Special section
Influence of density dependence on the detection of trends in unobserved life-history stages

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Abstract

In many species, certain life-history stages are difficult or impossible to observe directly, hampering management. Often more easily observed stages are monitored instead, but the extent to which various forms of uncertainty cloud our ability to discern trends in one critical life-history stage by observing another is poorly studied. We develop a stochastic simulation model for threatened California coho salmon *Oncorhynchus kisutch* to examine how well trends in one stage can be detected from observations of another. In particular, we use the model to examine the effect density dependence has on our ability to detect trends. We present a structural form for the transition between life-history stages that encompasses the common functional forms: density independence, Beverton–Holt compensatory density dependence and Ricker-type over-compensation. In small populations, such density dependence is often ignored. However, it may in fact be extremely important, for example if population decline was caused by a decrease in carrying capacity. Our results show that density dependence in any life-history transition significantly reduces the ability to detect trends in abundance; critical but inaccessible stages cannot generally be studied by monitoring more easily observed stages, especially if density dependence is present for any life-cycle transition.

Introduction

For any managed population, for example an endangered species or a newly invading non-native species, an important applied problem is the detection of trends in abundance. The situation is complicated when important life-history stages are difficult to observe, encouraging a reliance on other, more easily monitored stages. For example, if managers desire to eradicate a recently invasive weed, the above-ground abundances are most easily monitored, but it is the difficult-to-observe seed bank whose demise dictates the final extirpation of the exotic species (Kéry, 2004; Kéry, Gregg & Schaub, 2005), and hence the cessation of monitoring and control efforts. Many pest outbreaks are monitored by sampling adult densities, yet it is often larval stages that cause the damage (e.g. gypsy moth in the USA; Sharov *et al*., 1999). Similar issues arise in studies of threatened and endangered species. In certain amphibians, for example, adult stages may be very hard to locate in woodland, whereas floating egg masses and tadpoles are relatively simple to monitor (Rubbo & Kiesecker, 2005). Likewise, seal population abundances are estimated from counts of pups at breeding sites (Ward, Thompson & Hiby, 1987). Despite the fact that this is a common approach, the following question remains: to what extent is it valid to infer trends in one life-history stage by monitoring another?

Detecting trends in one life stage from observations of another seems feasible in principle. After all, if one stage dramatically increases or decreases, it seems only likely that other life stages will follow suit. However, the strong links between different life stages are potentially clouded by a number of uncertainties (Hilborn & Mangel, 1997). Some uncertainty arises as a consequence of external factors, for example environmental variability or anthropogenic influences. Some uncertainty is the inevitable outcome of sampling and observational error. Finally, some uncertainty arises from the possibility that our interpretation of the underlying biological processes (the model) does not

accurately reflect the true system dynamics. For example, we might assume that density dependence is negligible when it is in fact quite important or vice versa. In previous work (Shea & Mangel, 2001), we examined the effects that the former two types of uncertainty have on the probability of detecting trends. We found that statistical power decreases with decreasing autocorrelation in mortality, decreasing census durations and increasing observational error, and that these factors interact. Suitably designed monitoring programs with minimal observational uncertainty and accurate estimates of temporal autocorrelation in vital rates can succeed. However, all these results rest on the assumption that transitions in the life cycle are density independent.

The assumption that density dependence is unimportant is common in studies of endangered species, where populations are dramatically reduced from historical levels. Similarly, as a new species invades it is usual to assume that the invader will exhibit exponential, unbounded growth. If the population size is low because of a decline in vital rates, or because it has just arrived in the environment, such assumptions may be valid. But if the decline is caused by reduction of a limiting resource, competition for that resource may still be fierce even at lower population densities (e.g. Orciari, Mysling & Leonard, 1987), and density dependence should be considered.

Models can be useful in assessing the effectiveness of monitoring strategies (Katzner, Milner-Gulland & Bragin, in press). In this paper, we use a stochastic simulation model to assess the effect of the type and magnitude of density dependence on the detection of trends in abundance in one life-history stage from observations of another. We incorporate a functional form for density dependence that avoids the need for structural changes to address density independence, and compensatory and over-compensatory dynamics. The model is parameterized using data for the threatened California coho salmon *Oncorhynchus kisutch* as an example. California coho salmon *O. kisutch* are listed as threatened under the US Endangered Species Act (ESA; NMFS, 1995). Coho populations declined markedly in the 20th century (Brown, Moyle & Yoshiyama, 1994). ESA listings for coho salmon in most states pertain to adult numbers, but in California current assessments have focused strongly on surveys of juveniles in fresh water. For comparative purposes, there is a need to understand whether trends in observed juvenile abundances provide reliable information about adult trends (Shea & Mangel, 2001).

