$	P_d	ΔDIC	*w*
	Time	Space	Time	Space	Time	Space	Space				
124	Var	Grad	Con	Unim	Con	Con	Var	-4498.6	5.3006	0	1
72	Var	Unim	Var	Unim	Var	Con	Con	-5086.3	11.493	133.78	8.91E-30
88	Var	Grad	Var	Unim	Var	Grad	Con	-5091.1	11.725	143.56	6.70E-32
70	Var	Grad	Var	Unim	Var	Con	Con	-5091.5	14.451	147.01	1.19E-32
112	Var	Grad	Con	Con	Con	Con	Var	-4614.4	4.2239	230.56	8.60E-51
108	Var	Unim	Var	Unim	Var	Unim	Con	-5142	10.174	243.8	1.15E-53
106	Var	Grad	Var	Unim	Var	Unim	Con	-5145	8.7858	248.46	1.12E-54
64	Var	Grad	Var	Grad	Var	Con	Con	-5200.9	17.753	369.22	6.68E-81
84	Var	Unim	Var	Grad	Var	Grad	Con	-5210.4	17.234	387.61	6.79E-85
100	Var	Grad	Var	Grad	Var	Unim	Con	-5232.3	13.703	427.83	1.25E-93
54	Var	Unim	Con	Unim	Con	Unim	Con	-5237.7	5.9524	430.98	2.59E-94
82	Var	Grad	Var	Grad	Var	Grad	Con	-5243	16.507	452.15	6.56E-99
102	Var	Unim	Var	Grad	Var	Unim	Con	-5273.5	8.4662	505.12	2.06E-110
16	Var	Grad	Con	Unim	Con	Con	Con	-5277	4.3821	507.91	5.11E-111
34	Var	Grad	Con	Unim	Con	Grad	Con	-5277.2	6.3355	510.4	1.47E-111
52	Var	Grad	Con	Unim	Con	Unim	Con	-5289.9	10.868	540.32	4.69E-118
66	Var	Unim	Var	Grad	Var	Con	Con	-5299.4	8.5836	557.08	1.08E-121
12	Var	Unim	Con	Grad	Con	Con	Con	-5317.6	5.2518	590.09	7.30E-129
48	Var	Unim	Con	Grad	Con	Unim	Con	-5319.5	4.5107	593.1	1.62E-129
30	Var	Unim	Con	Grad	Con	Grad	Con	-5321.1	4.8638	596.61	2.80E-130
36	Var	Unim	Con	Unim	Con	Grad	Con	-5321.1	7.0608	598.88	9.01E-131
18	Var	Unim	Con	Unim	Con	Con	Con	-5360.8	5.4642	676.74	1.12E-147
10	Var	Grad	Con	Grad	Con	Con	Con	-5369.4	4.3187	692.73	3.76E-151
6	Var	Unim	Con	Con	Con	Con	Con	-5374.6	3.9979	702.9	2.33E-153

