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Using variance components to estimate power in a hierarchically nested sampling design

Improving monitoring of larval Devils Hole pupfish

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Abstract We used variance components to assess allocation of sampling effort in a hierarchically nested sampling design for ongoing monitoring of early life history stages of the federally endangered Devils Hole pupfish (DHP) (*Cyprinodon diabolis*). Sampling design for larval DHP included surveys (5 days each spring 2007–2009), events, and plots. Each survey was comprised of three counting events, where DHP larvae on nine plots were counted plot by plot. Statistical analysis of larval abundance included three components: (1) evaluation of power from various sample size combinations, (2) comparison of power in fixed and random plot designs, and (3) assessment of yearly differences in the power of the survey. Results indicated that increasing the sample size at the lowest level of sampling represented the most realistic option to increase the survey's power, fixed plot designs had greater power than random plot designs, and the power of the larval survey varied by year. This study provides an example of how monitoring efforts may benefit from coupling variance components estimation with power analysis to assess sampling design.

Keywords Devils hole · Power analysis · Nested sampling design · Variance components · Pupfish

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Introduction

Diversity of freshwater fishes is at risk in North America (Ricciardi and Rasmussen 1999) with an estimated 39% of freshwater and diadromous fishes considered endangered, threatened, or vulnerable (Jelks et al. 2008). The imperiled status of many freshwater fish species makes understanding population trends imperative to successful conservation. Monitoring populations can help prioritize management actions, thereby promoting efficient use of conservation funds (Nichols and Williams 2006). For monitoring to be useful in detecting population trends, the survey design must have high statistical

power. Statistical power in population monitoring represents the probability of detecting a real change in population abundance. Survey designs with low statistical power have a high probability of failing to detect population change and are likely to mislead managers by falsely concluding a population is stable (Peterman 1990; Taylor and Gerrodette 1993; Legg and Nagy 2006). Incorporating estimates of statistical power is therefore essential when choosing an appropriate sampling design structure (Legg and Nagy 2006; Field et al. 2007), which in turn affects monitoring schemes.

Trends in fish populations are difficult to detect due to high spatial and temporal variability in population abundance (Silliman 1946; Gibbs et al. 1998; Sammons and Bettoli 1998), so statistical power in surveys of fish populations tends to be low compared to power in surveys for other organisms (Gibbs et al. 1998). For instance, Cyr et al. (1992) estimated that about half of the surveys that focused sampling on the early life history stages of fish had less than 80% power to detect a one order of magnitude change in the abundance of larvae. Low power in surveys for larval fish is regrettable because mortality rate of larval fishes is often high in comparison to mortality at later life history stages, thus larval fish abundance may be an important indicator of year class strength (Diana 1995; Sammons and Bettoli 1998). One technique for increasing power is to conduct surveys at fixed locations if the spatial distribution of the population is predictable between surveys (e.g., Quist et al. 2006). However, surveys with fixed sites are less capable of detecting spatial patterns than surveys with random sites located throughout the survey area.

The Devils Hole pupfish (DHP) (*Cyprinodon diabolis*) is thought to inhabit the smallest habitat of any vertebrate species (Moyle 1976). It is endemic to Devils Hole, a small limestone cavern located in southwestern Nevada. In the late 1990s, the adult DHP population declined for unknown reasons, reaching a low of just 38 individuals (April 2006 and April 2007). Although population records for adult DHP date back to 1972, very little is known about its early life history stages. Gustafson and Deacon (1997) and Lyons (2005) studied the relationship between microhabitat characteristics and abundance of DHP larvae. Although both studies provided insight as to the distribution of larval DHP, neither was able to detect meaningful relationships between habitat characteristics and abundance. Consequently, surveys for larval DHP began in 2005 to monitor long-term trends in the abundance of larval fish with the hopes that the data would help elucidate mechanisms associated with recruitment.