Methods

Density-dependent population model

Coho salmon are anadromous and semelparous (Shapovalov & Taft, 1954; Sandercock, 1991), with three main life-history stages. Parr (juveniles) emerge in the spring, typically remaining in their natal streams for 1 year, before migrating to the ocean as smolts (immatures), where they live for

about 18 months. Late in the year, adults return to their natal streams to spawn and die. We developed a stage-structured, density-dependent population model, based on the coho salmon life cycle. We consider three life-history stages: juveniles (parr), immatures (smolts) and adults (Fig. 1). The model has annual time steps in January (between spawning and emergence), describes total population size in each stage, and assumes a 50:50 sex ratio.

The general stock–recruitment relationship, for 'recruits', R, into one life-history stage at time $t+1$, from 'stock', S, in the previous stage at time t, is given by

$$R(t+1) = S(t)\psi(S(t)). \qquad (1)$$

To maintain consistency between types of density dependence, we use a common structural form for $\psi(S(t))$, modified from Shepherd (1982) (see also a review of common functional forms of density dependence in Elliott, 1994):

$$R(t+1) = \frac{aS(t)}{1 + b(aS(t)/K)^b}. \qquad (2)$$

The parameter a is a productivity parameter, and relates to the rate of increase of the population at low densities (Shepherd, 1982). In the case of sequential life-history classes, a is a survivorship ($0 < a < 1$); in the case of transitions spanning a reproductive stage, a incorporates elements of both fecundity and survivorship. K is broadly defined as a capacity parameter (Moussalli & Hilborn, 1986). In this general formula, b is the 'shape' parameter that generates functional forms ranging from no density dependence to Beverton–Holt compensatory density dependence (Beverton & Holt, 1957) and Ricker-type over-compensatory density dependence (Ricker, 1954). Shepherd (1982) does not include b as a multiplier in the denominator. We do for the following reason. If $b = 0$ then there is no density
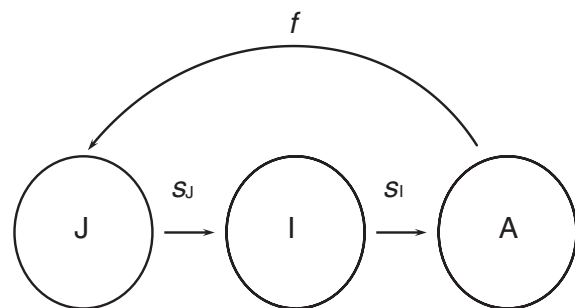
Figure 1 Life-cycle diagram for a species with three life-history stages. Circles represent the densities of juveniles, *J*, immatures, *I*, and adults, *A*, respectively, at any time *t*. Arrows represent transitions between these stages. The population parameter *f* represents the number of juveniles produced at time *t* by adult females at time *t*−1 (number of offspring per female × early survivorship). The parameter $s_J(t)$ represents survivorship of juveniles at time *t*−1 to immatures at time *t*, and $s_I(t)$ represents survivorship of immatures at time *t*−1 to adults at time *t*.

dependence, $R(t + 1) = aS(t)$, and a is thus the maximum R per S. If $b = 1$ then we recapture the Beverton–Holt function exactly. As b increases to 2 (and beyond) dependence increases and the resulting curve becomes Rickeresque in form. In the case where $b = 0$, the magnitude of K is irrelevant; however, for $b > 0$, lower K values lead to stronger effects of density in S on the value of R. Thus, both a and K have a single directly interpretable meaning. The parameter b broadly determines the shape of the curve, but as such it affects the rate of increase at low densities (i.e. it can affect what a affects), the maximum of the curve (i.e. it can affect what K affects) as well as the overall form of the curve. Examples of the form of the curve for different values of b are shown in Fig. 2.

The function in Equation (2) can take a different form (determined by b and K) for each life-history transition in the life cycle of the focal species. Juveniles are produced by adults according to

$$J(t) = \frac{fA(t-1)/2}{1 + b_J(fA(t-1)/2K_J)^{b_J}}. \tag{3}$$

We model total population size; hence $A(t-1)/2$ adults (the females) each produce f juveniles (of both sexes). Note again that this is maximum fecundity (achieved only at extremely low population densities or in the absence of density dependence; a is the slope at the axis in Fig. 2) and not an estimate of typical realized fecundity. Variation in fecundity is not included. K_J is the capacity parameter for juvenile

production by adults and b_J is the shape parameter for the same transition.