90	Var	Unim	Var	Unim	Var	Grad	Con	-5370.4	14.738	705.22	7.30E-154
24	Var	Unim	Con	Con	Con	Grad	Con	-5376.1	4.3109	706.1	4.70E-154
42	Var	Unim	Con	Con	Con	Unim	Con	-5377.9	7.8017	713.12	1.41E-155
28	Var	Grad	Con	Grad	Con	Grad	Con	-5379.4	13.716	722.06	1.61E-157
46	Var	Grad	Con	Grad	Con	Unim	Con	-5379.8	14.381	723.56	7.60E-158
60	Var	Unim	Var	Con	Var	Con	Con	-5389.7	10.327	739.41	2.75E-161
78	Var	Unim	Var	Con	Var	Grad	Con	-5390.7	8.4925	739.57	2.54E-161
96	Var	Unim	Var	Con	Var	Unim	Con	-5392.9	9.7942	745.27	1.47E-162
68	Var	Con	Var	Unim	Var	Con	Con	-5413.3	11.339	787.51	9.87E-172
104	Var	Con	Var	Unim	Var	Unim	Con	-5413.8	10.818	787.93	8.00E-172
4	Var	Grad	Con	Con	Con	Con	Con	-5439.4	3.8343	832.2	1.95E-181
22	Var	Grad	Con	Con	Con	Grad	Con	-5440.8	4.1158	835.35	4.04E-182
14	Var	Con	Con	Unim	Con	Con	Con	-5441.7	4.5533	837.58	1.32E-182
40	Var	Grad	Con	Con	Con	Unim	Con	-5442.2	4.8489	838.95	6.67E-183
32	Var	Con	Con	Unim	Con	Grad	Con	-5442.8	4.2472	839.52	5.02E-183
50	Var	Con	Con	Unim	Con	Unim	Con	-5444.8	5.8962	845.03	3.19E-184
58	Var	Grad	Var	Con	Var	Con	Con	-5452.7	7.8997	862.87	4.27E-188
76	Var	Grad	Var	Con	Var	Grad	Con	-5454	8.2014	865.8	9.86E-189
94	Var	Grad	Var	Con	Var	Unim	Con	-5456.3	8.3369	870.5	9.40E-190
62	Var	Con	Var	Grad	Var	Con	Con	-5465.2	9.064	889.03	8.90E-194
178	Var	Grad	Var	Unim	Var	Con	Var	-4942	10.78	892.24	1.79E-194
196	Var	Grad	Var	Unim	Var	Grad	Var	-4942.2	10.807	892.74	1.39E-194
198	Var	Unim	Var	Unim	Var	Grad	Var	-4944	11.728	897.24	1.47E-195
214	Var	Grad	Var	Unim	Var	Unim	Var	-4943.9	12.767	898.04	9.84E-196
180	Var	Unim	Var	Unim	Var	Con	Var	-4944.7	13.431	900.27	3.23E-196
98	Var	Con	Var	Grad	Var	Unim	Con	-5473.1	10.862	906.72	1.28E-197
80	Var	Con	Var	Grad	Var	Grad	Con	-5472.9	12.469	907.88	7.18E-198
86	Var	Con	Var	Unim	Var	Grad	Con	-5502.5	11.291	965.9	1.81E-210
216	Var	Unim	Var	Unim	Var	Unim	Var	-4985.3	13.133	981.28	8.27E-214
83	Con	Unim	Var	Grad	Var	Grad	Con	-5523.2	12.602	1008.5	1.02E-219
65	Con	Unim	Var	Grad	Var	Con	Con	-5530.5	6.9846	1017.5	1.13E-221
8	Var	Con	Con	Grad	Con	Con	Con	-5536.6	3.9827	1026.9	1.03E-223
26	Var	Con	Con	Grad	Con	Grad	Con	-5538.2	3.7534	1029.8	2.41E-224
44	Var	Con	Con	Grad	Con	Unim	Con	-5539.9	4.7321	1034.2	2.67E-225
101	Con	Unim	Var	Grad	Var	Unim	Con	-5549.4	7.1722	1055.5	6.33E-230
71	Con	Unim	Var	Unim	Var	Con	Con	-5555.4	7.2901	1067.7	1.42E-232
89	Con	Unim	Var	Unim	Var	Grad	Con	-5556.7	8.021	1071.1	2.59E-233
11	Con	Unim	Con	Grad	Con	Con	Con	-5560.3	1.9425	1072.2	1.50E-233
29	Con	Unim	Con	Grad	Con	Grad	Con	-5561.4	2.645	1075	3.69E-234
107	Con	Unim	Var	Unim	Var	Unim	Con	-5557.9	12.21	1077.7	9.56E-235
47	Con	Unim	Con	Grad	Con	Unim	Con	-5563.4	2.881	1079.2	4.52E-235
17	Con	Unim	Con	Unim	Con	Con	Con	-5571	2.2653	1093.8	3.05E-238
35	Con	Unim	Con	Unim	Con	Grad	Con	-5572.3	4.0837	1098.3	3.22E-239
53	Con	Unim	Con	Unim	Con	Unim	Con	-5573.7	3.4758	1100.4	1.13E-239
210	Var	Unim	Var	Grad	Var	Unim	Var	-5049.1	8.2749	1104	1.86E-240
208	Var	Grad	Var	Grad	Var	Unim	Var	-5050.6	9.4612	1108.2	2.28E-241
190	Var	Grad	Var	Grad	Var	Grad	Var	-5055.4	10.7	1118.9	1.08E-243
67	Con	Con	Var	Unim	Var	Con	Con	-5587	6.6728	1130.3	3.62E-246
192	Var	Unim	Var	Grad	Var	Grad	Var	-5060.6	13.586	1132.3	1.33E-246
69	Con	Grad	Var	Unim	Var	Con	Con	-5588.1	6.949	1132.7	1.09E-246