While estimating statistical power is fairly straightforward for simple survey designs, estimating power in complex designs requires more sophisticated techniques (Urquhart and Kincaid 1999; Larsen et al. 2001). Surveys for larval DHP are hierarchically nested and include samples, subsamples, and sub-subsamples. Decomposing these sources of survey variation into variance components can help determine the relative contribution of factors to overall variation in the survey (Lewis 1978; Matthews 1990; Morrissey et al. 1992; Kincaid et al. 2003). Increasing the sample size at levels of sampling with high variance will result in a survey design focused on minimizing variation, thereby maximizing the survey's power to detect changes in the population (Morrissey et al. 1992; Larsen et al. 2001). As a general rule, increasing the number of samples will result in a greater increase in power than increasing the number of subsamples or sub-subsamples (Urquhart and Kincaid 1999). However, increasing the number of samples is usually more cumbersome and costly than increasing subsamples. In this study, we estimated variance components for all levels of sampling in DHP larval surveys to determine how altering sample size in a hierarchically nested design affected statistical power. Then, we discuss these findings as they relate to modifications of the long-term monitoring scheme for the DHP. Other studies have combined variance components estimation with power analysis to quantitatively assess sampling designs.

Methods

Study area

Devils Hole is located in an open fault zone adjacent to Ash Meadows National Wildlife Refuge, an oasis in the Amargosa Desert in Nye County, Nevada. A fissure formed by tectonic activity, Devils Hole is part of a network of subterranean carbonate formations that transport water to springs in Ash Meadows. The depth of Devils Hole remains unknown, though divers have explored down to a depth of 133 m without seeing the bottom (Riggs and Deacon 2004). The DHP is the only aquatic vertebrate species living in Devils Hole. Pupfish habitat in Devils Hole can be divided into two separate strata: the "shallow shelf," a boulder face approximately 2×5.5 m in area submersed under

0.2–0.7 m of water, and the "deep pool," or the deeper waters of the cavern where pupfish inhabit the upper 25 m. Except for a few extremely rare occasions, pupfish larvae have been observed exclusively on the shallow shelf (Gustafson and Deacon 1997), suggesting that pupfish recruitment is highly dependent on habitat conditions associated with the shallow shelf. In addition, primary production and invertebrate biomass are greatest on the shallow shelf (Riggs and Deacon 2004). While water temperature, pH, and conductivity remain fairly constant in the deep pool at 32–33°C, 7.1–7.5, and 820 μS/cm, respectively (Shepard et al. 2000), the shallow shelf is more dynamic and experiences greater fluctuations of temperature (32–34.5°C) and dissolved oxygen (2–8 mg/l; Gustafson 1997; Shepard et al. 2000; Lyons 2005). In addition, the Devils Hole spawning shelf experiences large magnitude disturbances from earthquakes and flood events (Lyons 2005), though the influence of disturbance events on the DHP population remains unknown.

Survey design

Sampling effort in surveys for larval DHP was nested and included surveys (conducted every other week), counting events (conducted three times within a survey with 1 h in between each event), and plots (nine observational units in an event). Larval surveys were conducted by biologists from the National Park Service, U.S. Fish and Wildlife Service, and Nevada Department of Wildlife. Plots used in this study were 30×14.5 cm quadrants constructed from three pieces of white polyvinylchloride (PVC) piping which had been laterally bisected (Fig. 1). The three pieces of PVC were lashed together by monofilament fishing line. Bead spacers were placed on the fishing line to maintain a 6-mm gap between the PVC halves. Gaps allowed larvae to emerge from the sediment and settle on the plot. The white background contrasted with the darker substrate, thereby making small larvae more visible and easy to detect on plots. Nine plots were placed at fixed locations (Lyons 2005) on the floor of the shelf a few hours before dusk to avoid disturbing larvae during the survey (Fig. 1). Since DHP larvae typically emerge from the sediment at night (Lyons 2005), surveys commenced 3 h after sunset. Observers illuminated each plot with a headlamp and counted all larvae present on the plot for 1 min. After observers finished counting larvae on the nine plots (i.e., after one counting event), observers waited until 1 h after