Immatures develop from juveniles according to

$$I(t) = \frac{s_J(t)J(t-1)}{1 + b_I(s_J(t)J(t-1)/K_I)^{b_I}}. \tag{4}$$

Adults develop from immatures according to

$$A(t) = \frac{s_I(t)I(t-1)}{1 + b_A(s_I(t)I(t-1)/K_A)^{b_A}}. \tag{5}$$

K_I and K_A are the capacity parameters for juvenile to immature survivorship and immature to adult survivorship, respectively. Similarly, b_I and b_A are the shape parameters for juvenile to immature survivorship and immature to adult survivorship. The two annual survivorships, $s(t)$, are related to the instantaneous mortality rates, $M(t)$, by

$$s(t) = e^{-M(t)}. \tag{6}$$

A previous model for coho salmon, which assumed density independence, showed that both autocorrelation in mortalities and observational uncertainty affect the detection of trends (Shea & Mangel, 2001); hence both are included in the present model. We assume that instantaneous mortality is correlated from year to year because of environmental conditions, with autocorrelation parameter ρ:

$$M(t) = \rho M(t-1) + (1-\rho)Z(t)$$
$$M(0), Z(t) \sim N(\bar{M}, \sigma_M^2). \tag{7}$$

Thus there is a contribution ρ by the previous year's mortality and a contribution $1-\rho$ from the random variable $Z(t)$. Observational uncertainty in juveniles is assumed to follow a lognormal distribution. Observed juveniles, $J_{obs}(t)$, are related to true juveniles, $J(t)$, by

$$J_{obs}(t) = J(t)e^{(\sigma_{obs}X - \frac{1}{2}\sigma_{obs}^2)}. \tag{8}$$

$X(0,1)$ is a normally distributed random variable and σ_{obs} is the standard deviation of the observational uncertainty. We used the Box–Muller method (Press et al., 1989) to generate normal random variables. Parameters used in the coho model are summarized in Table 1.

Detection of trends in abundance

We explore how density dependence affects our ability to detect adult population trends from information about juvenile numbers by examining the relationship between correlations in the trends in adult and juvenile abundances through time. We simulated population trajectories of 300 years, ignoring the first 90 years of output to ensure the decay of transients. A subset of y years was randomly selected from the remainder of each trajectory; y is thus the survey length. We carried out regression analyses of abundance through time for each of three variables: true number of adults, $A(t-1)$, true juveniles, $J(t)$, and observed juvenile numbers, $J_{obs}(t)$. For each variable, the regression was calculated and tested against the null hypothesis that the
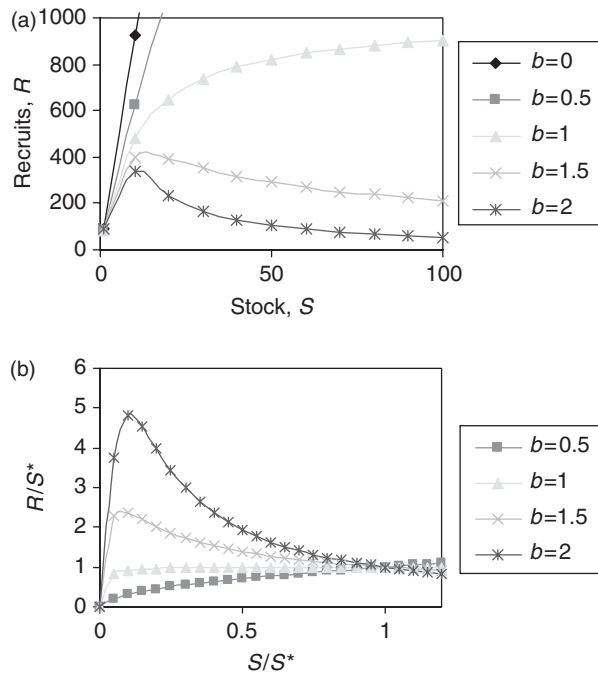
Figure 2 (a) Stock–recruitment relationship used in each life-history transition, showing the effect of altering the parameter b (for $a = 92.5$, $K = 1000$). (b) The same curves as in (a), scaled by the equilibrium stock size, S^*.

