

Detection of population trends in threatened coho salmon (*Oncorhynchus kisutch*)

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Abstract: Populations of coho salmon (*Oncorhynchus kisutch*) in California are listed as threatened under the U.S. Endangered Species Act. Such listings refer to adult populations, but often, juvenile life history stages are censused, so it is important to understand what affects the relationship between true adult and observed juvenile numbers. We present models to address how observational uncertainty, census length, and autocorrelation in vital rates affect our ability to observe trends. We ask two questions about our ability to detect declines in one life history stage from censuses of another. First, given an observed decline in parr numbers, what is the chance that this reflects a decline in adults? Second, given that adult numbers are declining, what is the chance that we see that decline in parr? Our results indicate that statistical power decreases with increasing observational uncertainty and decreasing census lengths and demonstrate how these two parameters interact. Power increases as the level of autocorrelation in mortality rates increases. Management recommendations include obtaining more accurate estimates of autocorrelation in mortality and of observational uncertainty.

Résumé : Les populations du Saumon coho (*Oncorhynchus kisutch*) de la Californie apparaissent sur la liste des espèces vulnérables conformément à la loi américaine sur les espèces menacées. Cette désignation concerne les populations d'adultes; comme il y a souvent des stades plus jeunes qui sont inclus dans les inventaires, il importe de comprendre les détails de la relation qui unit les nombres des vrais adultes et les nombres observés de jeunes. Des modèles permettent de comprendre comment l'incertitude des observations, la durée des inventaires et l'autocorrélation dans les taux vitaux affectent notre habileté à observer les tendances. Nous posons deux questions sur la possibilité de détecter les déclinés dans un stade du cycle biologique à partir d'inventaires faits sur un autre stade. Premièrement, quelle est la probabilité d'avoir un déclin dans la densité des adultes lorsqu'on observe une diminution des densités des tacons? Puis, quelle est la probabilité de discerner chez les tacons un déclin qui se produit chez les adultes? Nos résultats montrent que la puissance statistique diminue lorsque l'incertitude des observations augmente et la durée des inventaires diminue; ils illustrent aussi l'interaction entre les deux variables. La puissance croît à mesure que l'autocorrélation entre les taux de mortalité augmente. Pour fins d'aménagement, nous recommandons d'obtenir des estimations plus précises de l'autocorrélation de la mortalité, ainsi que de l'incertitude des observations.

[Traduit par la Rédaction]

Introduction

Several of the seven Pacific salmon species, including coho salmon (*Oncorhynchus kisutch*), have recently been listed as threatened under the U.S. Endangered Species Act. Californian populations of this species have declined considerably in the past century (Brown et al. 1994). In response to this decline, distinct populations of coho in California were defined and listed in terms of evolutionary significant units (National Marine Fisheries Service 1995; Weitkamp et al. 1995). Coho in the central California evolutionary significant units were listed in October 1996 and in the southern

Oregon – northern California evolutionary significant units in May 1997 (Spencer 1999).

Status reviews for this species in Washington and Oregon focus on spawner time series, which extend back to the 1950s (Weitkamp et al. 1995). In California, however, data are far less extensive (Brown et al. 1994; Weitkamp et al. 1995). Much of the focus is on presence-absence data, and few ongoing field surveys were commenced before 1990 (Spencer 1999). Furthermore, these surveys have mainly focused on river-dwelling juvenile stages (parr) and include snorkel surveys of juvenile numbers and electrofishing (P.B. Adams, National Marine Fisheries Service, Santa Cruz, CA 95064, U.S.A., personal communication). As U.S. Endangered Species Act listing and delisting assessments usually pertain to adult numbers (in the case of salmon, spawner escapement), it is necessary for there to be an understanding of the relationship between adult and juvenile numbers. Given that the endogenous and exogenous factors affecting the life history of this species are uncertain and that sampling efforts introduce additional uncertainty, this is not a trivial link to evaluate.

Uncertainty in this system arises from three main sources (Hilborn and Mangel 1997). Some of this uncertainty is endogenous, including uncertainty about biological processes such as mortality (particularly in the ocean-dwelling phase)

Received January 20, 2000. Accepted November 2, 2000.
Published on the NRC Research Press Web site on January 29, 2001.
J15539

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Table 1. Life history of coho salmon.

Year	Season	Event
t	Autumn	Spawning occurs and eggs are laid
$t + 1$	Spring	Parr emerge
$t + 2$	Spring	Smolts migrate
$t + 2$	Autumn	Jacks return (male only) (zero sea winters: 6 months)
$t + 3$	Autumn	Adults return (male and females) (one sea winter: 18 months)
$t + 4$	Autumn	Adults return (females only) (two sea winters: 30 months)

Note: For most of the range of coho, spring indicates April or May, while autumn indicates November. In California, the timing of events tends to be later in the year (Shapovalov and Taft 1954).

and demographic and genetic stochasticity. There are also exogenous sources of uncertainty: the amount of, and role played by, environmental stochasticity and catastrophes. Finally, there is observational uncertainty, arising from sampling efforts. This uncertainty limits our ability to detect changes in population levels and hampers management efforts.

Development of models for this system involves summarizing known biological and ecological aspects and hence will highlight important unknown quantities. Models will allow us to target which aspects are most important to understand fully, using different types of sensitivity analyses. Once developed, such models can also be used to direct empirical research efforts, to focus on management strategies that seem most likely to succeed in achieving conservation goals, and to ask ecological and management questions that are hard, or even impossible, to answer in the field.

We first present a model that summarizes the most general biology and life history of this species. This generic model comprises a series of nested, subsidiary models. Using this framework, we can compare models of increasing complexity (incorporating different life history and environmental factors) under different levels of observational uncertainty. This will highlight which parts of the life history it is important to know best (a target for future experimental research) and also whether existing sampling methodologies are sufficiently accurate to be useful in this system.

Sensitivity analyses allow us to estimate the relative "value" (i.e., usefulness) of different types of information for this system. Hence, we can ask which data are worth spending time and resources to obtain and which information we can manage without. Thus, our objective is to make recommendations to managers, not for management. Sensitivity analyses can be carried out at one of three levels. Sensitivity can be examined at the level of the model structure (e.g., by including or excluding different life history stages), at the level of the mathematical form (e.g., \pm environmental autocorrelation), or at the level of the parameter (e.g., differing amounts of autocorrelation). Some, or all, of these different types of analyses can be carried out for all factors about which there is uncertainty.