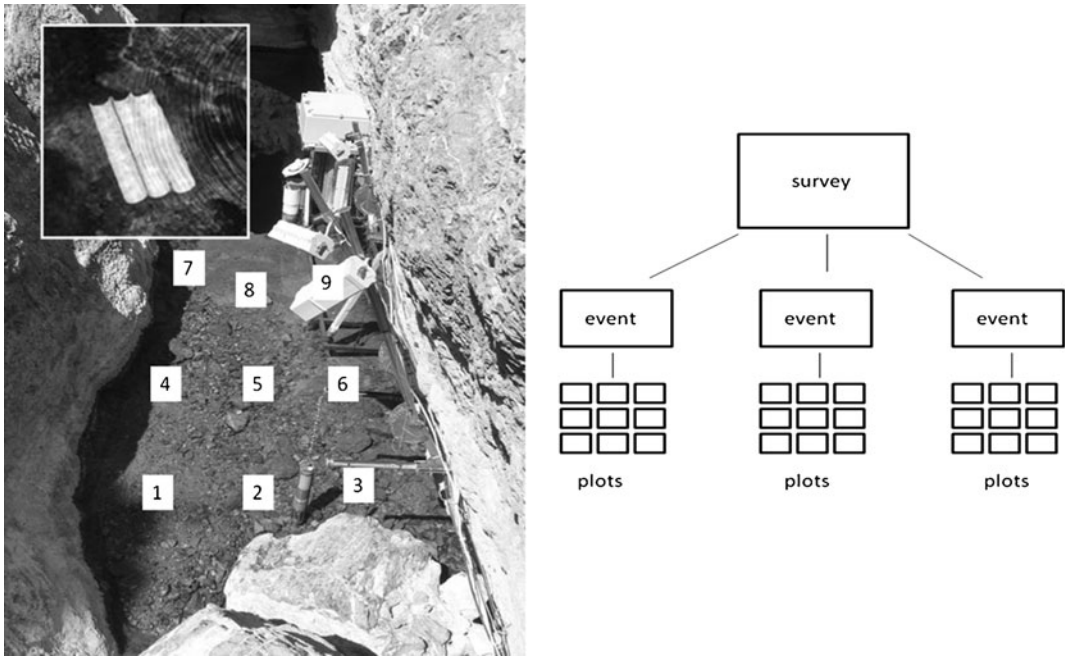

Fig. 1 Sampling design structure for surveys of larval Devils Hole pupfish. *Left photograph* Devils Hole spawning shelf with placement of fixed plots represented by numbers. *Upper left corner* a photograph of the sampling apparatus. *Right diagram* hierarchically nested structure of the sampling design

the commencement of the first counting event, and once again counted the number of larvae present on the nine plots. This process was repeated once more for a total of three counting events, each with nine plots. Since the shallow shelf was small in area (approximately 3×6 m), the plots sampled 3% of the habitat available for DHP larvae.

Previous studies assessing temporal trends in DHP larval populations have shown larval abundance to be greatest in spring (Gustafson 1997). Similarly, although spawning occurred 10 months out of the year, data from 2007 to 2009 surveys show larval abundance was greatest in early April, after which larval abundance declined until early autumn when another, albeit lesser, increase in larval abundance occurred. Five dates in mid-March to mid-May were used in our analysis (Fig. 2), because the large amount of variation in larval abundance between different seasons would have obscured comparison of population trends between years. We chose to analyze abundance data from spring sampling dates only because variation in larval abundance was greatest and power was lowest during this season. As such, estimates of statistical power from spring sampling dates would be most conservative when larval abundance estimates were compared within the same season across years.

Statistical analysis

All statistical analyses were conducted in SAS® version 9.2 ® (SAS Institute Inc., Cary, NC). Larval abundance was estimated from the mean number of larvae detected per plot during each survey. We analyzed ln-transformed larval abundance because preliminary inspection of the data suggested that the variance among plots within an event was not constant, and that events and surveys had multiplicative effects on the larval count. Values of 0 were replaced by 0.5 before ln-transformation. Evaluation of residuals showed that the log-transformation was reasonable and that relationships between means and variances were not sufficiently high to justify use of a Poisson distribution. The model describing ln-transformed abundance includes year (θ) and plot (β) as fixed effects; and surveys (b), events (c), and plots (e) as random effects:

$$y_{p(v(s(a)))} = \mu + \theta_a + \beta_p + b_{s(a)} + c_{v(s(a))} + e_{p(v(s(a)))} \quad (1)$$

where parameters are distinguished based on year (a), survey (s), event (v), and plot (p). The survey variance component represents short-term temporal variability, the event variance component is a larger-scale replicate of spatial variability, and the plot variance components represents small-scale spatial variability. Plots were treated in two different ways, corresponding to two different survey designs. If the same plot locations were used each survey (the fixed plot design), then plot effects were considered as fixed effects. The error variance was then the variance associated with each measurement. If new plot locations were used each survey (the random plot design), then plot effects (β_p) were deleted from the model; the error variance then included spatial variability.