Table 1 Parameters used in the coho simulation model

Parameter	Value
Productivity parameters, a	
Adult to juvenile ($a = f/2$)	92.5 parr per adult
Juvenile to immature ($a = s_J$)	0.28 smolts per parr
Immature to adult ($a = s_I$)	0.31 adults per smolt
Standard deviation of observational uncertainty for juveniles, σ_{obs}	0.4
Strength of temporal autocorrelation between mortalities, ρ	0.29
Length of census, y	20 years

The productivity parameter, *a*, for each life-cycle transition was estimated from data published in Shapovalov & Taft (1954) for coho salmon in Waddell Creek, CA. The maximum lifetime productivity parameter (the maximum number of new individuals produced by each individual) is the product of the three stage-specific productivity parameters, and is eight adults per adult. The standard deviation estimate and the estimate of temporal autocorrelation are from Berman (1999). The census length corresponds to the length of NMFS time series data sets for California.

slope was not significantly different from zero (at the 5% level). If the slope was significantly different, then the direction of the trend was found from the sign of the regression coefficient. This procedure was repeated 1000 times for each combination of parameters. Using this method, we then asked how often trends in adult abundance are accompanied by trends in observed juvenile number, and vice versa, under different levels and forms of density dependence in the different life-history transitions. Note that we are not discussing the relationship between the same individuals at one time and the next, or between individuals and their offspring; instead, we are focused on the trend in numbers in those stages across multiple years. We present the theory for a situation where we are interested in detecting a decline, but the same model could also be used to investigate the probability of detecting an increase (in de-listing or invasion scenarios).

We let $\Pr\{A\downarrow\}$ denote the probability that the true adult population is declining, $\Pr\{J_{obs}\downarrow\}$ the probability that the observed juvenile population is declining, and $\Pr\{J_{obs}\downarrow, A\downarrow\}$ the probability that both are declining. These probabilities were calculated as the proportion of the 1000 runs in which statistically significant declines were obtained. The first question is, 'Given a decline in observed juvenile numbers, what is the chance this reflects a decline in adults?', which is denoted as $\Pr\{A\downarrow|J_{obs}\downarrow\}$. Using the standard definition of conditional probability, we obtain

$$\Pr\{A\downarrow|J_{obs}\downarrow\} = \Pr\{J_{obs}\downarrow, A\downarrow\}/\Pr\{J_{obs}\downarrow\}. \tag{9}$$

The second question is, 'Given a decline in adult numbers, what is the chance that we see a decline in juveniles?' This can be denoted as $\Pr\{J_{obs}\downarrow|A\downarrow\}$, giving

$$\Pr\{J_{obs}\downarrow|A\downarrow\} = \Pr\{J_{obs}\downarrow, A\downarrow\}/\Pr\{A\downarrow\}. \tag{10}$$

Model investigation

We explored the model for threatened California coho salmon in three ways. First, we examined the literature for the best information on functional forms of density dependence in coho salmon and simulated the scenarios for which there is most support. Second, we systematically explored the general effects of variation in *b* and *K*, the parameters for which least information is known, in order to draw more general conclusions about the effect of density dependence. Third, we explored the model analytically, to explain and clarify the simulation model results.

A search of the literature revealed more than 100 papers in which the authors presented opinions or evidence regarding the possibility of density dependence in salmonid life-history transitions. The papers and their main conclusions are summarized here and presented in detail at http://www.soe.ucsc.edu/~msmangel/cohobib.pdf. In the transitions from spawner to emerging fry, emerging fry to fall parr (summer survival) and fall parr to outmigrating smolt (winter survival), most authors agree that survivorship decreases at high densities as a result of stream habitat limitation (e.g. Brown *et al.*, 1994; Bradford, 1997). Those authors who suggest a form for the stock–recruitment relationship generally produce something similar to a 'hockey stick' model or the Beverton–Holt equation, both of which reflect compensatory density dependence (Barrowman & Myers, 2000; Bradford, Myers & Irvine, 2000). Other support for compensatory density dependence comes from observations of consistent densities of fish within occupied habitats across years, increased numbers after habitat has been augmented and decreased numbers after habitat loss (e.g. Chapman, 1965; Nickelson *et al.*, 1992). These findings suggest both that a carrying capacity exists in streams and that the population is near it. Most authors seem to agree that mortality in the ocean is strongest shortly after ocean entry (Fisher & Pearcy, 1988; Emlen *et al.*, 1990), is dominated by ocean conditions (e.g. upwelling; Scarnecchia, 1981; Clark & McCarl, 1983; Lawson, 1997; Coronado & Hilborn, 1998), and correlates positively with size at ocean entry (at least in years of low upwelling) (Gowan & McNeil, 1984; Bradford, 1995). However, opinions regarding the presence or absence of density-dependent marine survival are nearly evenly split (e.g. *present:* McCarl & Rettig, 1983; Pearcy, 1997; *absent:* Nickelson, 1986; House & Crispin, 1990). A major confounding factor has been the release of increasing numbers of hatchery fish, which have lower survivorship than wild fish (Nickelson, 1986). The hypothesis of density-dependent marine survival in coho salmon remains to be satisfactorily tested (Peterman, 1989).

