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Fluctuations in food supply drive recruitment variation in a marine fish

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Reproductive rates and survival of young in animal populations figure centrally in generating management and conservation strategies. Model systems suggest that food supply can drive these often highly variable properties, yet for many wild species, quantifying such effects and assessing their implications have been challenging. We used spatially explicit time series of a well-studied marine reef fish (black surfperch *Embiotoca jacksoni*) and its known prey resources to evaluate the extent to which fluctuations in food supply influenced production of young by adults and survival of young to subadulthood. Our analyses reveal: (i) variable food available to both adults and to their offspring directly produced an order of magnitude variation in the number of young-of-year (YOY) produced per adult and (ii) food available to YOY produced a similar magnitude of variation in their subsequent survival. We also show that such large natural variation in vital rates can significantly alter decision thresholds (biological reference points) important for precautionary management. These findings reveal how knowledge of food resources can improve understanding of population dynamics and reduce risk of overharvest by more accurately identifying periods of low recruitment.

Keywords: population dynamics; stock recruitment; food limitation; marine fish; population regulation; biological reference points

1. INTRODUCTION

Properties governing reproductive rates and survival of young help shape a population's risk of extinction [1] and resilience to perturbation or harvest [2]. As a result, understanding how environmental change alters these properties remains a fundamental but elusive challenge that has direct implications for conservation [3] and resource management [4]. A large body of evidence suggests that food supply can influence population dynamics by, for example, altering reproductive performance of adults and/or survival of young. This has been documented for a range of vertebrates, including terrestrial mammalian herbivores [5,6], marine mammals [7], passerine birds [8], seabirds [7,9], and freshwater [10] and marine fish [11–13]. Although fluctuations in food supply are ubiquitous in nature, conservation and management strategies frequently assume that populations have constant mean vital rates through time. Such constancy is typically assumed for population viability analyses based on life tables or matrix projection models [14], as well as for many stock–recruit models in fisheries [15]. In marine fishes, for example, basic stock–recruitment models are expected to perform well only where there is comparatively low temporal variability in recruitment [16], which could be a major reason why many stock–recruit models account for little variation in the data [17]. If externally driven temporal variation in vital rates is high, then the application of such simplistic models could

lead to severe mismanagement, particularly if periods of recruitment failure are underestimated.

One solution to better predict or understand risk of recruitment failure has been to map variation in fecundity or survival onto physical environmental variables [15]. However, this correlative approach [18] appears best supported when species occupy harsh physical environments [19]. In stock–recruitment models of marine fish, difficulty in assessing food supply and other more direct drivers at appropriate scales has resulted in the use of environmental indices [20] or regime metrics ('good' versus 'poor') [21] to account for variation in adult reproduction and survival of young. Thus, even when there is strong environmental correlation with demographic rates, the descriptor variables (e.g. sea surface temperature [22]) are usually far removed from the underlying biological mechanism. As a result, such correlations often have not proved especially useful [4,23].

The growing availability of appropriate long-term data is enabling more direct assessments of the roles of food and other such drivers of dynamics for marine fishes and other species [11,12,24]. However, even when food has been considered explicitly, few empirical studies have addressed the dynamical consequences of the cumulative effect of fluctuations in food across multiple life stages over time. The replenishment of adult stock may not be limited by a bottleneck at a single life-history stage; rather a cohort may be susceptible to food stressors at multiple stages [11]. For example, low food availability to adults during the reproductive period may yield few offspring, but subsequent high food availability for those offspring may offset such effects owing to above normal survival. By contrast, successive years of low

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food may lead to low adult fecundity and poor offspring survivorship, which collectively result in recruitment failure. Thus, identifying the effect of food resources on multiple life stages may substantially improve predictions of recruitment failure in managed populations.

Here, we investigated (i) the extent to which food supply explained observed variation in reproduction and survival of a common marine reef fish (the black surfperch *Embiotoca jacksoni*), and (ii) how refined estimates of vital rates for this species altered a common decision threshold (i.e. a biological reference point, BRP) used for precautionary management of fisheries. We formulated *a priori* hypotheses from detailed knowledge of black surfperch feeding and reproductive ecology [25–28], and evaluated those using spatially explicit time-series data on age-structure and food availability. We first constructed several basic models for two important dynamical processes: production of young-of-year (YOY, age 0) by mature adults (age 2+ [29]); and subsequent survival of YOY to subadulthood (age 1, immature subadults). We then compared these basic models with those that incorporated food available to one or more age classes in the model (adults, YOY and subadults). In this manner, our model construction and selection framework served to quantitatively evaluate and describe functional relationships between availability of food known to be important and recruitment dynamics. This yielded insights regarding the circumstances under which incorporating such information can alter a common BRP used to forecast impaired recruitment (i.e. the adult stock size required to produce 50% of maximum recruitment [30]).