Variance components associated with each random effect were estimated by equating observed and expected

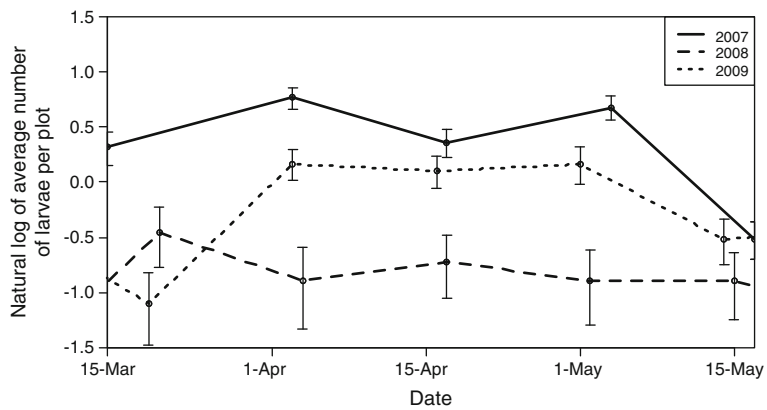

Fig. 2 Estimates of average larval density from mid-March to mid-May from 2007 to 2009. Average larval density was estimated as the average number of larvae occurring on plots during each survey

mean squares using PROC MIXED in SAS 9.2 (Littell et al. 2002). Equating observed and expected mean squares is a method of moments estimation procedure and does not require assumption of normality (Searle et al. 1992). Estimated variance components were then used to assess the effect of sample size on the variability in the mean observation (Snedecor and Cochran 1980) in the following equation:

$$\sigma_y^2 = \frac{\sigma_s^2}{n_s} + \frac{\sigma_v^2}{n_s \times n_v} + \frac{\sigma_p^2}{n_s \times n_v \times n_p} \quad (2)$$

where $\overline{y}$ is the sample mean, n is the sample size, and σ^2 is the variance component for the level of sampling indicated by the subscript.

Estimating power requires four pieces of information: (1) an estimate of variance, (2) the specified effect size, (3) the desired level of significance (α), and (4) the sample size. Variance of the mean was estimated using the variance components equation (Eq. 2). Effect size was the hypothetical difference in ln-transformed larval abundance between 2 years. For example, an effect size of ln(1.2) would estimate power to detect a 20% increase in abundance while an effect size of ln(0.8) would be used to detect a 20% decrease. The effect size and estimate of variance were used to calculate the noncentrality parameter from a *t*-distribution with degrees of freedom equal to two times the number of surveys minus two. Alpha was set to 0.05 for all analyses, and the sample size varied depending on the analysis. It is important to note that this method assesses hypothetical changes in larval abundance from year to year; it is ill advised to use this method to retrospectively estimate power with observed trends (Thomas 1997). Furthermore, we used a linear model to describe larval counts because of its relatively simple structure, which facilitates incorporation of multiple levels of sampling. Variance components were estimated separately for all 3 years (2007–2009) as well as for all years pooled together to compare annual variability. For each year, estimates of variance were used to calculate the power of the sampling design used from 2007 to 2009 (i.e., the power of five surveys, three events, and nine random plots). In addition, the number of plots, events, and surveys were manipulated to compare estimates of power resulting from various sampling design structures. Lastly, power from surveys with fixed plots and random plots were estimated by estimating variance components from models with (fixed plot) and without (random plot) "plot" as a fixed effect. Variance of the mean observation was then estimated separately for fixed- and random-plot designs using their respective estimates of the plot variance component (Eq. 2).