We then present a simplified life history model for coho. We use this specific model to assess the power that current sampling methods for juveniles (parr) have to tell us about trends in adult populations. We ask how observational uncertainty, length of time series, and autocorrelation in vital rates affect our ability to observe the true state of affairs. We pose two main questions. First, given an observed decline in parr numbers, what is the chance that this reflects a decline in

adults? Second, given that adult numbers are declining, what is the chance that we see that decline? We assess how the answers to these questions change in response to changes in observational uncertainty, census length, and autocorrelation in vital rates. The relative importance of these factors will highlight whether existing sampling methodologies are sufficiently accurate to be useful in this system.

Methods

Summary of coho salmon biology, life history, and ecology

Coho salmon is one of the seven Pacific salmon species (genus *Oncorhynchus*). Coho have a semelparous life history strategy (Shapovalov and Taft 1954; Sandercock 1991). Late in the year, adults migrate from the ocean to their natal streams, where spawning occurs. After spawning, they die. Parr emerge the next spring and usually remain in freshwater for 1 year before migrating to the sea as smolts. The majority of these fish remain in the ocean for 18 months before returning to freshwater to begin the cycle again. Some males, called jacks, return after only 6 months at sea. Some females may remain at sea for two winters, returning to spawn after 30 months. A summary of this cycle is shown in Table 1. For further details, see Sandercock (1991).

Coho salmon life history model

Figure 1a shows a life cycle diagram for coho salmon. A simplified version of this life cycle, in which the early-returning jacks and late-returning females (which form a minority of the population) are ignored, is presented in Fig. 1b. The model equations for the simplified life history are presented in the Appendix.

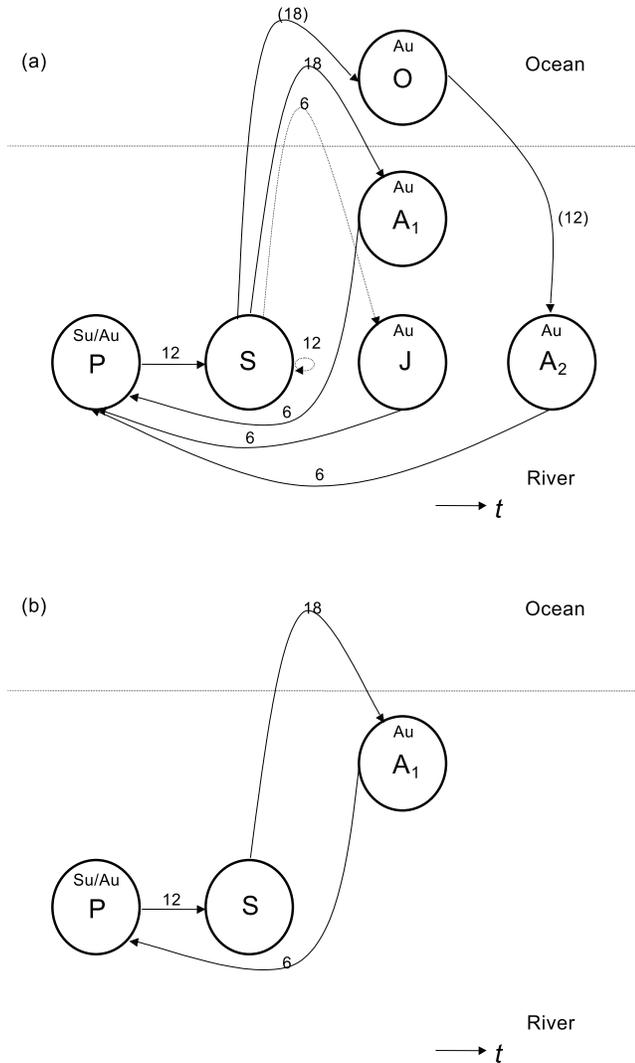
The model is a discrete-time, age-structured model, with time steps of 1 year. Censuses are modeled on an annual basis with a defining cutoff in January (i.e., after spawning and before emergence and migration). The number of individuals (both male and female) in a life history stage is considered either in summer and early autumn (juveniles) or in late autumn (adults) of any given year. Note that an egg stage is not included explicitly, due to the model timing, but that data on egg production are included in the parr stage formula. We assume a 50:50 sex ratio. We do not include density dependence in this version of the model, since populations of this species have been dramatically reduced from historical levels.

Observational uncertainty

Observational uncertainty in the models is assumed to follow a lognormal distribution, where X is $N(0,1)$ and σ_{obs} is the standard deviation of the observational uncertainty (see Hilborn and Mangel 1997, p. 146, 7.33). Thus, observed parr, P_{obs} , are related to true parr, P , by

$$(1) \quad P_{\text{obs}} = Pe^{(\sigma_{\text{obs}}X - \frac{1}{2}\sigma_{\text{obs}}^2)}.$$

Fig. 1. (a) Full and (b) simplified life cycle diagrams for coho salmon. Circles represent life history stages of the coho. P, S, O, A₁, A₂, and J refer to the densities of parr, smolts, ocean-dwelling salmon, one-sea-winter adults, two-sea-winter adults, and jacks, respectively, all at time *t*. Arrows represent transitions between these stages. Time *t* (in years) can be read from left to right, as indicated. Stages or transitions below the dotted line occur in the river. Stages and transitions above the line occur in the ocean. Su/Au or Au at the top of a stage indicates that that stage is counted in late summer – early autumn or in autumn, respectively. The number above any transition indicates the time (in months) between the two linked life history stages.



We used the Box–Muller method (Press et al. 1989) to generate normal random variables.

Detection of trends in abundance over time

This work concerns our ability to correctly detect trends in abundance. Type I errors occur when there is no trend in abundance, but we incorrectly conclude that one exists. Type II errors occur when there is a trend in abundance, but we falsely conclude that none exists. If the probability of making a Type II error is β , then the statistical power is $1 - \beta$.

Statistical power to detect trends in abundance (Gerodette 1987; Peterman and Bradford 1987; Peterman 1990) is especially vital in

endangered populations. In the present paper, we are interested in the statistical power to detect trends in true adult numbers from observed trends in juvenile numbers. In order to assess this, we examined how adult and juvenile numbers changed through time and how these trends were correlated.