85	Con	Con	Var	Unim	Var	Grad	Con	-5588.3	6.6205	1132.9	9.86E-247
174	Var	Unim	Var	Grad	Var	Con	Var	-5057.8	20.781	1133.9	5.98E-247
87	Con	Grad	Var	Unim	Var	Grad	Con	-5589.4	7.3179	1135.7	2.43E-247
103	Con	Con	Var	Unim	Var	Unim	Con	-5589.5	7.4766	1136.1	1.99E-247
105	Con	Grad	Var	Unim	Var	Unim	Con	-5590.2	7.1917	1137.2	1.15E-247
172	Var	Grad	Var	Grad	Var	Con	Var	-5062.5	21.376	1143.9	4.03E-249
61	Con	Con	Var	Grad	Var	Con	Con	-5647.5	6.3405	1251	2.23E-272
2	Var	Con	Con	Con	Con	Con	Con	-5649.3	3.1086	1251.3	1.92E-272
63	Con	Grad	Var	Grad	Var	Con	Con	-5647.5	6.704	1251.3	1.92E-272
79	Con	Con	Var	Grad	Var	Grad	Con	-5648.4	5.8378	1252.3	1.17E-272
81	Con	Grad	Var	Grad	Var	Grad	Con	-5648.9	6.6379	1254	4.98E-273
15	Con	Grad	Con	Unim	Con	Con	Con	-5651.4	2.1732	1254.6	3.69E-273
20	Var	Con	Con	Con	Con	Grad	Con	-5650.8	3.5842	1254.7	3.51E-273
13	Con	Con	Con	Unim	Con	Con	Con	-5651.9	1.6796	1255.1	2.87E-273
97	Con	Con	Var	Grad	Var	Unim	Con	-5650.1	5.4967	1255.2	2.73E-273
33	Con	Grad	Con	Unim	Con	Grad	Con	-5652.7	2.0401	1257.1	1.06E-273
38	Var	Con	Con	Con	Con	Unim	Con	-5652.2	4.0592	1258.1	6.41E-274
99	Con	Grad	Var	Grad	Var	Unim	Con	-5650.8	6.9808	1258.1	6.41E-274
31	Con	Con	Con	Unim	Con	Grad	Con	-5653.5	2.0773	1258.6	4.99E-274
49	Con	Con	Con	Unim	Con	Unim	Con	-5654.8	2.2418	1261.4	1.23E-274
59	Con	Unim	Var	Con	Var	Con	Con	-5661.1	5.447	1277.3	4.34E-278
56	Var	Con	Var	Con	Var	Con	Con	-5662.3	8.124	1282.3	3.57E-279
142	Var	Grad	Con	Unim	Con	Grad	Var	-5140.4	5.5295	1283.8	1.68E-279
74	Var	Con	Var	Con	Var	Grad	Con	-5663.4	7.7011	1284	1.52E-279
95	Con	Unim	Var	Con	Var	Unim	Con	-5664.4	6.9702	1285.3	7.96E-280
160	Var	Grad	Con	Unim	Con	Unim	Var	-5141.8	6.4649	1287.5	2.65E-280
92	Var	Con	Var	Con	Var	Unim	Con	-5665	8.229	1287.8	2.28E-280
120	Var	Unim	Con	Grad	Con	Con	Var	-5144.7	4.9199	1291.8	3.08E-281
138	Var	Unim	Con	Grad	Con	Grad	Var	-5145.7	4.6878	1293.6	1.25E-281
126	Var	Unim	Con	Unim	Con	Con	Var	-5145.7	5.2162	1294.2	9.29E-282
144	Var	Unim	Con	Unim	Con	Grad	Var	-5147	5.6515	1297.2	2.07E-282
156	Var	Unim	Con	Grad	Con	Unim	Var	-5147.6	4.6373	1297.4	1.88E-282
162	Var	Unim	Con	Unim	Con	Unim	Var	-5148.5	5.1441	1299.5	6.56E-283
114	Var	Unim	Con	Con	Con	Con	Var	-5163.2	4.9798	1328.9	2.71E-289
132	Var	Unim	Con	Con	Con	Grad	Var	-5164.6	5.9413	1332.6	4.26E-290
150	Var	Unim	Con	Con	Con	Unim	Var	-5165.9	4.6858	1334	2.12E-290
9	Con	Grad	Con	Grad	Con	Con	Con	-5694.3	1.9283	1340	1.05E-291
7	Con	Con	Con	Grad	Con	Con	Con	-5694.9	1.1254	1340.5	8.21E-292
27	Con	Grad	Con	Grad	Con	Grad	Con	-5695.7	1.7867	1342.8	2.60E-292
25	Con	Con	Con	Grad	Con	Grad	Con	-5696.3	1.4973	1343.8	1.58E-292
45	Con	Grad	Con	Grad	Con	Unim	Con	-5697.1	2.0611	1345.9	5.51E-293
43	Con	Con	Con	Grad	Con	Unim	Con	-5697.7	1.7868	1346.8	3.52E-293
168	Var	Unim	Var	Con	Var	Con	Var	-5178.1	7.6419	1361.4	2.38E-296
186	Var	Unim	Var	Con	Var	Grad	Var	-5179.9	8.736	1366	2.38E-297
204	Var	Unim	Var	Con	Var	Unim	Var	-5181.3	9.6522	1369.7	3.74E-298
118	Var	Grad	Con	Grad	Con	Con	Var	-5190.5	5.1501	1383.7	3.41E-301
136	Var	Grad	Con	Grad	Con	Grad	Var	-5191.5	4.7916	1385.3	1.53E-301
154	Var	Grad	Con	Grad	Con	Unim	Var	-5193.1	4.8553	1388.6	2.95E-302
197	Con	Unim	Var	Unim	Var	Grad	Var	-5723.4	8.1534	1404.5	1.04E-305
57	Con	Grad	Var	Con	Var	Con	Con	-5726.8	5.689	1408.9	1.15E-306