Results

Estimating power for different sample size combinations illustrated how increasing the number of samples (i.e., surveys) had the greatest influence on statistical power (Fig. 3). This result was expected, because increasing the number of samples decreases the contribution from every variance component (Eq. 2). A more surprising finding, however, was that the subsample (i.e., event) contributed negligibly to the overall variation in the mean observation. In fact, the estimated variance component for events in 2008 and 2009 was negative. As such, increasing the number of events had virtually the same effect as increasing the number of plots. To test whether negative variance components estimates could be attributed to the estimation procedure, we re-estimated variance components in SAS using restricted maximum likelihood and type I sums of squares (i.e., proc mixed method = reml and proc varcomp method = type1 in SAS, respectively). Variance components for event were negative using proc varcomp and zero using proc mixed method = reml; thus, we feel confident that the negative variance estimate was not a result of the estimation procedure. For years when variance components were estimated to be negative (e.g., 2008, 2009, grouped years), the restricted maximum likelihood method tended to provide lower estimates of variance components for positive variance components relative to the equating observed and expected mean squares. Nevertheless, power estimates from the from the two estimation procedures differed by less than 0.001 for survey design consisting of five surveys, three events, and nine random plots.

Surveys with fixed plots had slightly higher statistical power than surveys with random plots, although the difference in power between the two designs decreased as the total number of plots increased (Fig. 4). The higher power of the fixed plot design was due to fixed plot variance component being roughly 24% less than the random plot variance component. Estimates of larval density varied each year, with the greatest densities of larval DHP occurring in 2007 and the

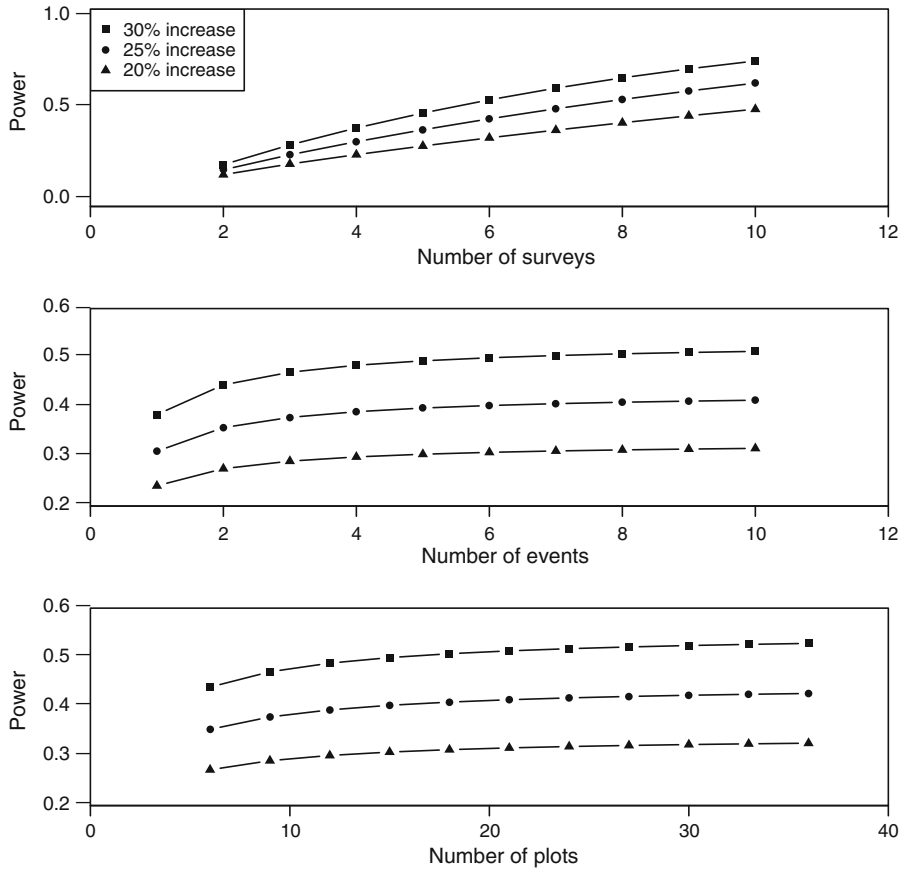

Fig. 3 Statistical power to detect increases in the abundance of Devils Hole pupfish larvae under different sample size combinations in a hierarchically nested sampling design. Estimates of variance components and power were attained from pooling abundance data from five survey days each year in mid-March thru mid-May in 2007–2009. In each panel, the sample sizes of two levels of sampling were held constant to show how increasing sample size at a specific level of sampling influenced statistical power. Power was estimated from sampling designs with **a** three events and nine random plots, **b** five surveys and nine random plots, and **c** five surveys and three events