2. METHODS

(a) Study system

Black surfperch occupy shallow temperate reefs. Females are viviparous and annually produce well-developed, locally retained young (for more details see [25,26]). This quality facilitates tracking of adults and offspring on a reef over multiple years. Young consume the same general taxa as adults [27], with diets dominated by caprellid and gammarid amphipods, and other small crustaceans living within benthic, reef-dwelling macroalgae [28].

(b) Time-series data

Data on age-specific abundance of black surfperch, the amount of foraging habitat and the availability of their food were collected at 11 sites on the north side of Santa Cruz Island, CA, annually in autumn (when fish copulate [31]), intermittently from 1982 to 1992 and annually from 1993 to 2008. At each site, three fixed 40 m transects at 3, 6 and 9 m depth contours (the typical depth range) were surveyed annually for black surfperch (in a 40 × 2 m swath), their foraging habitat and principal food using SCUBA. Counts of fish were always made by the same observer (R.J.S.), and included the number of YOY, subadults and mature adults. In this study, prey were identified as caprellid and gammarid amphipods that were within the gape limitation of black surfperch because they composed the majority of prey biomass in our algal samples (84%) and in diets of black surfperch [32,33]. Our index of food availability for a given year was calculated as the mean biomass of each prey taxon within suitable foraging habitats in that year multiplied by the cover of appropriate habitat at each site in each year.

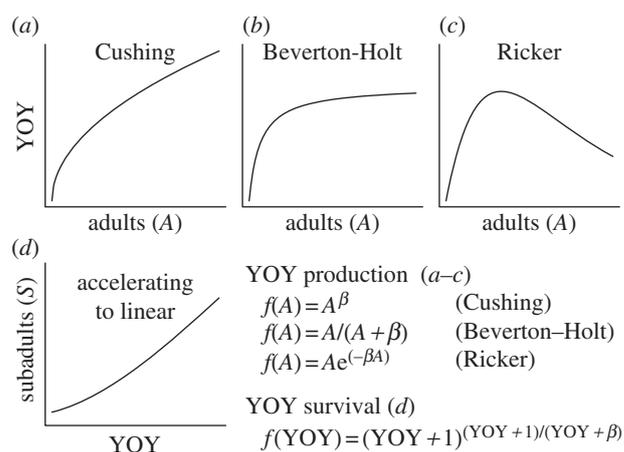


Figure 1. Nonlinear functional forms used in (a–c) YOY production models and (d) YOY survival models.

For further details, see electronic supplementary material, appendix S1. Data used in analyses are available from <http://metacat.lternet.edu/knb/metacat/knb-lter-sbc.60>.

(c) Young-of-year production

To examine the extent to which food availability influenced the production of YOY, we incorporated into stock–recruit (S–R) models (i) availability of food in the year that females became pregnant and (ii) availability of food in the following year when their newly produced YOY feed. We used three typical S–R models (Beverton–Holt, Cushing, Ricker) [15] as well as a density-independent (linear) form (figure 1a–c). We hypothesized that increasing food available to adults and/or YOY directly modified the YOY-per-adult relationship; thus, the S–R function was multiplied by the food variables (see the electronic supplementary material, appendix S2 for model construction). Because the food effect may taper with increasing food, we added a shape parameter in the exponent of each food variable that allowed this behaviour. The general structure of the full models used was

$$\text{YOY}_{t+1,i} = \alpha f(A_{t,i}) e^{\gamma_1 \ln(F_{t,i}) + \gamma_2 \ln(F_{t+1,i}) + \varepsilon_{t,i}} \quad (2.1)$$

$$= e^{\psi} f(A_{t,i}) (F_{t,i})^{\gamma_1} (F_{t+1,i})^{\gamma_2} e^{\varepsilon_{t,i}},$$

where $\alpha = e^{\psi}$ is the density-independent productivity parameter, $A_{t,i}$ is adult density in year t at site i , $f(A_{t,i})$ is one of the stock–recruit relationships in figure 1, $F_{t,i}$ is food available to those adults, $F_{t+1,i}$ is food available to the YOY they produce, γ_1 and γ_2 are shape parameters for the food variables, and $\varepsilon_{t,i}$ is an error term. ψ was allowed to vary randomly among sites to account for site variation, avoid pitfalls of pseudoreplication and induce correlation among multiple observations within a site among years. We fitted the relationships as nonlinear mixed effects models (NLMMs) [34], using a Gaussian likelihood after natural log transformation. Stock–recruit relationships tend to exhibit lognormal error structure so the models were natural log-transformed, with a small constant added to YOY (1/9, the minimum, non-zero mean density observed). By convention, both sides of the model were divided by the number of adults to fit models on a per capita basis (YOY per adult). Model predictions (in log-space) were back-transformed to the original scale using a bias correction (by adding $\sigma_{\text{residual}}^2/2$ before taking the antilog, where $\sigma_{\text{residual}}^2$ is the estimated within-site error variance [35]), which is necessary because back-transforming the mean of log-transformed data

otherwise yields the median on the original scale, which will be biased low.