In the general simulations, we also used the base parameters for the coho system from Table 1, and then systematically varied the parameters *b* and *K*. The parameter *b* was increased from 0 to 2.0 in steps of 0.2, and *K* was increased from 1 to 1 000 000 in multiples of 10 (1000 runs for each combination of parameters). We additionally explored how detection of significant trends related to the magnitude of the trends concerned.

In a full analytic exploration of this model, we would consider Equations (3–5) for juveniles, immatures and adults, evaluated at equilibrium (J^*, I^* and A^*). With three equations and three unknowns, we could then find an algebraic solution. However, for simplicity, we instead give an intuitive heuristic explanation by analyzing the one-step stock–recruitment relationship [Equation (2)].
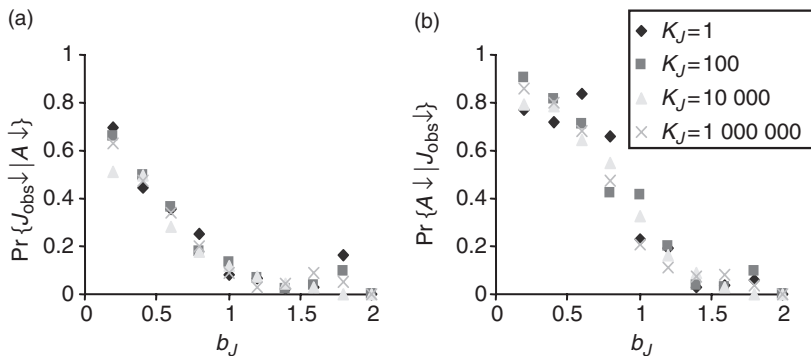
Results

Results for the two scenarios most closely corresponding to our best and current understanding of the natural coho
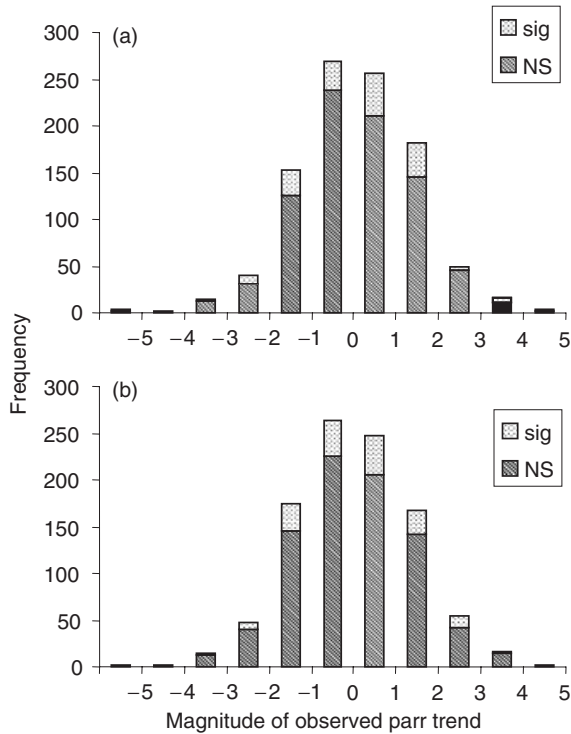

Figure 3 Frequency (out of 1000 runs) and significance of true adult trend plotted against the observed parr (juvenile) trend (change in population size per annum) for the case where all $K = 100$, and $b_J = 1.0$, $b_I = 1.0$ and $b_A = 0.2$ in (a), $b_A = 1.0$ in (b). These parameters correspond to our best understanding of the real state of affairs for coho (as outlined in the section on density dependence).

system are shown in Fig. 3. In both parts of the figure, based on a consensus in the literature, parr (juvenile) and smolt (immature) production are compensatory. Ocean survivorship may be either (1) density independent or (2) density dependent. Figure 3 shows that in both cases the ranges of parr population trends observed are the same. Both scenarios have similar proportions of significant observations of adult trends (16.5 and 16.2%, respectively), and these are distributed similarly across parr trend sizes: larger trends are more likely to be detected as significant, but a high proportion is not detected. Both scenarios also have similar $\Pr\{J_{\mathrm{obs}} \downarrow | A \downarrow\}$ (0.12 and 0.10, respectively) and $\Pr\{A \downarrow | J_{\mathrm{obs}} \downarrow\}$ (0.31 and 0.28, respectively). In this respect, therefore, we can say that the presence or absence of density-dependent ocean survival is relatively unimportant to our ability to detect trends, because the presence of density dependence elsewhere in the life cycle has already clouded our ability to draw conclusions about adult trends from juvenile surveys.

