

Investigating three sources of bias in hook-and-line surveys: survey design, gear saturation, and multispecies interactions

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Abstract: Hook-and-line surveys can be used to estimate population trends in fish species where conventional methods such as trawl, acoustic, visual, or pot surveys cannot be applied. Hook-and-line surveys allow for the collection of biological information, but the resultant indices of abundance may be biased. We designed simulations to address concerns around survey design, hook saturation, and competition among species and found that catch per unit effort (CPUE) declined more slowly than population size across all scenarios. This hyperstability was most prominent when fish were found in high-density patches, and these scenarios have median absolute relative error values roughly three to five times greater than those with more even distributions of fish density. Despite hyperstability, the surveys still had statistical power to detect changes in abundance. Interspecific competition for hooks caused bias in survey results when one species was more aggressive than another. Taken together, our results indicate hook-and-line surveys fill a niche in survey methodologies, but their use and interpretation can be challenged by hyperstability and competition among species.

Résumé : Les relevés à la ligne peuvent être utilisés pour estimer les tendances démographiques d'espèces de poissons quand des méthodes traditionnelles comme les relevés acoustiques, visuels, au chalut et au casier ne peuvent être employées. Si les relevés à la ligne permettent la collecte de renseignements biologiques, les indices d'abondance en découlant peuvent être biaisés. Nous avons conçu des simulations pour examiner les problèmes potentiels entourant la conception des relevés, la saturation des hameçons et la concurrence entre espèces et avons constaté que les captures par unité d'effort (CPUE) baissent plus lentement que la taille de la population pour tous les scénarios. Cette hyperstabilité est la plus prononcée quand les poissons se trouvent dans des groupements de haute densité, ces scénarios présentant des valeurs absolues médianes de l'erreur relative environ trois à cinq fois supérieures aux valeurs associées à des répartitions plus uniformes de la densité de poissons. Malgré l'hyperstabilité, les relevés ont la capacité statistique de détecter des variations d'abondance. La concurrence entre espèces pour les hameçons cause un biais dans les résultats des relevés quand une espèce est plus agressive qu'une autre. Collectivement, nos résultats indiquent que les relevés à la ligne ont leur place parmi les méthodes de relevé, mais que l'hyperstabilité et la concurrence entre espèces peuvent compliquer leur utilisation et l'interprétation des résultats qui en découlent. [Traduit par la Rédaction]

Introduction

Fisheries management is predicated on surveys that monitor changes in population levels. Biased and imprecise surveys can lead to uncertain population estimates that can complicate management strategies. In some cases, only fishery-dependent data are available, which require standardization to account for changes in catch per unit effort (CPUE) unrelated to fish abundance (Maunder and Punt 2004). Standardization of fishery-independent survey data is often necessary as well, particularly for design-based surveys. Surveys that miss key habitats, such as rocky reefs that cannot be trawled and deep waters beyond the reach of a survey, increase the potential for biased estimates of relative abundance and raise concerns about the magnitude of biomass that may be cryptic to standard surveys. Bias correction is difficult with inconsistently biased CPUE indices and will result in biased population assessments.

In the search for accurate fishery-independent population estimates, a wide variety of survey methods have been developed, including trawl, acoustic, trap, visual, and hook-and-line surveys —

each with different trade-offs. Assessments for commercial fisheries often rely on trawl survey data, which use survey data to calculate indices of abundance. Indices along with age, length, and mass information are incorporated to evaluate stock status, which on the West Coast of the US is done with statistical catch-at-age stock assessments (Methot and Wetzel 2013). However, trawl surveys are less effective at sampling rocky areas because of the increased likelihood of snags and gear damage, and bottom trawling gear can cause more harm to habitat and nontarget species than most other survey methods. As a result, trawl gear may not be able to sample rocky reef habitats well. Acoustic surveys are best used on densely schooling, abundant species such as Pacific hake (*Merluccius productus*; Berger et al. 2017). However acoustic surveys cannot adequately resolve demersal species in the acoustic dead zone near the ocean floor (Ona and Mitson 1996; Patel et al. 2009) and require additional extractive sampling to confirm species identification and collect biological information such as length, sex, age, and genetic data. Trap surveys are most useful for crabs and lobsters that are commercially caught using the same gear, but are affected by trap saturation (Fogarty and

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Addison 1997; Bachele et al. 2013a, 2013b) and other factors. Visual survey methods, including divers and underwater vehicles, are non-lethal and can collect both habitat information and species information (Yoklavich et al. 2000, 2007). However biological information is difficult to collect with visual survey methods, and behavioral responses to cameras, divers, and vehicles might bias survey results (Stoner et al. 2008; Laidig et al. 2013).