To test hypotheses, we compared models with (i) no food information, (ii) food information for either adults or YOY, and (iii) food information for both adults and YOY. All model comparisons in this study were performed using corrected Akaike information criterion (AICc). AICc values were compared using the following criteria: (i) the simplest model(s) within two units of the minimum is (are) favoured, (ii) models 4+ units from the minimum are rejected with caution, and (iii) models 10+ units greater than the minimum effectively have no statistical support and are rejected with confidence [36]. Comparing models with different fixed effects requires use of maximum likelihood (ML), yet comparing models with different random effects requires restricted maximum likelihood (REML) [37,38]. Thus, we first confirmed that parameters other than ψ should not vary randomly by site by comparing models fit using REML (see the electronic supplementary material, appendix S2), then compared models with different fixed effects fit using ML, and finally refit models using REML to get unbiased parameter estimates. In the best-fit models, we detected no significant effect of residual autocorrelation using AICc (see the electronic supplementary material, appendix S3).

(d) Young-of-year survival

We evaluated the effect of food on indices of YOY survival to subadulthood by including food available to YOY in year (t) at the i th site and food available to subadults in year ($t + 1$) in models of YOY survival. Note that we use the term survival to mean an index of survival, not a true estimate of survival *per se* because YOY are cryptic in comparison with subadults. As a result, YOY densities are assumed to be underestimated, particularly at low densities, and therefore the ratio of subadults in year ($t + 1$) and YOY in year (t) can exceed 1 when YOY are scarce.

In the same fashion as for YOY production, we used a general relationship for YOY survivorship:

$$S_{t+1,i} = \delta f(\text{YOY}_{t,i}) e^{[\gamma_1 \ln(F_{t,i}) + \gamma_2 \ln(F_{t+1,i}) + \epsilon_{t,i}]} \quad (2.2)$$

$$= e^{\xi} f(\text{YOY}_{t,i}) (F_{t,i})^{\gamma_1} (F_{t+1,i})^{\gamma_2} e^{\epsilon_{t,i}},$$

where $\delta = e^{\xi}$ is the density-independent subadult–YOY ratio, $F_{t,i}$ is food available to YOY in year (t) at the i th site, $F_{t+1,i}$ is food available to subadults in year ($t + 1$) at the i th site, γ_1 and γ_2 are shape parameters for the food variables, and $f(\text{YOY}_{t,i})$ is either: (i) a linear relationship between YOY and subsequent subadults (figure 1, constant survival) or (ii) an accelerating to linear function (figure 1d); this accommodates subadult/YOY ratios more than 1 caused by low biased YOY estimates (see the electronic supplementary material, appendix S4). NLMs were fitted in log-space (fitted as subadults + 1/9 per YOY, with 1/9 again being the smallest non-zero value) using a Gaussian likelihood (after log-transformation) and back-transformed predictions were bias-corrected. Only δ was allowed to vary by site (see the electronic supplementary material, appendix S2 for results for comparison of random effect structures). For model selection, we used the same process as outlined for YOY production models. For precautionary purposes, we used a first order autoregressive model (AR(1)) to account for potential autocorrelation as its inclusion allowed the model to conform to residual normality (see the electronic supplementary material, appendix S3) and slightly modified model parameter estimates.

(e) Subadult abundance predicted by reproductive adults and food availability

We combined the most statistically supported YOY production and YOY survival models into a single, parametrized model to assess how well these models together explained variation in subadult abundance. We compared the predictions of this best combined model with those that combined the previously parametrized standard Beverton–Holt, Cushing or Ricker models, with the standard linear YOY survival models (each lacking food information) hereafter referred to as the standard (non-food) combined models. For each, we estimated variance explained in subadult densities as well as mean bias of the predictions (predicted–observed) for each combined model.

(f) Impact of food information on the biological reference point B50%R

To explore how explicit information on food might alter BRPs, we examined a major BRP used to indicate stock thresholds for impaired recruitment. The adult stock size required to produce 50 per cent of the maximum estimated recruitment produced at high biomass (B50%R) is a generally reliable threshold [30]. Ricker and Beverton–Holt models have estimable theoretical maximum recruitment levels, whereas the Cushing model requires estimating recruitment at historical adult mean–maximum densities (13 adults per 80 m² in this case). We solved the best-fit YOY production model with food to estimate how proportional reductions in mean food availability would alter B50%R in comparison with that from the corresponding model without food and used residual bootstraps to calculate 95% CIs (999 iterations), whereby we (i) added randomly sampled residuals (with replacement) to the fitted values, (ii) re-estimated model parameters using these data, and (iii) calculated 2.5 per cent and 97.5 per cent quantiles.