215	Con	Unim	Var	Unim	Var	Unim	Var	-5726.2	9.7275	1411.8	2.70E-307
75	Con	Grad	Var	Con	Var	Grad	Con	-5728.6	6.2569	1413	1.48E-307
5	Con	Unim	Con	Con	Con	Con	Con	-5732.4	1.6928	1416.2	2.99E-308
93	Con	Grad	Var	Con	Var	Unim	Con	-5730	7.0387	1416.6	2.45E-308
23	Con	Unim	Con	Con	Con	Grad	Con	-5733.8	2.0215	1419.3	< 2.45E-308
41	Con	Unim	Con	Con	Con	Unim	Con	-5735.3	2.1183	1422.3	< 2.45E-308
130	Var	Grad	Con	Con	Con	Grad	Var	-5217.1	5.2169	1437	< 2.45E-308
148	Var	Grad	Con	Con	Con	Unim	Var	-5218.7	5.4052	1440.4	< 2.45E-308
176	Var	Con	Var	Unim	Var	Con	Var	-5216.6	10.036	1440.7	< 2.45E-308
194	Var	Con	Var	Unim	Var	Grad	Var	-5218	9.2011	1442.6	< 2.45E-308
212	Var	Con	Var	Unim	Var	Unim	Var	-5219	8.8352	1444.2	< 2.45E-308
51	Con	Grad	Con	Unim	Con	Unim	Con	-5748.3	2.3224	1448.4	< 2.45E-308
166	Var	Grad	Var	Con	Var	Con	Var	-5231.6	8.465	1469.2	< 2.45E-308
177	Con	Grad	Var	Unim	Var	Con	Var	-5758.9	6.0829	1473.4	< 2.45E-308
202	Var	Grad	Var	Con	Var	Unim	Var	-5234.1	9.2799	1475	< 2.45E-308
184	Var	Grad	Var	Con	Var	Grad	Var	-5233.4	12.356	1476.6	< 2.45E-308
195	Con	Grad	Var	Unim	Var	Grad	Var	-5761.2	7.3221	1479.3	< 2.45E-308
77	Con	Unim	Var	Con	Var	Grad	Con	-5761.4	7.2625	1479.6	< 2.45E-308
213	Con	Grad	Var	Unim	Var	Unim	Var	-5763	7.4724	1483.1	< 2.45E-308
122	Var	Con	Con	Unim	Con	Con	Var	-5252.1	4.5968	1506.3	< 2.45E-308
140	Var	Con	Con	Unim	Con	Grad	Var	-5253.6	4.6158	1509.4	< 2.45E-308
158	Var	Con	Con	Unim	Con	Unim	Var	-5255	4.8801	1512.5	< 2.45E-308
3	Con	Grad	Con	Con	Con	Con	Con	-5785.5	1.2848	1521.9	< 2.45E-308
21	Con	Grad	Con	Con	Con	Grad	Con	-5787.1	2.0744	1526	< 2.45E-308
173	Con	Unim	Var	Grad	Var	Con	Var	-5784.7	7.1223	1526.2	< 2.45E-308
39	Con	Grad	Con	Con	Con	Unim	Con	-5788.4	2.0583	1528.6	< 2.45E-308
191	Con	Unim	Var	Grad	Var	Grad	Var	-5785.9	9.0291	1530.4	< 2.45E-308
209	Con	Unim	Var	Grad	Var	Unim	Var	-5787.4	7.7818	1532.3	< 2.45E-308
188	Var	Con	Var	Grad	Var	Grad	Var	-5263.8	8.3816	1533.4	< 2.45E-308
206	Var	Con	Var	Grad	Var	Unim	Var	-5264.6	9.7337	1536.4	< 2.45E-308
170	Var	Con	Var	Grad	Var	Con	Var	-5267.6	11.409	1544	< 2.45E-308
179	Con	Unim	Var	Unim	Var	Con	Var	-5793.4	8.2531	1544.6	< 2.45E-308
175	Con	Con	Var	Unim	Var	Con	Var	-5823	6.5967	1602.2	< 2.45E-308
193	Con	Con	Var	Unim	Var	Grad	Var	-5824.3	6.9004	1605.1	< 2.45E-308
211	Con	Con	Var	Unim	Var	Unim	Var	-5825.2	7.0086	1606.9	< 2.45E-308
55	Con	Con	Var	Con	Var	Con	Con	-5839.9	5.3576	1634.8	< 2.45E-308
73	Con	Con	Var	Con	Var	Grad	Con	-5841.2	5.2995	1637.4	< 2.45E-308
91	Con	Con	Var	Con	Var	Unim	Con	-5843.4	6.4626	1642.9	< 2.45E-308
167	Con	Unim	Var	Con	Var	Con	Var	-5850.2	6.191	1656.2	< 2.45E-308
185	Con	Unim	Var	Con	Var	Grad	Var	-5851.5	7.7816	1660.5	< 2.45E-308
203	Con	Unim	Var	Con	Var	Unim	Var	-5852.5	6.0857	1660.7	< 2.45E-308
119	Con	Unim	Con	Grad	Con	Con	Var	-5854.9	2.5713	1661.9	< 2.45E-308
116	Var	Con	Con	Grad	Con	Con	Var	-5330.2	4.5058	1662.5	< 2.45E-308
137	Con	Unim	Con	Grad	Con	Grad	Var	-5856.1	3.0454	1664.9	< 2.45E-308
134	Var	Con	Con	Grad	Con	Grad	Var	-5331.7	4.2779	1665.2	< 2.45E-308
155	Con	Unim	Con	Grad	Con	Unim	Var	-5857.1	3.2271	1667.1	< 2.45E-308
152	Var	Con	Con	Grad	Con	Unim	Var	-5332.8	4.4322	1667.6	< 2.45E-308
161	Con	Unim	Con	Unim	Con	Unim	Var	-5858.9	4.2458	1671.6	< 2.45E-308
143	Con	Unim	Con	Unim	Con	Grad	Var	-5862.3	3.516	1677.7	< 2.45E-308
125	Con	Unim	Con	Unim	Con	Con	Var	-5877.6	2.4636	1707.4	< 2.45E-308