The simulation study shows that our ability to discern correctly the relationship between observed juvenile and actual adult number, as defined by $\Pr\{A \downarrow | J_{\mathrm{obs}} \downarrow\}$ and $\Pr\{J_{\mathrm{obs}} \downarrow | A \downarrow\}$, is in general reduced by the presence of density dependence. The effect is generated by the functional form of the density dependence, that is by the parameter b, which describes the transition from density independence (or almost so, $b = 0.2$), through compensatory density dependence ($b = 1.0$) to over-compensatory density dependence ($b = 1.8$; Fig. 4). There is little or no effect of the capacity parameter, K (Fig. 5); see the analytical results below for an explanation. As the strength of density dependence increases (from $b \approx 0$ to $b > 1$), there is a strong decline in our ability to detect trends, although this increases slightly as b increases toward 2. The increasing spread in probabilities seen over a given range of K for increasing values of b, with all other b's and K's fixed (e.g. Fig. 4a as b increases from 1.5 to 2), arises because as b increases beyond 1.5 (i.e. as the over-compensatory density dependence becomes stronger) the population becomes more tightly regulated and the number of runs in which either adults or juveniles exhibit a measurable decline decreases, so that our sample size is reduced and the numbers in the denominators of the probability estimates decline. As found previously (Shea & Mangel, 2001), $\Pr\{A \downarrow | J_{\mathrm{obs}} \downarrow\}$ is in general higher

Figure 4 Probability of trend detection $\Pr\{J_{\mathrm{obs}} \downarrow | A \downarrow\}$ in (a) and $\Pr\{A \downarrow | J_{\mathrm{obs}} \downarrow\}$ in (b) against b_J. All other K's are 10^6 and all other b's are 0.2. The results for b_I and b_A are qualitatively similar.
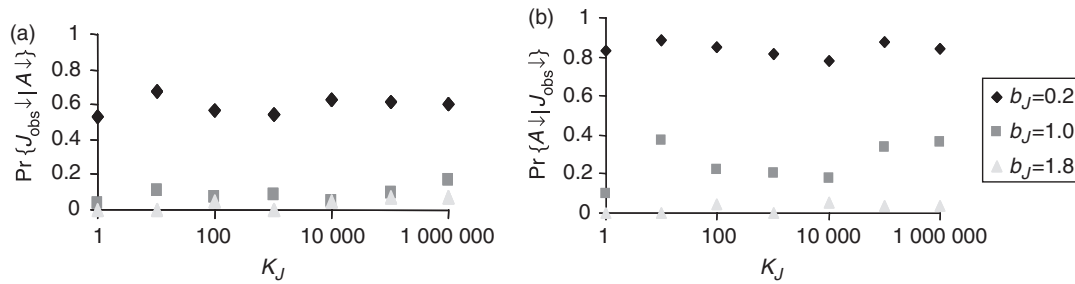
Figure 5 Probability of trend detection $\Pr\{J_{\mathrm{obs}} \downarrow | A \downarrow\}$ in (a) and $\Pr\{A \downarrow | J_{\mathrm{obs}} \downarrow\}$ in (b) against K_J. All other K's are 10^6 and all other b's are 0.2. The results for K_I and K_A are qualitatively similar.
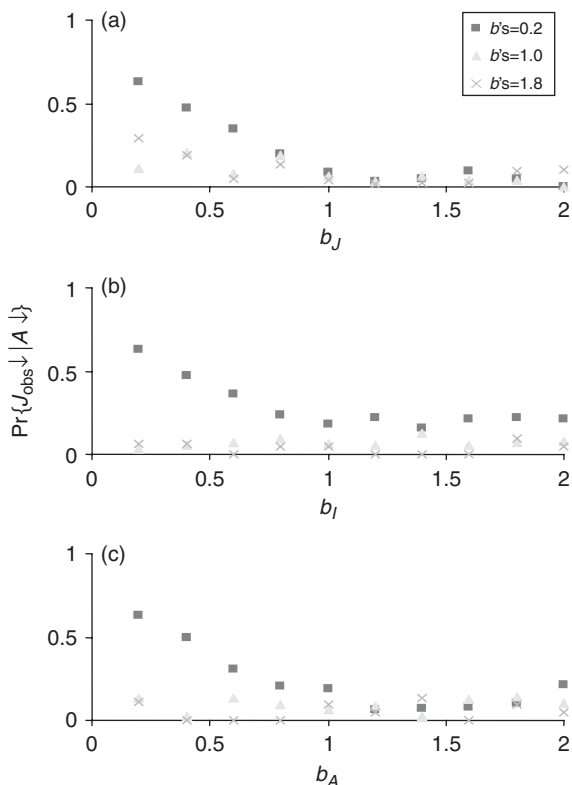
Figure 6 Probability of detecting a trend, $\Pr\{J_{\mathrm{obs}} \downarrow | A \downarrow\}$, against b_J in (a), b_I in (b) and b_A in (c). In each plot, the other two parameters, b, are set at 0.2, 1.0 or 1.8, corresponding to no, compensatory or over-compensatory density dependence. All $K = 10^6$.