3. RESULTS

(a) Temporal variation in the study system

Abundances of adult black surfperch and their foraging habitat were highest in the early years of the study, and declined substantially during the late 1980s and early 1990s (figure 2a,b). From 1993 to 2008, the densities of all age classes exhibited an increase (figures 2b and 3a). Food availability showed substantial inter-annual variability (figure 3b, s.d. of site means = 3.714) with much smaller inter-site variability (s.d. of annual means = 0.940).

(b) Young-of-year production

The Cushing model that included food levels for both adults and YOY explained 41 per cent of the variance and was strongly supported as the best of the models tested (AICc value 7.7–50.0 units less than all other models; table 1). The model indicated that YOY production was positively influenced by adult density ($A_{t,i}$), food available to adults (figure 4a,b) and food available to YOY. In the model, the food effect decreased as food became more available, indicated by shape parameters with values less than 1 ($\gamma_1 = 0.68 \pm 0.12$ s.e., $p < 0.001$; $\gamma_2 = 0.46 \pm 0.11$ s.e., $p < 0.001$). Random site effects for ψ varied substantially ($\psi = -1.70 \pm 0.20$ s.e., $p < 0.001$, $\sigma_y = 0.43$; s.d. of random effects), suggesting substantial

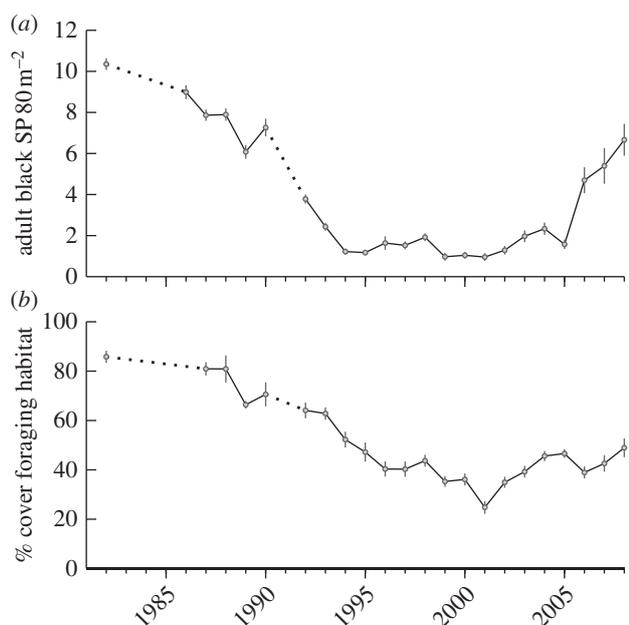


Figure 2. Temporal patterns of (a) adult black surfperch densities (mean \pm s.e.) and (b) percentage cover of foraging habitat. Foraging habitat is defined as foliose understory and turfing algae in which black surfperch feed.

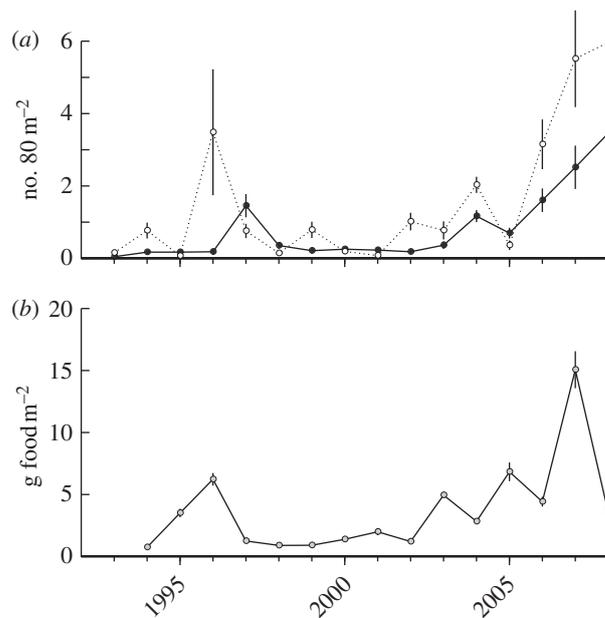


Figure 3. Temporal patterns (mean \pm s.e.) of (a) YOY and subadult black surfperch densities; and (b) index of food available to black surfperch. Open circle, YOY; filled circle, subadults.