123	Con	Grad	Con	Unim	Con	Con	Var	-5878.3	3.365	1709.7	< 2.45E-308
171	Con	Grad	Var	Grad	Var	Con	Var	-5875.9	8.6537	1710.1	< 2.45E-308
189	Con	Grad	Var	Grad	Var	Grad	Var	-5877.1	6.7278	1710.5	< 2.45E-308
141	Con	Grad	Con	Unim	Con	Grad	Var	-5879.7	3.1501	1712.1	< 2.45E-308
159	Con	Grad	Con	Unim	Con	Unim	Var	-5881.6	3.0602	1715.8	< 2.45E-308
207	Con	Grad	Var	Grad	Var	Unim	Var	-5879	10.191	1717.8	< 2.45E-308
187	Con	Con	Var	Grad	Var	Grad	Var	-5881.5	6.6798	1719.4	< 2.45E-308
169	Con	Con	Var	Grad	Var	Con	Var	-5881.6	7.4208	1720.3	< 2.45E-308
205	Con	Con	Var	Grad	Var	Unim	Var	-5884.5	9.035	1727.7	< 2.45E-308
121	Con	Con	Con	Unim	Con	Con	Var	-5889.9	3.1674	1732.6	< 2.45E-308
139	Con	Con	Con	Unim	Con	Grad	Var	-5890.7	2.3466	1733.3	< 2.45E-308
157	Con	Con	Con	Unim	Con	Unim	Var	-5892.1	2.4809	1736.2	< 2.45E-308
1	Con	Con	Con	Con	Con	Con	Con	-5896.9	0.94216	1744.3	< 2.45E-308
19	Con	Con	Con	Con	Con	Grad	Con	-5898.3	1.2735	1747.5	< 2.45E-308
37	Con	Con	Con	Con	Con	Unim	Con	-5899.8	1.5749	1750.7	< 2.45E-308
165	Con	Grad	Var	Con	Var	Con	Var	-5914.5	6.5072	1785.1	< 2.45E-308
183	Con	Grad	Var	Con	Var	Grad	Var	-5915.6	6.9927	1787.8	< 2.45E-308
201	Con	Grad	Var	Con	Var	Unim	Var	-5916.8	6.5867	1789.8	< 2.45E-308
113	Con	Unim	Con	Con	Con	Con	Var	-5922.8	2.4677	1797.8	< 2.45E-308
131	Con	Unim	Con	Con	Con	Grad	Var	-5923.8	2.1219	1799.4	< 2.45E-308
117	Con	Grad	Con	Grad	Con	Con	Var	-5925.4	2.3822	1802.7	< 2.45E-308
149	Con	Unim	Con	Con	Con	Unim	Var	-5925.3	2.6094	1802.9	< 2.45E-308
135	Con	Grad	Con	Grad	Con	Grad	Var	-5926.1	2.637	1804.4	< 2.45E-308
153	Con	Grad	Con	Grad	Con	Unim	Var	-5927.6	2.4026	1807.3	< 2.45E-308
115	Con	Con	Con	Grad	Con	Con	Var	-5931.8	1.7758	1814.9	< 2.45E-308
133	Con	Con	Con	Grad	Con	Grad	Var	-5932.3	2.2329	1816.5	< 2.45E-308
151	Con	Con	Con	Grad	Con	Unim	Var	-5934.5	2.342	1821	< 2.45E-308
110	Var	Con	Con	Con	Con	Con	Var	-5426.3	4.1734	1854.2	< 2.45E-308
128	Var	Con	Con	Con	Con	Grad	Var	-5427.7	4.3629	1857.2	< 2.45E-308
146	Var	Con	Con	Con	Con	Unim	Var	-5429.2	4.4139	1860.4	< 2.45E-308
164	Var	Con	Var	Con	Var	Con	Var	-5440	9.7701	1887.2	< 2.45E-308
182	Var	Con	Var	Con	Var	Grad	Var	-5440.5	9.2519	1887.7	< 2.45E-308
200	Var	Con	Var	Con	Var	Unim	Var	-5443.1	10.34	1894	< 2.45E-308
111	Con	Grad	Con	Con	Con	Con	Var	-5976.4	1.6769	1904.1	< 2.45E-308
129	Con	Grad	Con	Con	Con	Grad	Var	-5977.3	2.2504	1906.5	< 2.45E-308
147	Con	Grad	Con	Con	Con	Unim	Var	-5978.8	1.8202	1909.1	< 2.45E-308
163	Con	Con	Var	Con	Var	Con	Var	-6067.7	5.8882	2090.9	< 2.45E-308
181	Con	Con	Var	Con	Var	Grad	Var	-6068.4	7.0763	2093.5	< 2.45E-308
199	Con	Con	Var	Con	Var	Unim	Var	-6069.7	6.4013	2095.4	< 2.45E-308
109	Con	Con	Con	Con	Con	Con	Var	-6126.6	1.1829	2204.1	< 2.45E-308
127	Con	Con	Con	Con	Con	Grad	Var	-6127.7	1.71	2206.8	< 2.45E-308
145	Con	Con	Con	Con	Con	Unim	Var	-6129.4	2.0904	2210.4	< 2.45E-308

Table 5B. Summary of posterior distributions of parameters from most parsimonious model (model 124 from Table 6A). See Appendix 5 for more details on model equations.

Model term	Posterior mean	95% credible interval
Recruitment $R_{i,t} = \exp(r_t + r_{grad} d_i)$		
r_{2000}	-6.4436	-8.6608 – -4.6144
r_{2001}	-6.9229	-9.1542 – -5.2130
r_{2002}	-5.9342	-7.8655 – -4.5074
r_{2003}	-2.7611	-3.1174 – -2.4403
r_{2004}	-8.0957	-9.0007 – -7.3250
r_{2005}	-9.9277	-11.4696 – -8.6270
r_{2006}	-9.8759	-11.3901 – -8.5776
r_{2007}	-7.0518	-9.0064 – -5.4451
r_{2008}	-4.2579	-4.8078 – -3.7731
r_{2009}	-6.3983	-6.8140 – -6.0032
r_{grad}	0.2630	0.2459 – 0.2833
Juvenile mortality $M_J = exp(m_J)$		
m_J	-1.8128	-3.3211 – -0.3289
Adult mortality $M_{A,i} = exp(m_A + m_{unim,A}(d_i - m_{offset,A})^2$		
m_A	-1.5434	-1.7782 – -1.3088
$m_{linear,A}$	0.0306	0.0261 – 0.0360
$m_{offset,A}$	9.5401	9.1532 – 9.9657