than $\Pr\{J_{\mathrm{obs}} \downarrow | A \downarrow\}$ because the elevated variance in observed juvenile numbers (because of observational uncertainty) makes significant observed juvenile trends ($J_{\mathrm{obs}} \downarrow$) rare compared with significant adult trends ($A \downarrow$). Thus the probability of declines occurring both in A and in J_{obs}, $\Pr\{A \downarrow | J_{\mathrm{obs}} \downarrow\}$, depends more strongly on $\Pr\{J_{\mathrm{obs}} \downarrow\}$ than on $\Pr\{A \downarrow\}$.

Fairly strong density dependence (high b) in any one transition strongly reduces the probability of detecting a trend, regardless of the strength of density dependence in the other life-history transitions. This effect can be understood

with reference to Figs 5 and 6. For example, in Fig. 5a, both immature and adult production are density independent. If this is true of juvenile production also, then the probability of detecting an existing adult trend by observing juveniles is greater than 0.5 (for all K_J; see the diamonds). As soon as there is some density dependence in parr production, however, the probability of detecting a trend dips well below 0.5 (squares and triangles). This is also true for density dependence in immature and adult production and similarly for all cases where we ask what our chance is of there being an adult trend if we see one in juveniles (Fig. 5b). We can see this in more detail in Fig. 6. In Fig. 6a, b_J is varied across its entire range, with b_I and b_A both set to either negligible, compensatory or over-compensatory density dependence. Only when all three values of b equal 0.2 do we have a greater than 0.5 probability of detecting an actual adult trend using parr surveys. Similar results are obtained for b_I and b_A (Fig. 6b, c).
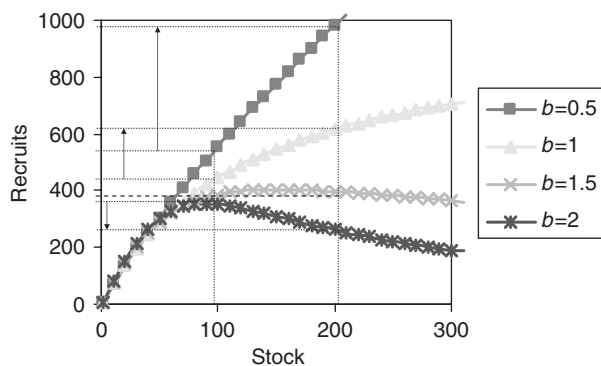
The probability of detecting a trend reaches a minimum at values of b somewhere between 1.0 and 1.5. This can be understood with reference to Fig. 7 and to the analysis of the one-step stock–recruitment relationship. At low values of b, when density dependence is weakly compensatory or non-existent, a small change in the stock in one class can cause a large change to the recruitment into the next class. As the stock–recruitment curve becomes saturating ($b = 1$) this effect declines, and reaches a minimum at a value of b between 1.0 and 1.5. Then as b continues to increase, the effect of a given change in the stock on the corresponding recruitment into the next class begins to increase again. The minimum can be found by evaluating $\mathrm{d}R/\mathrm{d}S = 0$ [using Equation (2)] at the equilibrium, S^*. Some minimal density dependence (non-zero b) must be assumed in this evaluation, because without it there is no equilibrium. The equilibrium, when $S = R = S^*$, is given by

$$S^* = \frac{K}{a}\left(\frac{a-1}{b}\right)^{1/b} \tag{11}$$

so that

$$\frac{\mathrm{d}R}{\mathrm{d}S} = \frac{a(1+x-bx)}{(1+x)^2} = 0, \quad \text{where} \quad x = b\left(\frac{aS^*}{K}\right)^b. \tag{12}$$

This gives the result that the minimum in dR/dS is at $a + b = ab$. Thus, the value of K is immaterial to the location of the minimum. One coho adult produces *at most* an average of eight new adults in the next generation (Table 1). In the one-step stock–recruitment relationship system, this estimate gives a value of $b = 1.14$ at the minimum of dR/dS, which agrees with our Monte Carlo results. This result means that monitoring one stage from observations of another is least likely to be successful when $b \approx 1$; unfortunately, this is a very likely scenario for coho salmon. The sensitivity of our results to changes in a is illustrated in Fig. 8. The location of the minimum is sensitive to decreases in overall a (e.g. from a maximum of eight to a maximum of three adults per adult) but relatively insensitive to increases

in overall a (e.g. from a maximum of eight to a maximum of 100 adults per adult).