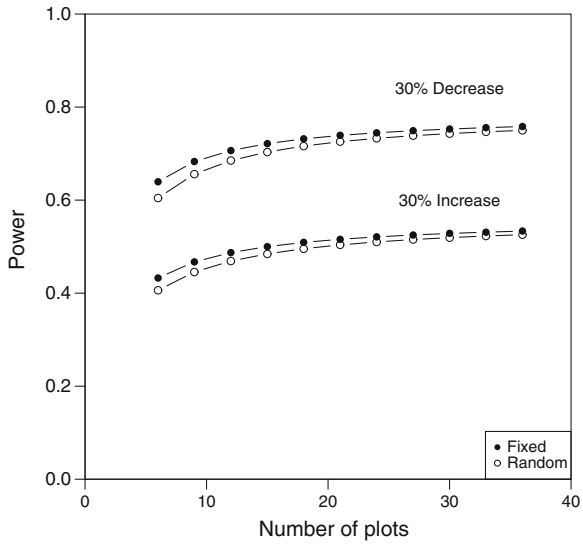

Fig. 4 Comparison of power from sampling designs with fixed plots and random plots. Power was calculated from pooled estimates of variance in spring 2007–2009 from sampling designs with five surveys and three events

lowest in 2008. Likewise, statistical power in the larval survey varied each year; the survey had its lowest power in 2007 and its highest power in 2008 (Table 1). The power to detect a decrease was always greater than the power to detect an increase of the same magnitude because the effect size was ln-transformed. Variance component estimates from all 3 years of data showed that the survey design with five surveys, three events, and nine random plots had low power to detect a 20% increase ($1-\beta$=0.30) or decrease (0.40) in population abundance, however, power to detect a 50% increase (0.80) or decrease (0.99) was relatively high.

Discussion

Other fish monitoring studies have assessed variance partitioning at spatial and temporal scales in hierarchically nested survey designs. Gray et al. (2009) found that variability in abundance of ten fish species in

Table 1 Variance components and their associated estimates of statistical power in hierarchically nested surveys of Devils Hole pupfish (DHP) larvae

	Plot effect	Total variance	CV	Survey variance	Event variance	Plot variance	Power 50% decrease	Power 50% increase
2007	Random	0.571	0.878	0.084	0.005	0.482	0.927	0.570
2008	Random	0.241	0.522	0.001	−0.015	0.255	1.000[a]	1.000[a]
2009	Random	0.335	0.631	0.059	−0.004	0.280	0.985	0.726
All years	Random	0.380	0.680	0.048	−0.007	0.339	0.993	0.781
2007	Fixed	0.357	0.655	0.084	0.005	0.268	0.943	0.600
2008	Fixed	0.182	0.447	0.001	−0.015	0.196	1.000	1.000
2009	Fixed	0.299	0.590	0.059	−0.004	0.244	0.987	0.734
All years	Fixed	0.301	0.593	0.048	−0.007	0.260	0.995	0.800

Values were attained from ln-transformed abundance estimates of DHP larvae from mid-March to mid-May. Power was estimates from sampling designs with five surveys, three events, and nine plots. Power estimates calculated from variance components estimated using restricted maximum likelihood (a method which constrains variance components to be greater than or equal to zero) did not differ from power estimates from the ANOVA method by more than 0.001 (not shown)

[a] The variance component estimates in 2008 were very low and thus caused problems in estimating power for some sample size combinations in 2008 (not shown)

southeast Australian lakes was greatest at the lowest level of sampling (sites located 50–100 m apart) relative to larger spatial scales (1–20 km apart). Similarly, variation in reef fish assemblages in northeastern New Zealand was greatest between transects (tens of meters) compared to sites (hundreds to thousands of meters), locations (hundreds of kilometers), and years (Anderson and Millar 2004). In a literature review of 39 studies of algal and macroinvertebrate abundance in coastal habitats, variability in biomass was typically greatest at small spatial scales (Fraschetti et al. 2005). However, the relative magnitude of variability in abundance of eight different taxa of benthic macrofauna in Botany Bay, Australia, was variable across different spatial scales (Morrissey et al. 1992).