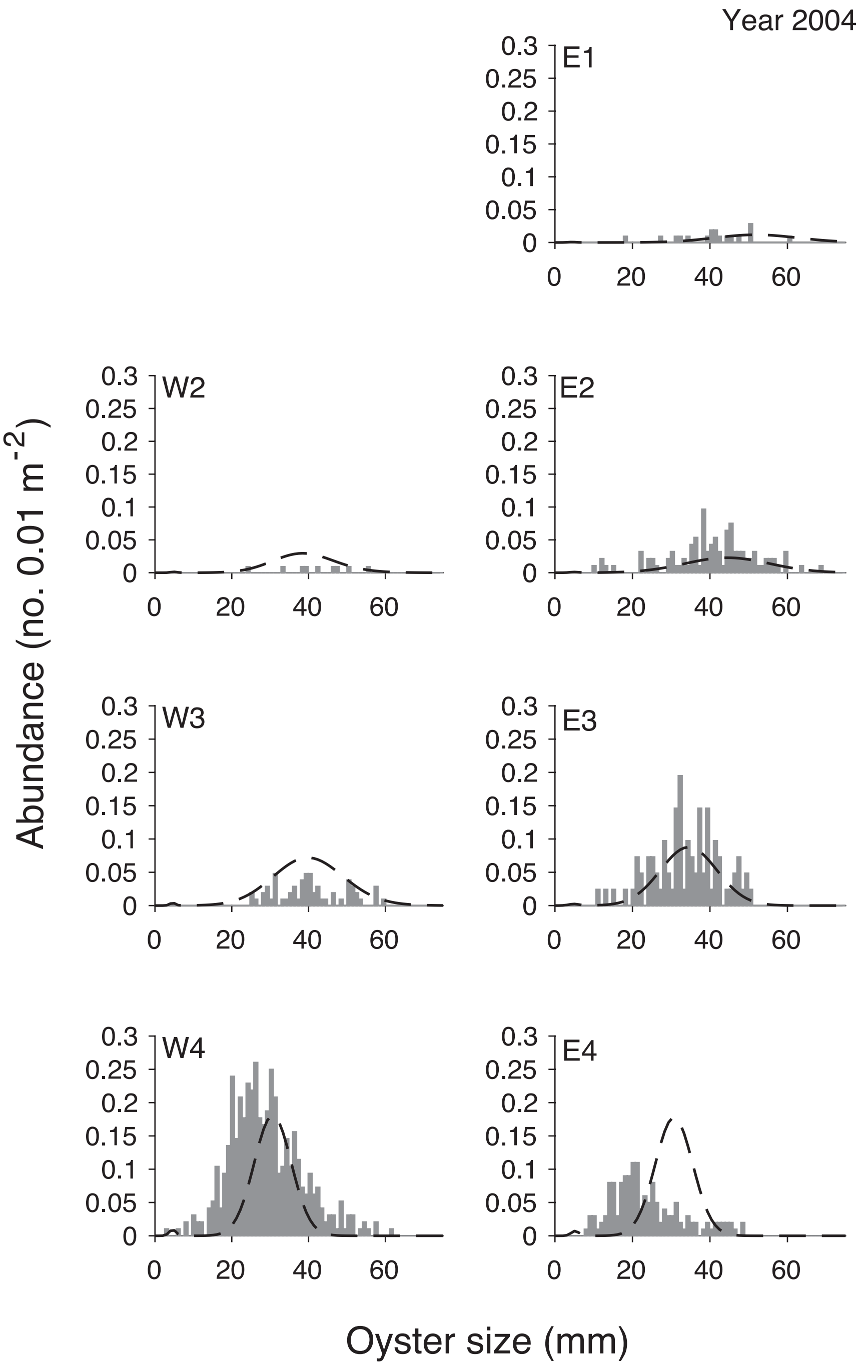

Figure 5A. Fit of the SSIPM for the most parsimonious model (curves) to observed size distributions (bars) at each site in 2004.