Population trajectories of 300 years were simulated using the specific model. All analyses were carried out after at least 90 years to ensure that transients had disappeared. Regression analyses were based on subsets of the full trajectory of 5-, 10-, 15-, or 20-year observation windows. For each trajectory, regression analyses of abundance through time were carried out for each of three variables: true adult numbers, $A(t - 1)$, true parr numbers $P(t)$, and observed parr numbers $P_{obs}(t)$. In each case, a regression slope was calculated and tested against the null hypothesis that the slope was not significantly different from zero (i.e., the population size is staying the same) in a two-tailed *t* test at the 5% level (Sokal and Rohlf 1995). If the slope was significantly different from zero, the sign of the regression coefficient indicated whether the trend was positive or negative. We also carried out a parallel analysis for a scenario with the burden of proof placed on showing that there is a trend. Such analyses have been called for in fisheries management (Peterman 1990) and clearly would be of use in conservation situations also. In this case, we tested for significant declines or increases using two one-tailed *t* tests, again at the 5% level (thus, in effect, we tested overall for a 10% chance of a change in population size). All these analyses were repeated 1000 times for each combination of four lengths of observation window ($w = 5, 10, 15, \text{ and } 20$ (at least 3 years of data are required for a complete life cycle to be observed)) over all values of year-to-year autocorrelation in mortality, ρ (from 0 to 1 in increments of 0.05), and over all values of observational uncertainty, σ_{obs} (from 0 to 2 in increments of 0.05). The results of the 1000 runs for each parameter combination were used to calculate the probabilities of the different possible outcomes.

For any parameter set, we can then see how trends in one variable (e.g., true adult numbers) related to trends in any other variable (e.g., observed parr numbers). This allows the estimation of a measure of the power that we have to assess population trajectories correctly. There are two main questions of interest for the simulated population.

Question 1. Given that we see a decline in parr numbers, what is the chance that this reflects a decline in adults?

We let $\Pr\{A \downarrow\}$ denote the probability that the true adult population is declining and $\Pr\{P_{obs} \downarrow\}$ the probability that the observed parr population is declining. The question that we are asking concerns the conditional probability that true adult numbers are declining, given that observed parr are declining, $\Pr\{A \downarrow | P_{obs} \downarrow\}$. Using the standard definition of conditional probability, we obtain

$$(2) \quad \Pr\{A \downarrow | P_{obs} \downarrow\} = \Pr\{P_{obs} \downarrow, A \downarrow\} / \Pr\{P_{obs} \downarrow\}.$$

The complement of this probability, $1 - \Pr\{A \downarrow | P_{obs} \downarrow\}$, lets us ask “when adults are not declining, what is the chance that we mistakenly see that it is, i.e., that we see juveniles declining?” If we are wrong in answering these questions, we are making a Type I error.

Question 2. Given that adult numbers are declining, what is the chance that we see a decline in parr?

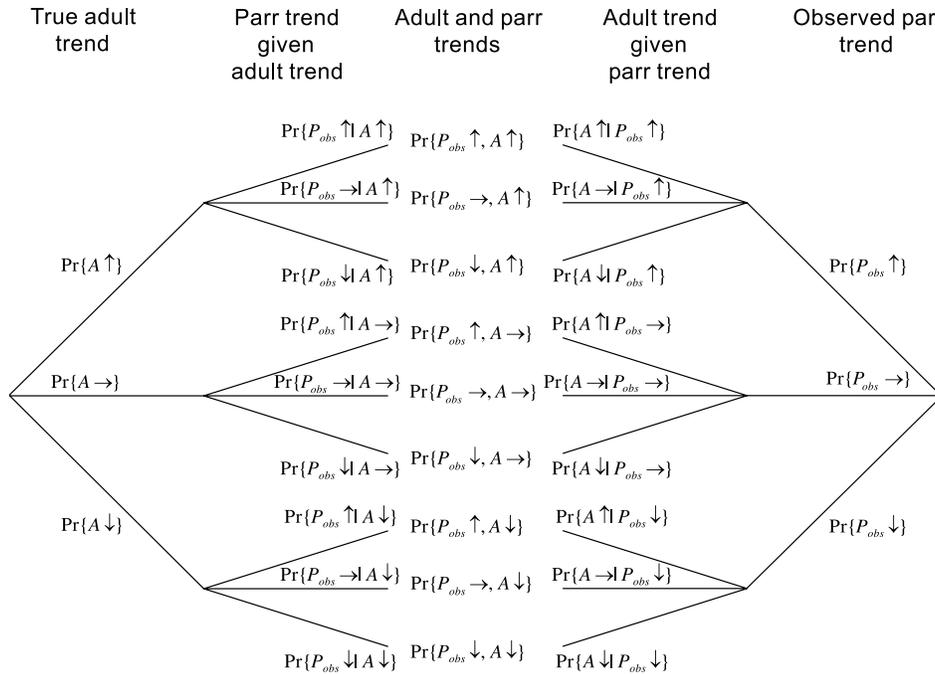
This question asks what is the conditional probability that observed parr are declining, given true adults are declining, $\Pr\{P_{obs} \downarrow | A \downarrow\}$?

$$(3) \quad \Pr\{P_{obs} \downarrow | A \downarrow\} = \Pr\{P_{obs} \downarrow, A \downarrow\} / \Pr\{A \downarrow\}.$$

If we are wrong, then we are making a Type II error.

The results for both these questions can be presented in a probability tree (Fig. 2), following the method of Peterman and Bradford (1987). These two results are linked by Bayes’ theorem:

Fig. 2. Possibility tree for the trends in coho salmon true adult population and observed parr population sizes. Population trajectories for each can either increase (↑), remain the same (→), or decline (↓). Thus, for example, $\Pr\{A\downarrow\}$ denotes the probability of a decline in true adult numbers, $\Pr\{P_{obs}\rightarrow\}$ denotes the probability of the observed parr population size remaining constant, $\Pr\{A\downarrow, P_{obs}\uparrow\}$ denotes the probability that observed parr and true adult populations both increase, and $\Pr\{P_{obs}\downarrow|A\downarrow\}$ denotes the probability that we observe a decline in parr given a decline in the true adult population. See Fig. 3 for a specific example.



$$(4) \quad \Pr\{A\downarrow|P_{obs}\downarrow\} = \Pr\{P_{obs}\downarrow|A\downarrow\}\Pr\{A\downarrow\}/\Pr\{P_{obs}\downarrow\}.$$

An example of the calculation of the conditional probabilities $\Pr\{A\downarrow|P_{obs}\downarrow\}$ and $\Pr\{P_{obs}\downarrow|A\downarrow\}$ is shown in Fig. 3 for the case where the window of observation $w = 20$, the autocorrelation in mortalities $\rho = 0.5$, and the observation uncertainty $\sigma_{obs} = 1.0$. From this tree, it can be seen that

$$(5) \quad \Pr\{P_{obs}\downarrow|A\downarrow\} = \Pr\{P_{obs}\downarrow, A\downarrow\}/\Pr\{A\downarrow\} \\ = 0.096/0.196 = 0.490$$

and

$$(6) \quad \Pr\{A\downarrow|P_{obs}\downarrow\} = \Pr\{P_{obs}\downarrow, A\downarrow\}/\Pr\{P_{obs}\downarrow\} \\ = 0.096/0.112 = 0.857.$$

Note that there are two sources of uncertainty in the relationship between true adult numbers and observed parr. First, there is the relationship between observed juvenile numbers and actual juvenile numbers. Second, there is the relationship between actual juvenile numbers and actual adult numbers. Thus, these questions involve the true parr number as a hidden state variable.