The decision of whether to use fixed or random sites should depend on whether the goal of monitoring is to assess spatial or temporal trends, as well as how much variation in the data can be explained by site location. If site location explains a substantial amount of variation, fixed sites will result in greater power than random sites (Urquhart and Kincaid 1999; Quist et al. 2006). Conversely, trends from fixed sites may not be representative of regional trends, even when great care is taken with site selection (Stoddard et al. 1998). Urquhart and Kincaid (1999) assessed power in various sampling designs that used both fixed and random plots, such as designs with random site revisits, and discussed the advantages of various sampling design strategies. Other studies comparing fixed and random sites in aquatic ecosystems have found either no difference in variation between fixed and random sites (King et al. 1981), or lower variability for fixed sites (Van der Meer 1997). In our study, although fixed plots had 24% less variation than random plots, the difference in power between fixed and random site designs was small. However, differences in power between fixed and random sites would be greater if plots represented samples, not sub-subsamples. Due to the small area of Devils Hole shallow shelf, detecting spatial patterns of DHP larvae is of less interest than detecting temporal changes in the larval population. Although the fixed plot design has greater power than the random plot design, the high power comes with the price of an added assumption that abundance patterns occurring on fixed plots are representative of the entire spawning shelf. Using combinations of fixed and random sites presents a practical solution if the goal of larval monitoring is to relate larval abundance to microhabitat characteristics such as water depth, substrate composition, dissolved oxygen concentration, or macroinvertebrate abundance.

Surveys conducted from 2007 to 2009 had different abundances as well as different estimates of power (Table 1). Estimates of power in surveys for larval DHP were high compared to surveys for other species of larval fish (Cyr et al. 1992). The higher power for surveys of DHP larvae was likely attributed to a

relatively large proportion of habitat on the Devils Hole shallow shelf being exposed to sampling. Although power was relatively high compared to surveys for other larval fishes, power to detect increases or decreases less than 30% magnitude was still low. One option to increase power in surveys is to increase the type I error probability (α). Increasing α is wise if the population of interest is threatened by inaction (Gryska et al. 1997; Daulwater et al. 2009) because a greater α improves the survey's ability to detect population trends at the cost of increasing the probability of a false detection. Additionally, tests for negligible trend can be used as a complement to traditional hypothesis testing (Dixon and Pechmann 2005). With this method, the alternative hypothesis tests whether the 90% confidence interval falls within a specified (by the researcher) interval around zero. As such, it is possible for poorly estimated trends to be not significantly different from zero and not significantly negligible with the same level of confidence for both tests (Dixon and Pechmann 2005).

The event variance component was estimated to be negative by the mixed model used to estimate variance components for the three levels of sampling in surveys for DHP larvae. However, because variance is a squared value, in theory it cannot be negative. Negative variance components can occur if variation between samples is lower than variation between subsamples. Numerous interpretations of negative variance components exist, and, as a consequence, there are multiple methods to solve the "problem" of a negative variance component. One perspective is that negative variance components are impossible; therefore, they arise due to random variation around zero. According to this perspective, negative variance components should be set to zero, effectively removing the source of variation from the model (Thompson and Moore 1963; Fletcher and Underwood 2002). Alternatively, restricted maximum likelihood estimates of variance components, which by definition cannot be negative, can be used instead of observed and expected mean squares (Fletcher and Underwood 2002). Yet another approach, which differs from the two above-mentioned approaches because it allows negative variance components to remain in the model, is to view parameters from analysis of variance as covariances rather than as variances (Smith and Murray 1984). When all variance components are estimated positive and data are balanced, restricted maximum likelihood method is equivalent to equating observed and expected mean squares (Littell et al. 2002). When variance components are estimated negative, the restricted maximum likelihood method produces biased estimates of other positive variance components (Searle et al. 1992). We thought it was reasonable to retain the negative variance component in the model, because it realistically depicted patterns of variation in larval abundance and allowed estimates of variance components to remain non-biased. Specifically, if larvae were found on a certain plot, they might be less likely to be found on other plots because of limited space on the Devils Hole spawning shelf. Under such a circumstance, the variation in the sum of larvae on all plots (i.e., the variation of events) would be less than the variation in the number of larvae on separate plots.