Table 1. Fit of YOY production models with columns indicating the stock–recruit model functional form, food variables included (food available to adults year (t) at site i ($F_{t,i}$) and/or to YOY the next year ($F_{t+1,i}$)), number of estimated parameters (k), corrected Akaike information criterion (AICc), increase in AICc over the best model and variance explained in YOY produced per adult by the model.

stock–recruit function	food variables included		k	AICc	Δ AICc	R^2
Cushing	$F_{t,i}$	$F_{t+1,i}$	6	447.0	0.0	0.41
Beverton–Holt	$F_{t,i}$	$F_{t+1,i}$	6	454.7	7.7	0.40
Cushing	$F_{t,i}$	—	5	462.2	15.2	0.31
Ricker	$F_{t,i}$	$F_{t+1,i}$	6	468.6	21.6	0.27
Beverton–Holt	$F_{t,i}$	—	5	471.3	24.3	0.30
Ricker	—	$F_{t+1,i}$	5	473.7	26.7	0.23
Cushing	—	$F_{t+1,i}$	5	478.9	31.9	0.18
Beverton–Holt	$F_{t,i}$	—	5	482.0	35.0	0.16
Ricker	$F_{t,i}$	—	5	482.5	47.5	0.16
Cushing	—	—	4	494.6	47.6	0.04
Linear	—	—	3	495.2	48.2	0.01
Beverton–Holt	—	—	4	497.1	50.1	0.01
Ricker	—	—	4	497.2	50.1	0.01

variation by site not accounted for by our measure of food (see the electronic supplementary material, appendix S2). The best model fit did not violate normality assumptions for residuals or random effects (see the electronic supplementary material, appendix S5).

Removing the effects of food availability to either adults or YOY significantly reduced the quality of the fit of the Cushing model. Variance explained dropped to 16–31% for models with food information for one life stage and to 1–4% for traditional models lacking food information altogether (table 1). The Beverton–Holt and Ricker models that included food levels for both adults and YOY were both improvements over models with no food information, but nonetheless had little statistical support when compared with the full Cushing model (table 1).

(c) Young-of-year survival

The model for young-of-year survival with the best statistical support included an accelerating to linear YOY to subadult function, and positive effects of food available to YOY in year (t) and food available to subadults in year ($t+1$; table 2 and figure 5a,b). This model explained 72 per cent of the variance. The effect of food decreased as food became more available, as indicated by shape parameters with values less than 1 ($\gamma_1 = 0.57 \pm 0.10$ s.e., $p < 0.001$; $\gamma_2 = 0.26 \pm 0.11$ s.e., $p = 0.019$). There was substantial variation in survival by site ($\zeta = -1.73 \pm 0.29$ s.e., $p < 0.001$, $\sigma_z = 0.61$; s.d. of random effects). The best model fit did not violate normality assumptions for residuals or random effects (see the electronic supplementary material, appendix S5).

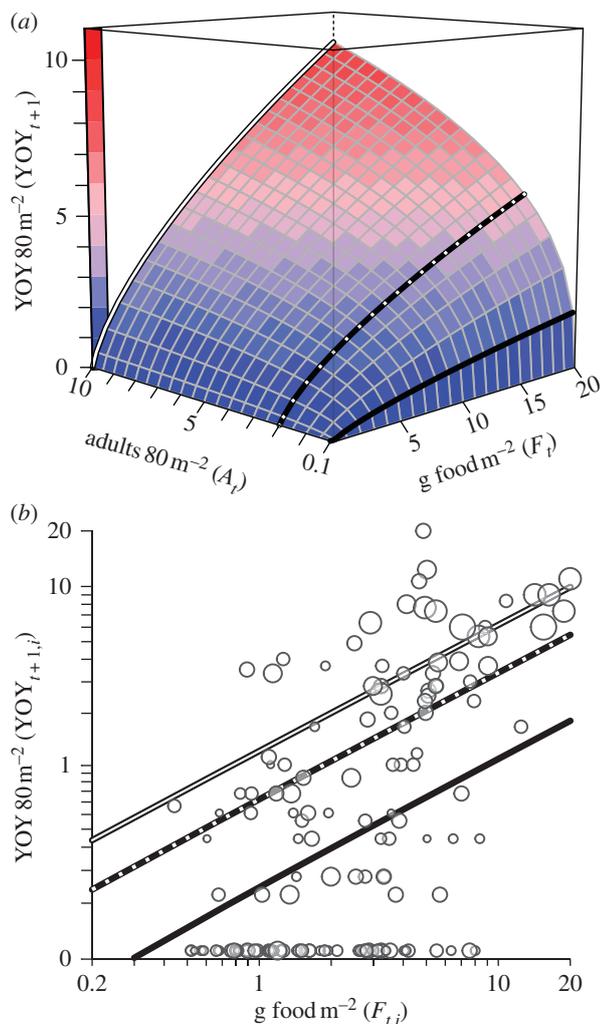


Figure 4. (a) Cushing YOY production model predictions, made with food available to YOY in year (t) fixed at its mean value of 3.5 g m^{-2} . Lines are selected predictions along this surface that correspond to those in (b). The vertical axis represents densities of YOY in year ($t+1$) that were produced by adults in year (t) on the left axis. The right axis represents food available to adults in year (t). (b) Log-scale density of YOY in year ($t+1$) versus log-scale food in year (t). Larger points indicate more adults in year (t) at that site-year combination. Lines correspond with those in (a).