Results

The ability to correctly discern the relationship between observed parr and actual adult number, as defined by $\Pr\{A\downarrow|P_{obs}\downarrow\}$ and $\Pr\{P_{obs}\downarrow|A\downarrow\}$, depends on the number of years for which surveys are carried out (the “window”), w , on the amount of autocorrelation in stage mortalities from one year to the next, ρ , and on the observational uncertainty, σ_{obs} (Figs. 4 and 5). Note that all of the uncertainty in the relationship between true adult numbers and observed parr

numbers in this model was due to the uncertainty in the relationship between actual and observed parr numbers, i.e., due to observational rather than biological uncertainty. True adult and true parr numbers always (i.e., for all simulations, for all w , ρ , and σ_{obs}) showed the same trends (↑, →, ↓).

In general, as σ_{obs} increases, $\Pr\{P_{obs}\downarrow|A\downarrow\}$ and $\Pr\{A\downarrow|P_{obs}\downarrow\}$ tend to decrease. Figure 4 shows these results for fixed ρ and different values of w . As the observational uncertainty increases, it becomes increasingly difficult to see the true state of affairs. As w increases, both $\Pr\{P_{obs}\downarrow|A\downarrow\}$ and $\Pr\{A\downarrow|P_{obs}\downarrow\}$ increase (Figs. 4 and 5), and variation in these estimates decreases. Thus, longer census windows increase our ability to see clearly what is going on in the system. Finally, as ρ increases, $\Pr\{P_{obs}\downarrow|A\downarrow\}$ and $\Pr\{A\downarrow|P_{obs}\downarrow\}$ both tend to increase. Figure 5 shows these results for fixed σ_{obs} and different values of w . Increased correlation in mortality rates improves our ability to correctly detect trends in population size.

The result for ρ is less obvious than those obtained for σ_{obs} and w and deserves further examination. If autocorrelation is low or zero, then mortalities can quickly vary from high to low between years. If, however, autocorrelation is high, mortalities will tend to remain the same for long periods of time, i.e., a trend is set up. If, for example, mortality is high in one year, it is likely to remain high for several years in a row. Consistent high mortality rates will drive the population size down, and we are more likely to see a strong decline. Similarly, with consistent low mortality rates, we are more likely to observe an increase in population size than we would in the absence of autocorrelation. Closer examination of the probability of generating a decline in true

Fig. 3. Probability tree illustrating how the general method is applied (window of observation $w = 20$, autocorrelation in mortalities $\rho = 0.5$, observation uncertainty $\sigma_{\text{obs}} = 1.0$). Note that the probabilities in each of the three columns sum to unity.

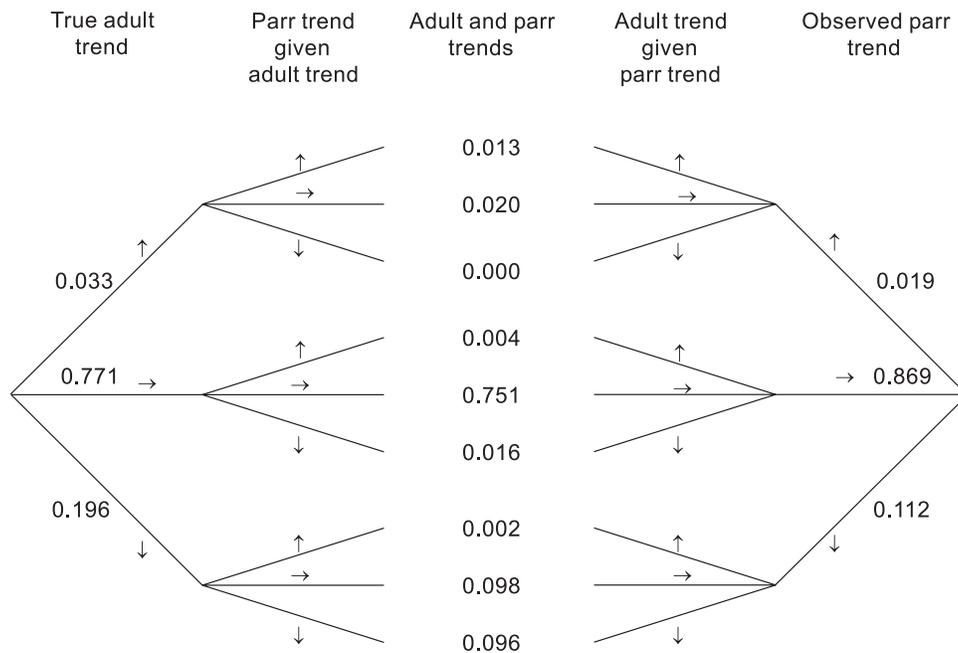


Table 2. Conditional probabilities for $\sigma_{\text{obs}} = 0.4$ (estimated from marine survival data; Berman 1999) and $\rho = 0.29$ (estimated from coho data from the Oregon Production Area).

Census window, w (years)	Change in size*		Increase or decrease in size†	
	$\Pr\{P_{\text{obs}}\downarrow A\downarrow\}$	$\Pr\{A\downarrow P_{\text{obs}}\downarrow\}$	$\Pr\{P_{\text{obs}}\downarrow A\downarrow\}$	$\Pr\{A\downarrow P_{\text{obs}}\downarrow\}$
5	0.000	0.000	0.200	0.333
10	0.600	0.750	0.639	0.793
15	0.697	0.852	0.789	0.849
20	0.786	0.911	0.838	0.928

*Two-tailed t test.