Hook-and-line surveys may fill a methodological niche as they are well suited to collect biological information from rocky reef habitats. Previous studies have used data from hook-and-line surveys to study growth (Zhao et al. 1997), survey fish communities (Chester et al. 1984), estimate size selectivity of hook-and-line gear (Ralston 1990), and assess population status (Collins and Sedberry 1991). However, relative to other survey methods, hook-and-line surveys are not well studied and likely have their own specific sources of bias. Here we develop a simulation framework to investigate two potential sources of bias: density-based sampling and gear saturation.

Randomized or design-based sampling is desirable in surveys of fish populations as it results in unbiased inference. However simple random sampling is often highly inefficient and may impose logistical constraints. Habitat-stratified random sampling requires substrate maps of sufficient resolution and spatial coverage to identify all potential sampling locations that may not be available for all habitat types and target species (Pope et al. 2010). These obstacles may require survey design where sampling occurs with greater probability in areas of high densities, which we refer to as density-based sampling. We evaluate the bias associated with density-based sampling in the context of hook-and-line surveys, although the results will be applicable to surveys with other gears as well.

Hook-and-line surveys are also susceptible to gear saturation, which may lead to a nonlinear relationship between abundance and CPUE (Cadigan 2012). Specifically, gear saturation in hook-and-line surveys may result in hyperstability, where CPUE declines more slowly than abundance (Harley et al. 2001). Bias from gear saturation can occur because there are many more fish than available hooks, and this bias may be exacerbated when multiple species with behavioral differences are present (Etienne et al. 2010).

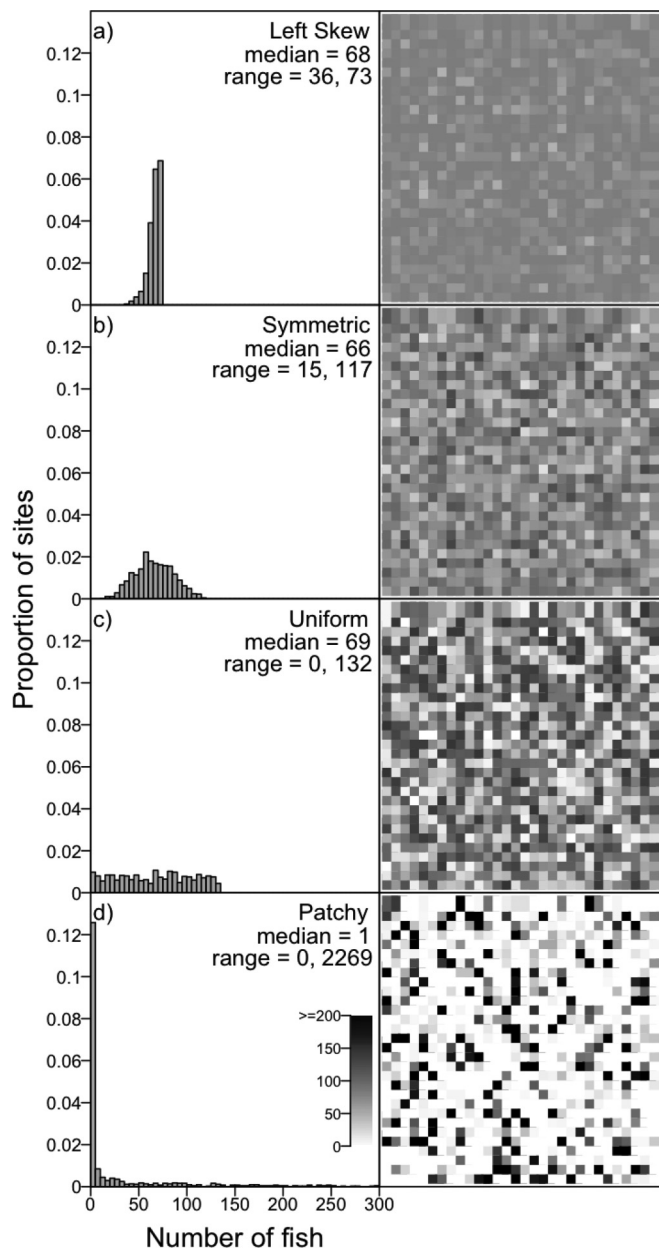
We designed a simulation framework to evaluate bias and imprecision from density-based sampling and gear saturation and assess their impact on the relationship between survey CPUE and relative abundance. Several of the simulation parameters and assumptions are informed by a case study, the Southern California Shelf Rockfish Hook and Line Survey (hereinafter, “California hook-and-line survey”), which targets several demersal species of the genus *Sebastes* in rocky habitats in the Southern California Bight. Simulation characteristics such as survey design, number of sites, number of hooks deployed, population sizes aimed at reflecting overfished, rebuilding, and rebuilt stocks, and exploration of how multispecies competition interacts with gear saturation were included to improve the analysis of data collected on the California hook-and-line survey but also provide useful insight for more generalized applications (Cadigan 2012). We conclude the analysis by comparing simulation results with empirical data collected on this survey.