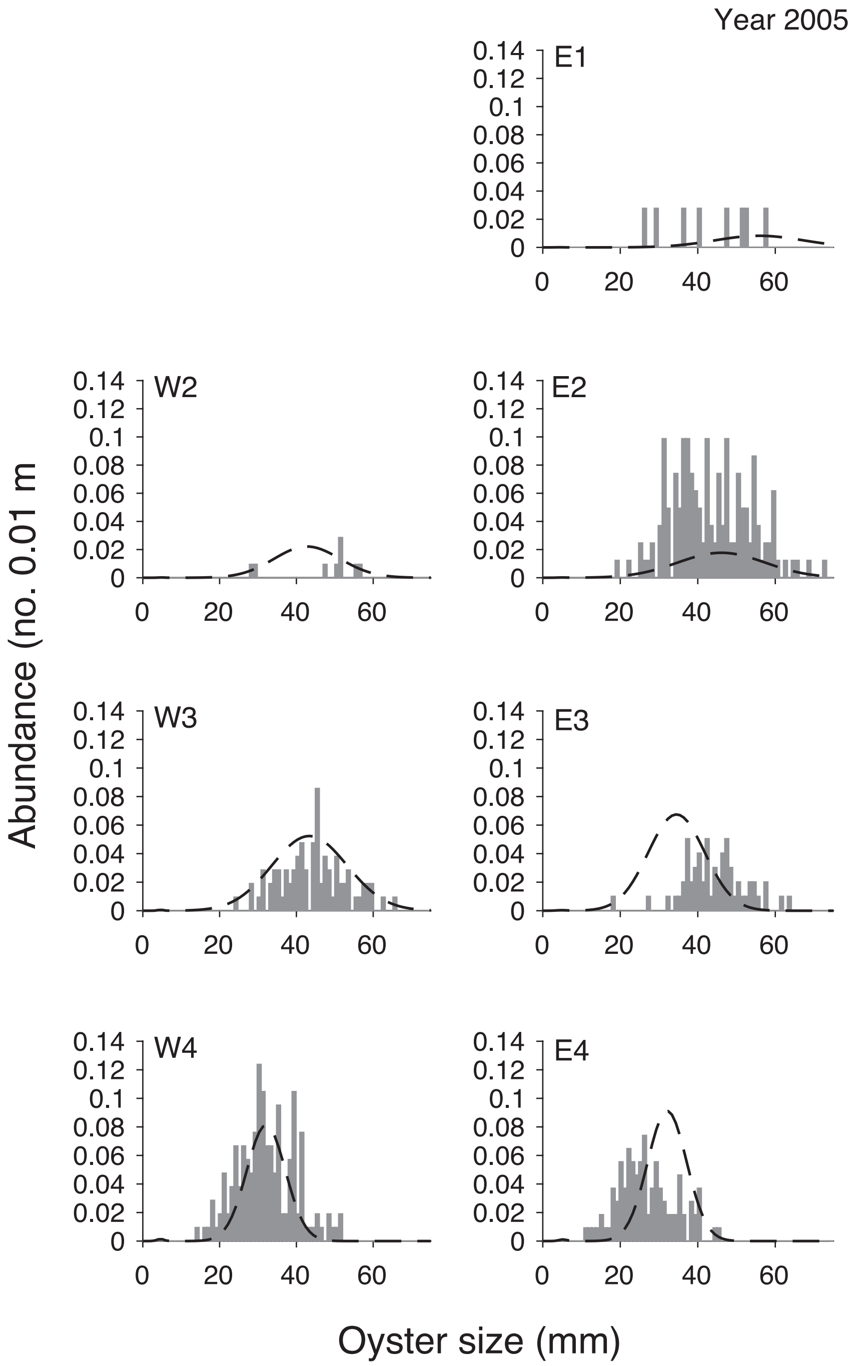

Figure 5B. Fit of the SSIPM for the most parsimonious model (curves) to observed size distributions (bars) at each site in 2005.

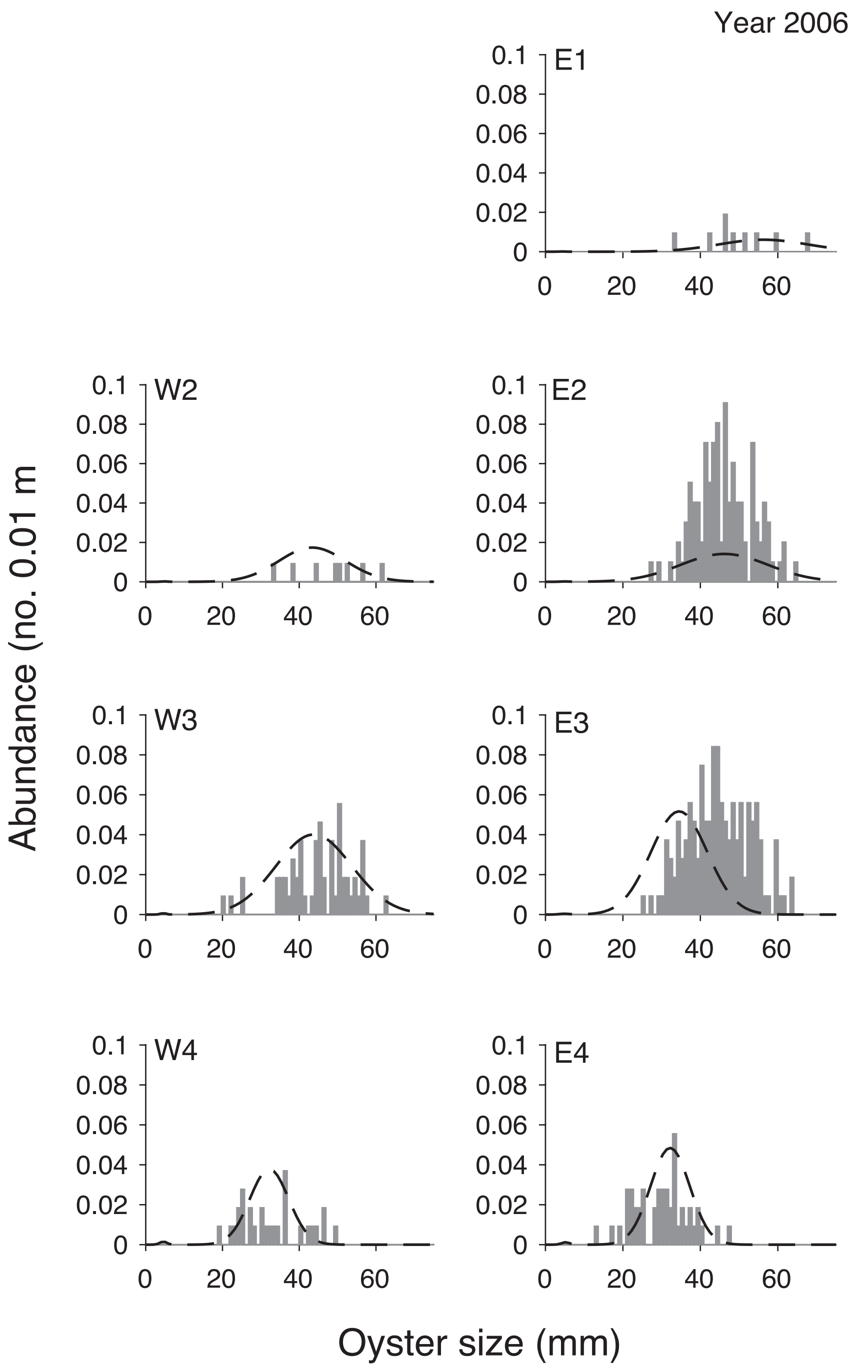

Figure 5C. Fit of the SSIPM for the most parsimonious model (curves) to observed size distributions (bars) at each site in 2006.