†One-tailed t tests.

adults, $\Pr\{A\downarrow\}$, or in observed parr, $\Pr\{P_{\text{obs}}\downarrow\}$, in the model substantiates this idea. Both probabilities increase as ρ increases. The effect is stronger, and increases more quickly, for longer censuses, w , when there is more opportunity to pick up a trend. In other words, there is an interaction between w and ρ . There is also an interaction with the observational uncertainty; as σ_{obs} increases, the true adult trend is unaffected (as is the true parr trend), yet we are less likely to observe it clearly. Hence, the probability of a true adult trend, $\Pr\{A\downarrow\}$, tends to be higher than the probability of an observed parr trend, $\Pr\{P_{\text{obs}}\downarrow\}$. The probability of both occurring, $\Pr\{A\downarrow, P_{\text{obs}}\downarrow\}$, thus closely mirrors that of the observed parr. For this reason, in general, $\Pr\{A\downarrow|P_{\text{obs}}\downarrow\} > \Pr\{P_{\text{obs}}\downarrow|A\downarrow\}$ for any particular parameter combination (e.g., see Table 2; Figs. 6 and 7).

Interaction of survey length, autocorrelation, and observational uncertainty

More detailed contour plots (Figs. 6 and 7) show that the factors w , ρ , and σ_{obs} interact to determine statistical power. Thus, for a given ρ , we can assess whether it is more useful to improve sampling methods or to increase census times in

order to be able to observe population trends at a required level of statistical power. The best approach to answering such a question depends strongly on the question itself. For example, a comparison of Figs. 6 and 7 indicates that our power to observe a parr decline given a decline in true adult numbers increases relatively slowly as the census time w is increased. There is a strong improvement between $w = 5$ and $w = 10$ but much less between $w = 15$ and $w = 20$. On the contrary, increasing w substantially improves our ability to infer a decline in true adult numbers given an observed decline in parr.

The best way to improve power also depends on the values of these parameters and on our ability to improve them. For coho salmon, very little is known about the values of ρ (over which value we have no influence) and σ_{obs} (which value we may be able to improve in future census work); this was, in part, the motivation of this study. Preliminary estimates from coho data from the Oregon Production Area indicate that ρ is approximately 0.29. From marine survival data on the observation of adult numbers, σ_{obs} may be about 0.4 (Berman 1999). These values are not strictly applicable to the system in question (Californian coho populations

Fig. 4. $\Pr\{P_{obs} \downarrow | A \downarrow\}$ and $\Pr\{A \downarrow | P_{obs} \downarrow\}$ versus σ_{obs} for the case where $\rho = 0.29$. (a and e) $w = 5$; (b and f) $w = 10$; (c and g) $w = 15$; (d and h) $w = 20$.

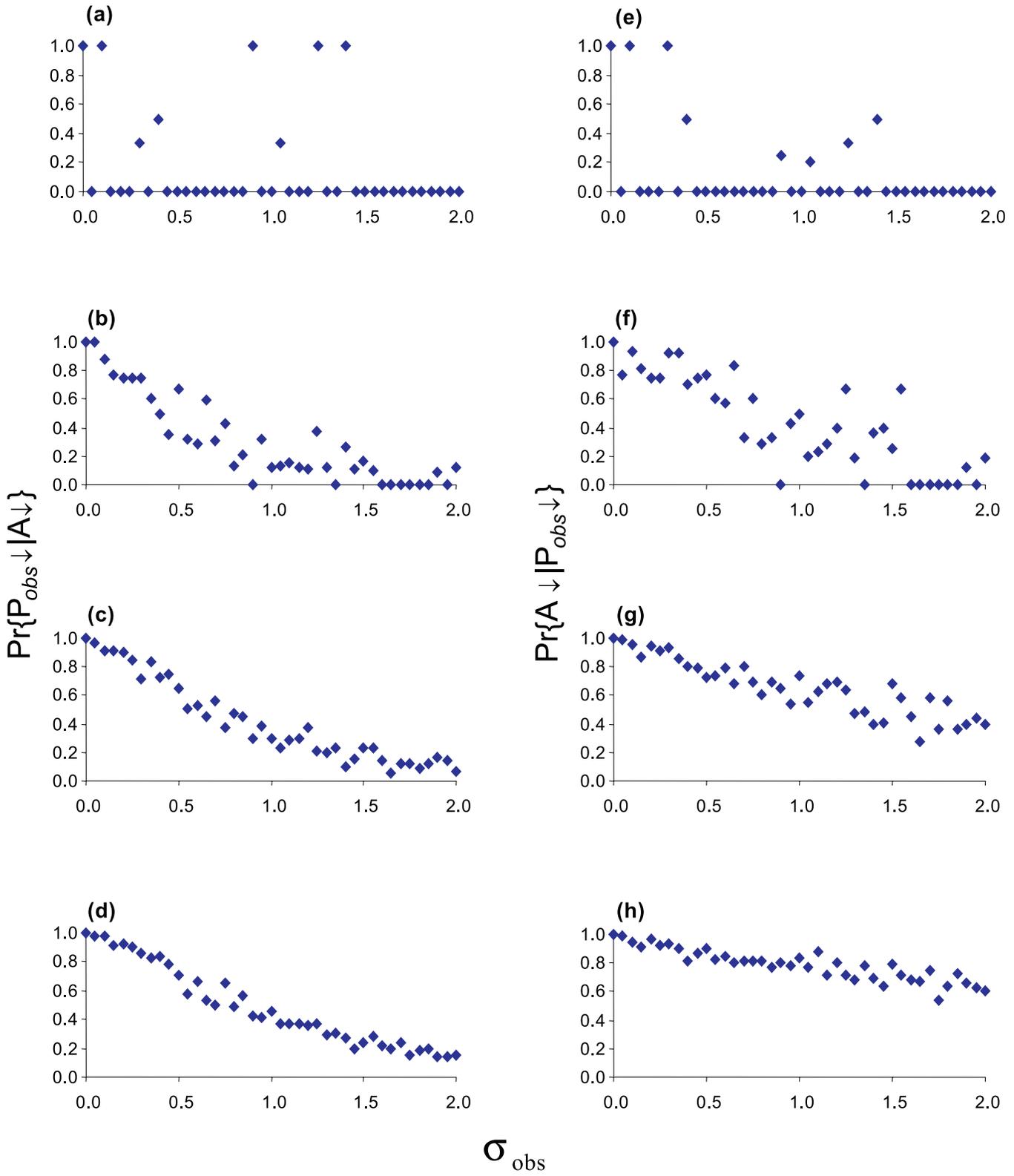


Fig. 5. $\Pr\{P_{obs} \downarrow | A \downarrow\}$ and $\Pr\{A \downarrow | P_{obs} \downarrow\}$ versus ρ for the case where $\sigma_{obs} = 0.4$. (a and e) $w = 5$; (b and f) $w = 10$; (c and g) $w = 15$; (d and h) $w = 20$.