Conclusion

Although the results of the power analysis are easy to interpret mathematically, using the findings of this study to recommend an "optimal" sampling design is more complex due to obstacles such as limited staff time, financial constraints, and concerns with disturbance due to sampling. Year-to-year differences in

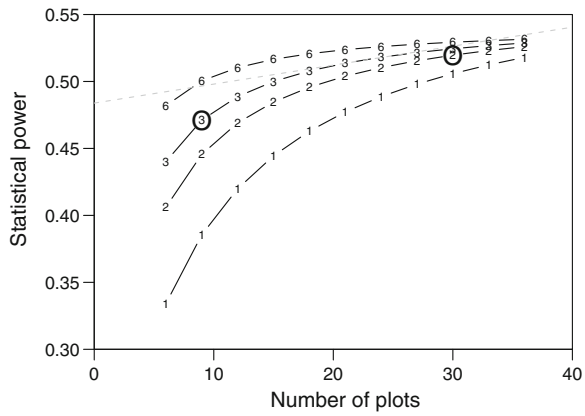

Fig. 5 Statistical power of different sampling design structures to detect a 30% increase in Devils Hole pupfish larvae population abundance. *Symbols* on the graph represent the number of events in each survey; *dotted line* represents a constant sampling effort of 30 plots partitioned differently among events (i.e., for five plots and six events versus 30 plots and one event). The line slopes gently upwards, indicating that maximizing the number of plots per event will result in a survey design with higher power. The number of surveys was held constant at five. Symbols representing power of the previous (three events, nine plots) and proposed (two events, 30 plots) sampling designs are circled

power due to dissimilarities in larval abundance further complicate construction of the "optimal" survey design for DHP larvae. Thus, developing a sampling design to consistently yield a certain level of statistical power was an unrealistic goal. Instead, we used the results of our study to compare relative differences in power from different combinations of sample sizes at each level of sampling. While increasing the number of surveys presented the best method to increase power, surveys are more demanding on resources and time. In contrast, the finding that event contributed negligibly and plot substantially to variation illustrates that increasing the number of plots per event is a relatively easy way to increase power in the sampling design without increasing sampling effort considerably. However, since surveys for larval DHP sample a fairly large proportion of larval DHP habitat, there is an upper limit to the number of plots which can be placed on the shallow shelf. If too many plots are placed on the shelf, larvae could swim onto multiple plots during one counting event, thus violating the assumption of independence between plots. Hence, because the results showed that the difference in power was minimal between surveys with three events and surveys with two events, a sampling design that includes two events, each with 30 plots is a practical alternative to the previous design because there is little difference in power and it requires less effort while still allowing for plots to maintain independence (Fig. 5). Specifically, a survey design with 30 plots and two events lasts ca. 1 h and 15 min, whereas a survey design with three events and nine plots lasts ca. 2 h and 5 min. Importantly, increasing the number of plots and(or) events will not substantially affect power to detect 30% (or lower) increases or decreases in larval abundance. Hence, if detecting fine-scale changes in larval abundance is of interest (e.g., hypothesis testing), the number of surveys must be increased to attain reasonable power. Because the sampling design of surveys for larval DHP is still in an experimental phase, its structure has been altered multiple times since 2005. Maximizing statistical power to detect year to year differences in larval density will help managers assess the influence of earthquakes and flood events on survival of DHP larvae. Furthermore, as data accumulate, year-to-year variability can be estimated as a random effect, thus allowing estimation of the survey's power to detect long-term trends. Hopefully, monitoring of DHP larvae will continue far into the future and become a long-term record of larval abundance that will accompany surveys of adult DHP as well as current habitat monitoring surveys. This holistic monitoring approach will provide valuable insight as to the life history and habitat requirements of the DHP, thus aiding managers make decisions on where to focus future management actions. Although the results of this study are specific to Devils Hole, many other monitoring efforts may benefit from coupling variance components estimation with power analysis.

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