Discussion

Our results show that the form of density dependence can make a major difference to the ability one has to discern trends in the abundance of one life-history stage from surveys of another. There is a negligible effect of varying the capacity parameter K, but a strong effect of the functional form of the density dependence, as mediated by the parameter b. As the strength of density dependence in the life history as a whole increases, the probability of detecting a trend declines. Only in the case where there is little density dependence in all three life-history transitions is there an appreciable chance of detecting trends in population abundances. These results are the same for each of the three life-history transitions. If there is density dependence in any stage, that quickly reduces the probability of detecting a trend at all, irrespective of the stage affected.

Although in any particular instance a strong trend may be observed in juveniles, our results reinforce previous studies that show that even large trends may not in fact be statistically (or biologically) significant. A failure to estimate statistical power is still a significant problem in resource management (Gerrodette, 1987; Peterman & Bradford, 1987; Peterman, 1990; Schmitt & Osenberg, 1996; Shea & Mangel, 2001; Jonzen, Rhodes & Possingham, 2005; Maxwell & Jennings, 2005). For example, many studies conclude that trends are absent, when in fact they may have insufficient power to justify such claims (e.g. Mangel, 1993; Musick, 1999).

Carrying capacity and other parameters related to density dependence have been notoriously difficult to measure with any level of accuracy for California coho salmon (see Taylor, 1999 for a similar story in Oregon and Washington). Our best understanding of the real forms of density dependence in different life-history stages leads us to estimate that the chance of detecting a decline in parr, given an actual decline in adults, is *c.* 10% (the signal was missed in 90.1 and 88.5% of the runs for the two ocean scenarios in Fig. 3). The chance that an observed decline in parr mirrors a real decline in adults is *c.* 30% (a false signal was obtained in 72.4 and 69.4% of the runs for the two ocean scenarios). Furthermore, these rates are worse than they first appear: in around 20% of cases where both parr (juvenile) and adult trends were significant, the trends were in opposite directions. The implication of our work is that unless one is confident that density dependence is not acting at any stage of the life history, an attempt to monitor the status of adults through juvenile surveys may be futile. That is, adults themselves need to be monitored.

These general insights are likely applicable to any species with a multiple-stage life cycle similar to the one presented here. If life cycles also involve either individuals which remain in stages for more than one transition or additional complications such as delayed density dependence, then the situation would be exacerbated even further. Certainly we

Figure 7 Effect of a change in stock, S, on the change in recruitment, R, for different forms of density dependence. When there is over-compensatory density dependence ($b = 2$), a doubling in stock, S, from 100 to 200 individuals leads to an overall decline in recruits, R (see the lowest arrow, pointing down). At intermediate levels of density dependence (when $b = 1.5$), the same change in S has no effect on R. When $b = 1$ (which corresponds to the Beverton–Holt compensatory density-dependent form), the result is an increase in R (see the middle arrow, pointing up). As the strength of density dependence declines further ($b = 0.5$ and below), the magnitude of the increase in R itself increases (see the large top arrow, pointing up).
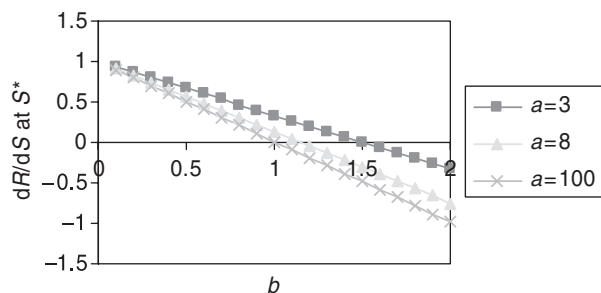
Figure 8 Rate of change in recruits, R, resulting from a change in stock, S, evaluated at the equilibrium value, S^*. The rate of change of dR/dS is at a minimum when $a + b = ab$. If lifetime $a = 8$, then the value of b at the minimum is $b = 8/7 = 1.14$. As a increases, the value of b at the minimum converges to 1. The parameter K does not appear in this result and so the value of K makes no difference.

recommend an analysis of the kind we present here to assess whether monitoring other stages would be informative or just a waste of time and resources. For example, some species may exhibit dynamics that would be well described by higher values of b; a detailed exploration of a case study for such a situation would be very informative. However, if such an analysis is not feasible, then we suggest a rule of thumb: if it is important to monitor one life-history stage of a species, then, unless there is great confidence that trends in different stages do track each other closely, another life stage should not be used as a proxy.

Acknowledgements

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