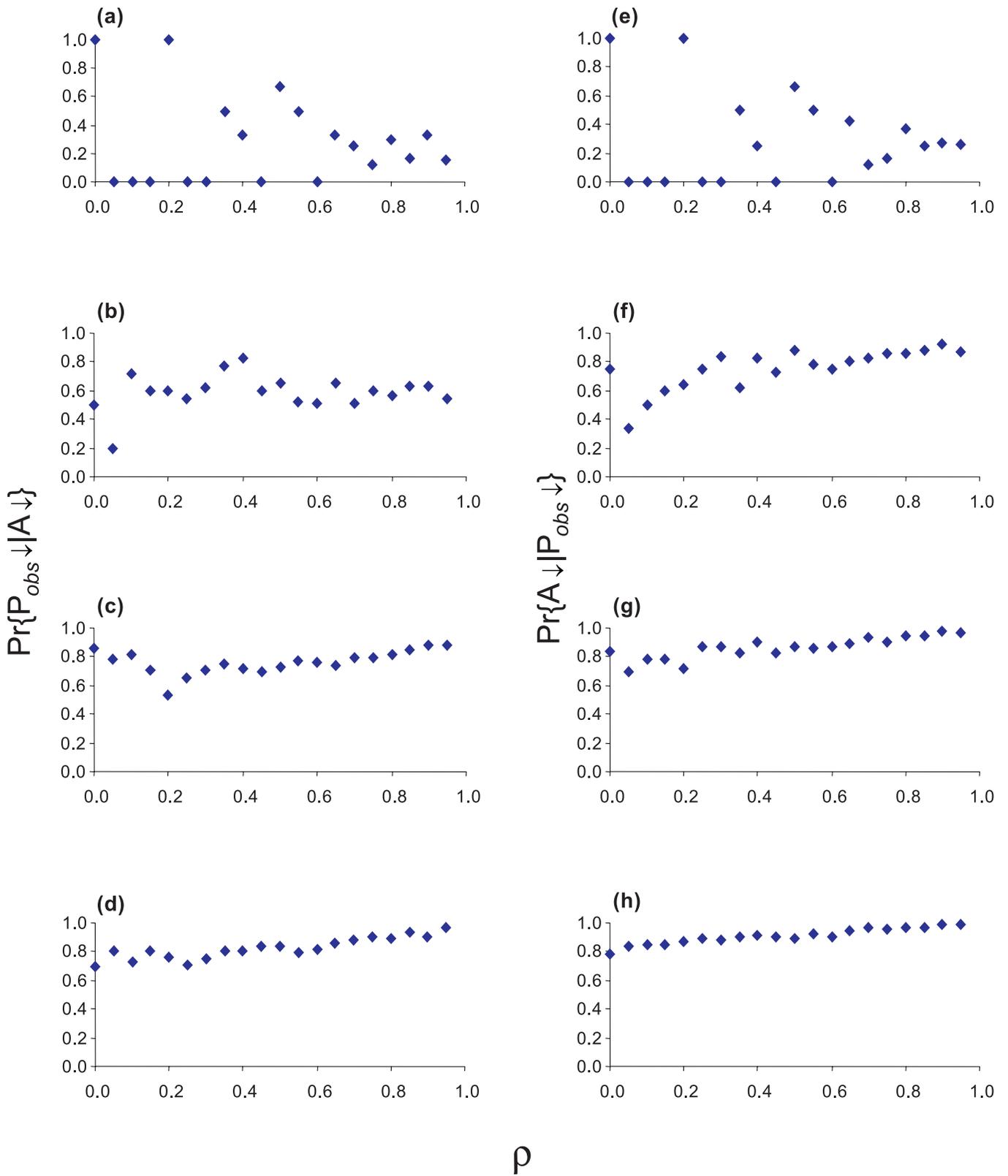
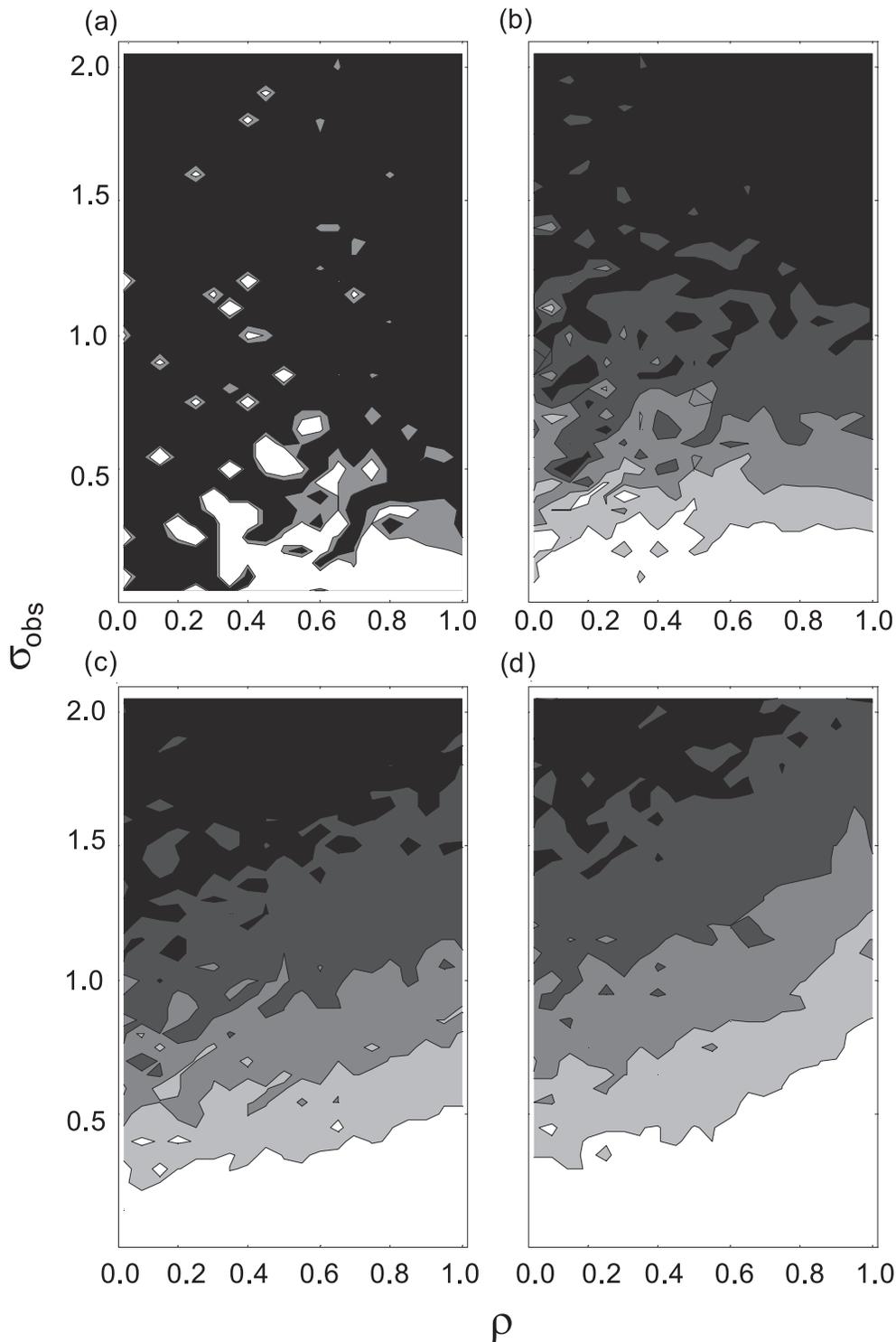