Removing food components of the model structure significantly reduced explanatory power, but the far more important one was food available to YOY (indicated by an increase in AICc of only 3.0 when food to subadults was removed in contrast to an increase of 20.2 when food to YOY was removed; table 2). However, food variables became statistically significant only when the nonlinear functional relationship between YOY and subadults was incorporated (table 2).

(d) Subadult abundance predicted by reproductive adults and food availability

The best combined model (predicting subadult densities from adult densities 2 years prior and food covariates from lags 0, 1 and 2 years using parameter estimates shown above) far outperformed the standard (non-food) combined models that did not include food as explanatory

variables. The best combined model explained much more of the variation in subadult densities ($R^2 = 0.68$, figure 6) than the standard combined models ($R^2 = 0.31\text{--}0.36$). Furthermore, the best combined model did not exhibit significant bias (bias = 0.07, $t_{129} = 1.02$, $p = 0.31$, figure 6), whereas the standard (non-food) combined models showed significant, positive bias (overprediction) ranging from 0.66 to 0.69 (see the electronic supplementary material, appendix S5).

(e) Impact of food information on the biological reference point B50%R

When reductions in mean annual food availability were greater than approximately 35 per cent, the estimated number of adults required to produce 50 per cent of maximum mean-recruitment (B50%R) by the best model significantly exceeded B50%R estimated by the model without food information (figure 7). For black surfperch, such reductions in mean annual food availability may be due to either changes in availability of foraging habitat or density of prey within such habitat. Once food is reduced by more than 40 per cent, the number of adults required to produce sufficient recruitment is equal to or greater than the historical mean maximum (indicated by the arrow in figure 7). In contrast, with no or modest change in food availability, the number of adults is less than or equal to that estimated by the model without food information because of stronger density dependence in the full model (a smaller β).

4. DISCUSSION

Our findings not only show that fluctuations in food to a marine fish can substantially shape both the production of young and their subsequent survival; more importantly they demonstrate the serious consequences that can arise from failing to account for such food limitation in models used to describe population dynamics or guide management decisions. Relatively simple models are still the dominant choice to characterize complex population dynamics and at times can prove to be as effective as models with more biological realism [39]. In the realm of such realism, food limitation remains a central research frontier in fisheries science and population dynamics, particularly of marine vertebrates. Although a plethora of research demonstrates direct and often cascading roles of predators in regulating populations in both marine and terrestrial systems [40], top-down influences do not necessarily render bottom-up forcing unimportant, including for marine fishes [41,42]. In the case of black surfperch, whose individual and population attributes indeed are affected by predators [43,44], we found that more than an order of magnitude of natural variation in several vital rates was driven by natural fluctuations in the amount of food available to multiple life stages. In systems exhibiting such food limitation, knowledge of food supply can substantially alter estimates of useful BRPs, particularly when reductions in food are severe.

Food-driven variability in the number of young black surfperch produced by adults challenges traditional assumptions made by many population models that fecundity and survival of young is purely intrinsic. Such effects result from either increased survival of newly

Table 2. Fit of YOY survival models with columns indicating the functional form of survival, the food variables included (food available at the i th site to YOY and in year (t) at site i ($F_{t,i}$) and/or to subadults the next year ($F_{t+1,i}$)), number of estimated parameters (k), corrected Akaike information criterion (AICc), increase in AICc over the best model, and variance explained in survival by the model.

survival function	food variables included		k	AICc	Δ AICc	R^2
accelerating to linear	$F_{t,i}$	$F_{t+1,i}$	7	197.8	0.0	0.72
accelerating to linear	$F_{t,i}$	—	6	200.8	3.0	0.67
accelerating to linear	—	$F_{t+1,i}$	6	218.0	20.2	0.62
accelerating to linear	—	—	5	221.9	24.1	0.57
linear	—	—	4	240.7	42.9	0.26
linear	—	$F_{t+1,i}$	5	262.7	64.9	0.17
linear	$F_{t,i}$	—	5	263.0	65.2	0.19
linear	$F_{t,i}$	$F_{t+1,i}$	6	264.5	66.7	0.17