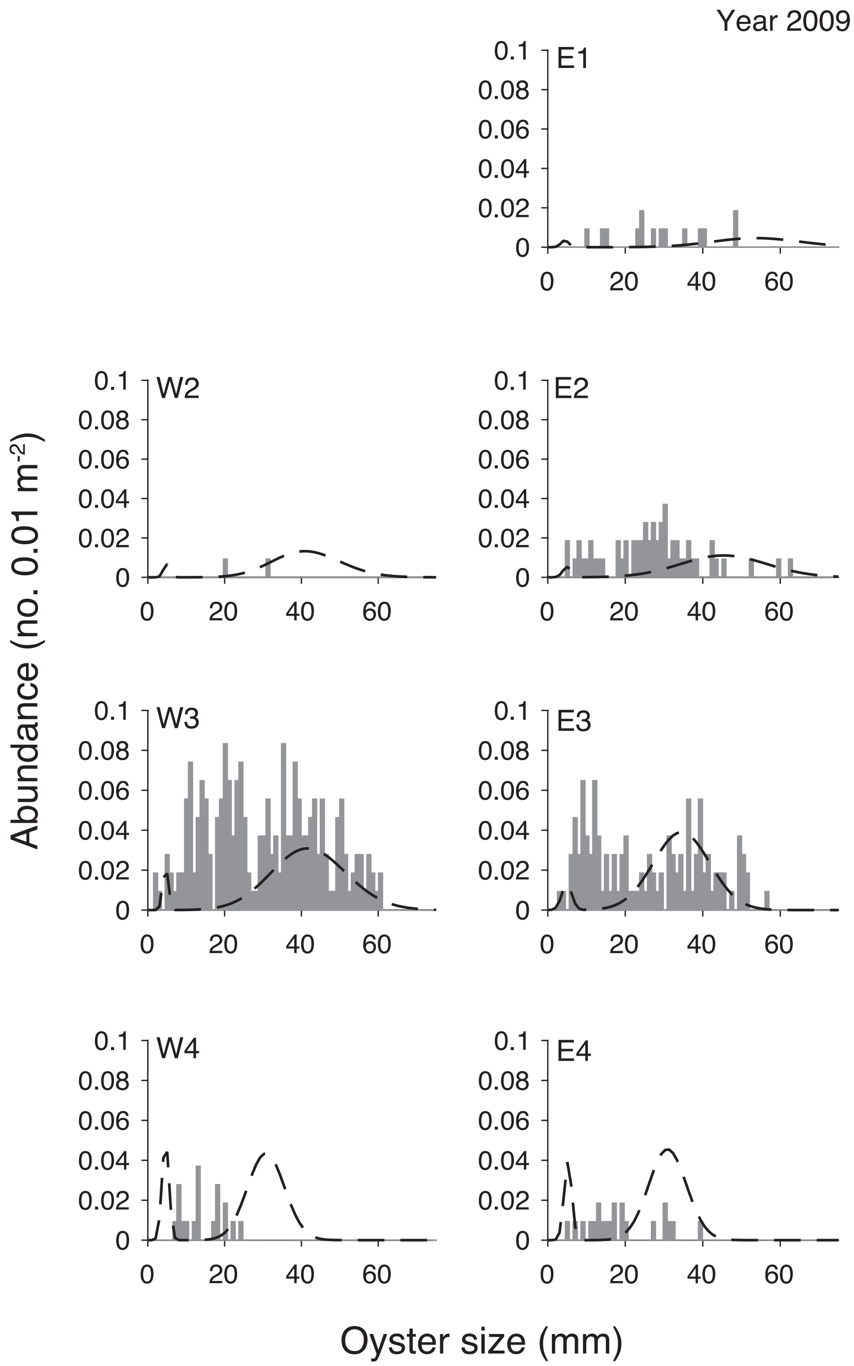

Figure 5D. Fit of the SSIPM for the most parsimonious model (curves) to observed size distributions (bars) at each site in 2009.

Appendix 6

Larval recruitment monitoring

In August of 2002, we began to monitor oyster recruitment by deploying seven 15 × 15 cm PVC tiles at five-meter intervals along an intertidal transect at sites E4 and W4. These tiles were removed after one month and oyster recruitment was quantified in the laboratory. Given the high abundance of oyster recruits in 2002, we used smaller tiles (10 × 10 cm) and added six more sites the following year. On a monthly basis from May to September of 2003, we exchanged tiles in the field with new tiles and quantified oyster recruitment on each recovered tile. Because we observed zero recruitment during the summers of 2003, 2004 and 2005, we monitored monthly recruitment without interruption from March to August 2006. From August 2006 to August 2007, recruitment was monitored at three-month intervals. In the summer of 2008, oyster recruitment was monitored monthly from May–September.

Appendix 7

Summary of results from Analysis of Deviance on the number of live and dead adult oysters from the post-settlement mortality experiment during 2011 in Tomales Bay

Table 7. Results from analysis of deviance on the number of live and dead adult oysters from the cage and control treatments during post-settlement mortality experiment. Results were fit with logistic regression analysis (binomial GLM with logit link). An asterisk denotes a statistically significant effect at an $\alpha = 0.05$.

Source	df	Deviance Residuals	df	Residual Deviance	p-value
Treatment (cage versus control)	1	11.58	45	280.61	< 0.001*
Distance	1	12.0272	42	61.548	0.04*
Distance:Treatment (cage versus control)	1	0.7306	40	54.619	0.49