Fig. 6. Contour plots for $\Pr\{P_{\text{obs}} \downarrow | A \downarrow\}$ showing σ_{obs} against ρ for the case where (a) $w = 5$, (b) $w = 10$, (c) $w = 15$, and (d) $w = 20$. Contours are plotted at $\Pr\{P_{\text{obs}} \downarrow | A \downarrow\} = 0.2, 0.4, 0.6,$ and 0.8 with shading from black at $\Pr\{P_{\text{obs}} \downarrow | A \downarrow\} < 0.2$ to white at $\Pr\{P_{\text{obs}} \downarrow | A \downarrow\} > 0.8$.



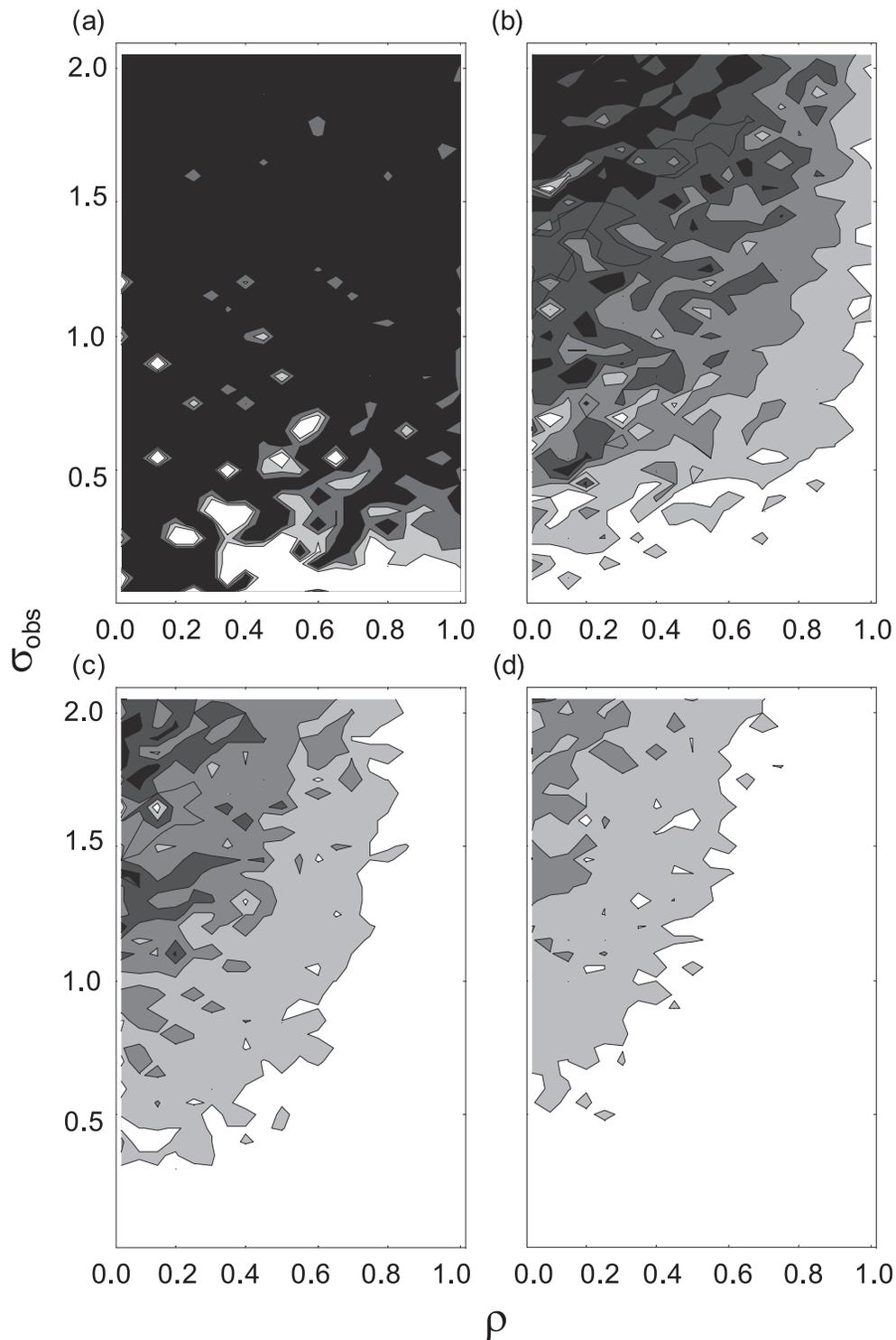
where observations are made on juvenile fish in freshwater); however, conditional probabilities based on these values provide an indication of the potential statistical power available (Table 2). Note that the results depend also on the placing of the burden of proof. For the case where we asked whether a change in population size was detected (using one two-tailed t test, i.e., 2.5% in each tail), the probabilities are in general lower than for the cases where we asked whether

a positive or negative trend was detected (using two one-tailed t tests, 5.0% in each tail). These results are consistent across the entire parameter space presented here.

Discussion

Discerning population trends, especially for endangered aquatic species, is difficult. The work that we present here

Fig. 7. Contour plots for $\Pr\{A \downarrow | P_{\text{obs}} \downarrow\}$ showing σ_{obs} against ρ for the case where (a) $w = 5$, (b) $w = 10$, (c) $w = 15$, and (d) $w = 20$. Contours are plotted at $\Pr\{A \downarrow | P_{\text{obs}} \downarrow\} = 0.2, 0.4, 0.6,$ and 0.8 with shading from black at $\Pr\{A \downarrow | P_{\text{obs}} \downarrow\} < 0.2$ to white at $\Pr\{A \downarrow | P_{\text{obs}} \downarrow\} > 0.8$.



asks how best to achieve our observation goals for coho salmon in the face of biological and observational uncertainties.