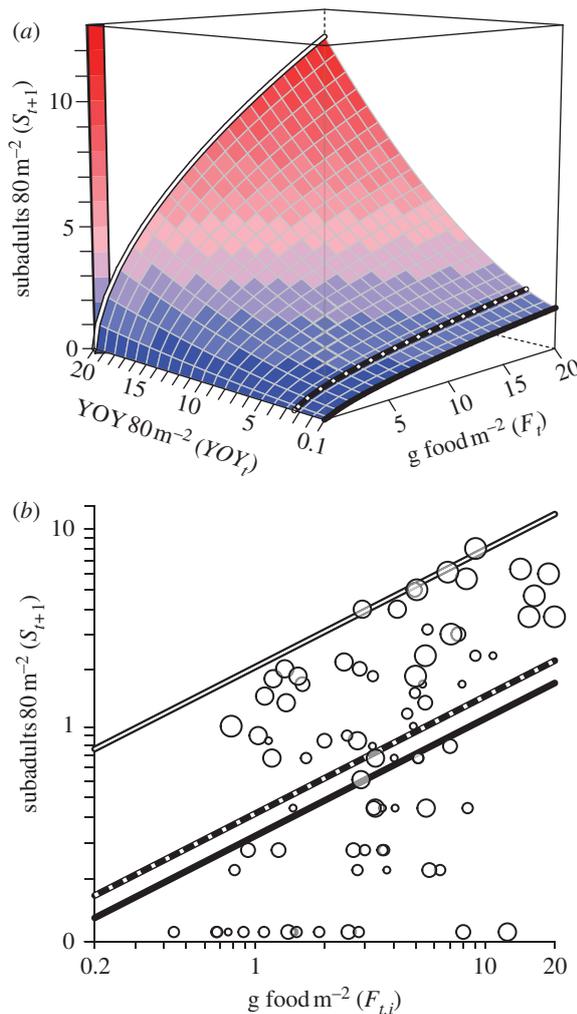


Figure 5. (a) YOY survival model predictions visualized with food in year (t) fixed at its mean value of 3.5 g m^{-2} . Lines are selected predictions along this surface that correspond to those in (b) and represent predictions for different YOY densities (the maximum, mean and minimum). The vertical axis represents density of subadults in year ($t+1$) that survived from YOY in year (t) shown on the left axis. The right axis represents g of food in year (t). (b) Log-scale density of subadults in year (t) versus log-scale food in year (t). Larger points indicate more YOY in year (t) at that site-year combination. Lines correspond to those in (a).

produced offspring or increased reproductive output. The latter may result from increased size-specific fecundity in response to food [45] or increased growth rates of adults

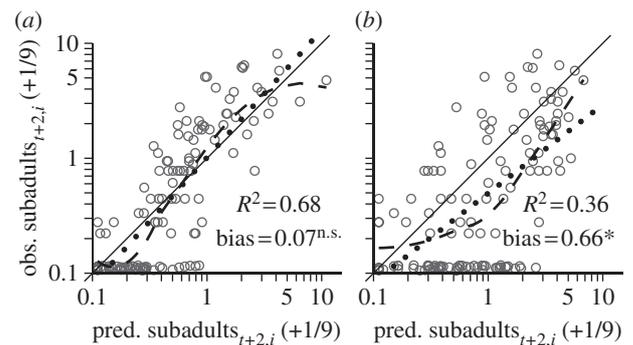


Figure 6. Observed versus predicted values for the combined models using: (a) the best-fit models with food variables, and (b) the Cushing model and linear YOY survival without food variables. Solid lines represent the 1:1 lines, dotted lines represent a fitted linear regression and dashed lines represent a fitted Loess smoother; unbiased model predictions will yield no difference between the 1:1 line and the others. R^2 values are for variance in subadults explained by each model; bias values are the average difference between the predicted and the observed values. * $p < 0.001$. n.s., not significant.

when food availability is high, allowing higher fecundity via a consistent length–fecundity relationship. Species such as surfperch that exhibit the capacity to abort or resorb embryos in response to stress [46], show plasticity in their size–fecundity relationship [47] or exhibit increased growth rates in response to food [25,42] may be especially susceptible to such size-specific fecundity effects when either foraging habitat or the density of food therein changes substantially through time. In either case, we found strong effects of food in all model forms, with the most pronounced in the Cushing. The strong fit in the Cushing model may have resulted from the fact that adult densities were seldom at or above historically high levels throughout the period of this study, limiting the opportunity for asymptotic recruitment or overcompensation to occur. Like the production of young by adults, the effect of food availability on survival of juveniles has been widely suspected, especially for marine fish [12,48], and was also strongly supported by our analyses.