Our results show that statistical power decreases as observational uncertainty increases, as population censuses decrease in length, and as autocorrelation in mortality rates decreases. The power to observe populations clearly also de-

pends on the level of statistical significance used. We addressed this in our examination of results for different burdens of proof (also see Peterman and Bradford 1987; Peterman 1990) rather than in the context of standard time series analysis (Box and Jenkins 1976) because the burden of proof is a more relevant framework for conservation problems. Our two questions were “given an observed decline in parr

numbers, what is the chance that this reflects a decline in adults?" and "given that adult numbers are declining, what is the chance that we see that decline?" We have presented measures of statistical power for these questions, spanning the entire reasonable state space for the parameters w , ρ , and σ_{obs} .

These results generate several clear recommendations for managers wishing to improve detection of population trends and hence their ability to manage coho salmon in California. The most obvious recommendation is, of course, to acquire longer time series of data. We have shown that, other factors aside, the chance of detecting trends in population abundance is, in general, increased the longer the time series of data available. However, our results also provide estimates of statistical power to detect trends following an environmental change such as a regime shift or some other large-scale disturbance. A regime shift is a climatically induced shift in productivity, and there is growing evidence that such changes occur approximately every 30 years (MacCall 1996; Beamish et al. 1999). Population trends before and after such a shift are unlikely to be closely related. For this reason, even long time series may need to be truncated if evidence of a regime shift occurs, with concomitant loss of power. This work shows how markedly our ability to discern trends will decrease following such a shift.

This loss of power can, of course, be ameliorated by minimizing observational uncertainty, σ_{obs} . Just as increasing observational window length increases power, so does decreasing observational uncertainty. A further recommendation also arises: it is vital to have an accurate estimate of the level of uncertainty itself. This conclusion also applies to ρ ; knowing its value is important, even though this is not a parameter that can be directly manipulated by a manager. Only with accurate estimates of ρ and σ_{obs} for coho salmon in California will a manager be able to assess the statistical power available for the detection of trends from time series of a particular length.

Analogous results, relating the observational uncertainty in abundance estimates to the number of samples required to estimate the cohort replacement rate (the number of future spawners produced by each spawner), have been obtained for other Californian salmonids (Botsford and Brittnacher 1998). Their work complements ours in the sense that their conclusions pertain to the specifics of management (what is the probability of extinction of the stock, under given assumptions?), while our work deals with the operational considerations that managers face (what is the chance of correctly observing a trend, under given assumptions?). Both their study and ours show that for a required level of statistical certainty, and for known ρ , observational uncertainty and observation window length must be considered simultaneously in the design of any sampling regime. Thus, in order to obtain meaningful results, it is necessary to frame any question explicitly, including an indication of where the burden of proof will lie. As we demonstrate, different questions can be answered with different levels of statistical power when all other parameters are the same.

Our results are based on a simplified model for coho life history. This model is in fact a special case of the generic model presented in this study. The generic model comprises

a conceptual suite of models that can incorporate many or all factors addressed in previous theoretical work on Pacific salmon (e.g., Emlen 1995; Nickelson and Lawson 1998; Spencer 1999). This suite of models can incorporate all the sources of variability that have been deemed important in populations of salmon (genetic, environmental, demographic). For example, demographic/genetic effects could be modeled with compensatory survivorship. Coupled versions of the model would allow different rivers, with different life history parameters, linked by straying individuals, to be modeled. Regime shifts could be explicitly modeled using a two-state Markov model. Catastrophes could be modeled by sudden increases in mortality rates across all stages. All parameters can be made functions of time and also functions of density measures at those times as required. A further extension would be to use the models to carry out population viability analyses in order to assess relative extinction risk, either without intervention or under different management regimes.

The fact that we have a suite of models, rather than just a single model, will allow an ongoing research agenda to investigate exactly which additional information would be most usefully acquired. In the specific version of the model presented in this paper, we have looked at the importance of observational uncertainty and autocorrelation in mortalities. Different simplifications of the general model could be used to ask questions about the importance of different structural components of coho life history. Our next immediate question concerns the effects of different types of density dependence (K. Shea and M. Mangel, unpublished data). Looking only at a single model begs the question of whether the results seen are somehow dependent on the biology that has been included and that which has been left out. By comparing related models, we can explicitly address that question, something that has not systematically been done before for coho.

Acknowledgements

Many thanks to Pete Adams, Suzanne Alonzo, Ottar Bjørnstad, Chris Wilcox, and two anonymous reviewers for helpful discussions. This work was funded in part by cooperative agreement NOAA 22567-447637 from the National Oceanic and Atmospheric Administration. The views expressed herein are those of the authors and do not necessarily reflect the views of the National Oceanic and Atmospheric Administration or any of its subagencies. The U.S. Government is authorized to reproduce and distribute for government purposes.

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Appendix. Specific coho salmon model

State variables

$P(t)$ = density of parr at time t

$S(t)$ = density of smolts at time t

$A_1(t)$ = density of one-sea-winter adults at time t

Parameters

Fecundities

f_1 = number of eggs laid by one-sea-winter females

Survivorships (see mortality below)

$s_p(t)$ = survivorship of parr at time $t - 1$ to smolts at time t

$s_{RO}(t)$ = survivorship of smolts moving from the river to the ocean at time t (emigration survivorship); this can be thought of as a product of river migration survivorship and early ocean survivorship

$s_O(t)$ = survivorship of salmon in the ocean over one winter from time $t - 1$ to time t

$s_{OR}(t)$ = survivorship of salmon moving from the ocean to the river at time t (immigration survivorship)

Survivorships and mortality

The four annual survivorships, $s_i(t)$, are related to the instantaneous mortality rates, $M_i(t)$, by

$$s_i(t) = e^{-M_i(t)}.$$

Instantaneous mortality is correlated from year to year with autocorrelation parameter ρ using a mixing model of the form

$$M(t) = \rho M(t - 1) + (1 - \rho)Z(t)$$

$$M(0), Z(t) \sim N(\bar{M}, \sigma_M^2).$$

Thus, there is a contribution, ρ , by the previous year's mortality and a contribution, $(1 - \rho)$, from the random variable $Z(t)$.

Equations

For parr:

$$P(t) = \frac{1}{2} f_1 A_1(t - 1).$$

A 50:50 sex ratio is assumed. Eggs are produced only by females. Variation in fecundity is not included.

For smolts:

$$S(t) = P(t - 1)s_p(t).$$

For one-sea-winter adults:

$$A_1(t) = S(t - 1)s_{RO}(t - 1)s_O(t)s_{OR}(t).$$