For black surfperch, the large effect of food on production and survival of young diminished as food supply increased. Because fecundity must have an upper limit, survival cannot exceed 100 per cent and fish are likely to become food satiated at some point, it is

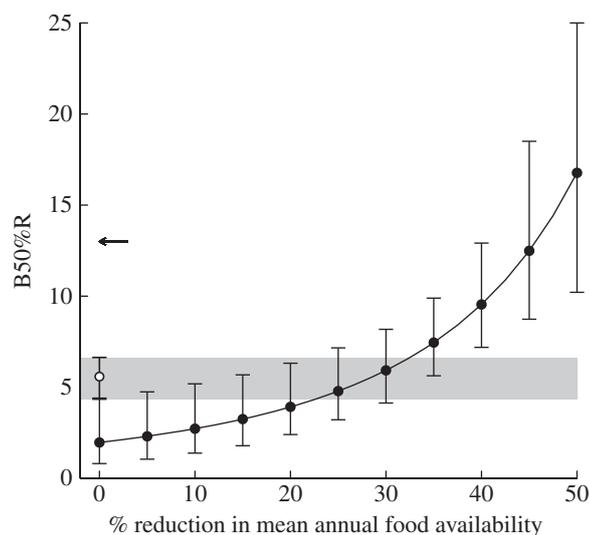


Figure 7. Number of adults required to produce 50% of maximum mean YOY recruitment (i.e. the biological reference point B50%R) as estimated under the Cushing model with food (filled circle) and without (open circle) with the arrow indicating the historical mean-maximum adult density. Error bars represent 95% CIs; the grey band represents the 95% CI for the no-food Cushing model projected across x -axis values.

biologically sensible that their positive relationships with food decelerate and they become increasingly influenced by other factors. While black surfperch is not a fished species, our analyses do not include the effects of other factors that affect demographic rates such as the density of their main predator (kelp bass *Paralabrax clathratus*) [43], structural complexity of refuge habitat [44] and competition with other species (e.g. *Embiotoca lateralis* [49]). Because our best combined model (which included food) explained 68 per cent of observed variation in subadult density, these types of external factors could account for some portion of the unexplained variance. Furthermore, for a given supply of food, production of young and survival to subadulthood varied substantially among our study sites, suggesting the potential importance of external factors. As YOY and, to a lesser extent, subadults are subject to predation, variation in predator densities and/or the abundance of foliose algae that provide refuge may account for some of the unexplained variation. However, our analyses cover population trends of black surfperch during a period when both predator densities [50] and foliose algae (figure 2) were consistently low. We expect that large fluctuations in predator densities, although not seen since the late 1980s, may give rise to synchronous changes in survival of young.

Given that food rarely will be the sole constraint of populations, an approach such as ours that focuses on food resources is perhaps best suited to predict recruitment failure (via low reproductive or survival rates) rather than to predict production of banner year classes. Models that incorporate only food resource information are likely to be less accurate in predicting high recruitment events because other factors probably increase in importance as food availability increases. By contrast, large reproductive output or high survival of young is not expected when food is scarce, regardless of predator densities or other external factors. Thus, management

decisions and conservation measures should carefully consider resource-driven predictions when conditions are poor, but place less confidence in such predictions when food is abundant. Such conclusions are evident from our analyses of the BRP based on the adult stock that produces 50 per cent of the maximum number of recruits (i.e. B50%R). Inclusion of food information had no substantive effect on estimates of B50%R when food availability remained constant, but a large decline in food supply, such as observed in the black surfperch system in the 1980s, predicted such dramatic reductions in productivity that the stock would be considered impaired with respect to recruitment even if the stock was at its historical mean-maximum density. Thus, basing inference upon models and associated BRPs that ignore food information can be imprudent. While calculations as performed here require high-quality food information that is often unavailable, adaptive BRPs could be estimated in the absence of such data where annual demographic vital rates such as adult survival, adult fecundity and mortality of young can be measured in season. Such measurements may, in some cases, provide better estimates of BRPs than those provided by resource informed models, but would lack the capacity to anticipate and evaluate environmental versus anthropogenic effects on demographic rates. For species subject to changes in foraging habitat, such as black surfperch, evaluating the subsequent effect on vital rates and BRPs has the potential to substantially alter recruitment-based management policies in an adaptive setting.

It is reasonable to infer that, for many fishes and other taxa, adult fecundity and survival can exhibit strong plasticity to the availability of food in a manner similar to black surfperch. We suggest that populations exposed to highly variable environments may be more likely to exhibit recruitment dynamics that fluctuate as a result of substantial changes in food availability to a host of life-history stages. Moreover, the history of environmental forcing matters; multiple years of low food will probably lead to recruitment failure in such systems. By contrast, alternating years of high food may buffer a cohort against a single low food year. The surprising lack of definitive evidence for such phenomena stems historically from logistical and analytical limitations, and because high-quality long-term data series of food information are often unavailable. However, accrual of more long-term data and continued advancement of our understanding of ecological systems should lessen such constraints. Tandem investment in time-series estimates of population abundance, age-structure and known food resources coupled with experimentation and modelling should improve our ability to assess and manage populations whose food resources vary through time.

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