Methods

Survey simulations

Each survey simulation has three components: an initial fish distribution, method of site selection, and number of sample sites. The initial fish distribution is a characteristic of the system, which can influence survey design (e.g., fish with patchy initial distributions may be best surveyed with 100 sites with density-based site selection). The method of site selection was random or density-based. Sites that have the highest numbers of fish are sampled more frequently with density-based sampling. Surveys

Fig. 1. Histograms of the numbers of fish per site (left) for the four initial distributions when 60 000 fish are distributed among 900 fishing sites, including the median and range of numbers of fish in each site. Plots in the right column show the numbers of fish (darker colors for higher numbers) in each site (squares) in the 900 fishing sites.



occur in 5, 20, 50, or 100 sites. Our simulations occurred over a 30×30 matrix, where each cell represents a site. Survey simulations had one or two species, and simulations with two species included interspecies competition for bait on hooks.

Fish density distribution refers to the statistical distribution of numbers of fish across the 900 sites. We designed the simulations to account for a wide range of population distributions, which are influenced by species' life histories as well as habitat distribution. Initial fish distributions range from few fish in many areas to many fish in few areas (Fig. 1). Specifically, we used four forms of a beta distribution (which has two parameters, α and β) to determine the statistical distribution of density used to initially allocate fish among sites: left skew ($\alpha = 10$, $\beta = 1$; Fig. 1a), symmetric (5, 5;

Table 1. Ranges (minimum–maximum) and median numbers of fish for each level of relative abundance and initial distribution type.

No. of fish	Relative abundance	Ranges			Medians				
		Left skew	Normal	Patchy	Uniform	Left skew	Normal	Patchy	Uniform
20 000	0.1	12–25	5–39	0–756	0–44	23	22	0	23
40 000	0.2	24–50	10–78	0–1512	0–88	46	44	0	46
60 000	0.3	36–73	15–117	0–2269	0–132	68	66	1	69
80 000	0.4	47–98	20–156	0–3025	0–176	91	88	1	92
100 000	0.5	59–122	25–195	0–3781	0–220	114	110	1	114
120 000	0.6	71–147	29–234	0–4537	0–264	137	131	1	137
140 000	0.7	83–171	34–273	0–5294	0–308	160	153	1	160
160 000	0.8	95–195	39–312	0–6050	0–352	183	175	1	183
180 000	0.9	107–220	44–351	0–6806	0–397	205	197	2	206
200 000	1	118–244	49–390	0–7562	0–441	228	219	2	229

Fig. 1b); uniform (1, 1; Fig. 1c), and patchy (0.1, 10; Fig. 1d). The descriptions refer to the beta distribution form, thus a uniform distribution means that there is an equal probability of a small number of fish or a large number of fish at a given site, while a symmetric distribution implies most sites will have an intermediate number of fish and few will have large or small numbers of fish. Fish in rocky reef habitats are most closely represented by initial distributions with many fish in few areas (patchy initial distribution). These four scenarios were designed to represent a spectrum of possible fish distributions, while the California hook-and-line survey is probably most closely represented with a patchy initial distribution. Fish were spatially distributed by sampling 900 values (one for each site) from the corresponding beta distribution, normalizing the values to sum to one and multiplying the normalized values by the total number of fish in the entire survey area. Initial numbers of fish ranged from 20 000 to 200 000 in increments of 20 000 (Table 1). Patches were not redistributed as the initial numbers of fish varied.

Survey site selection was either random or density-based. For random sampling, a selection of sites was chosen at random from all sites. For density-based sampling, sites were sampled with probabilities proportional to the numbers of fish in each site, ensuring that sampling was more likely to be in sites with more fish. In reality, information for density-based sampling could come from fisher knowledge or information about habitats preferred by the target species, such as rocky reefs. The precision of the survey estimates was modelled across different numbers of sampling sites: 5, 20, 50, or 100. At each site, 75 hooks were deployed to match our real-world scenario.

Simulations did not have a temporal component and did not include processes like recruitment, mortality, movement, and local depletion. Simplifying the simulations in this manner, while adjusting population levels, allowed us to focus on the effects of survey design and gear saturation. Inclusion of these processes would improve realism of the simulations, but we decided to simplify the simulations to focus on the effects of survey design and gear saturation.

Sampling probabilities

The probability of a particular hook catching a fish was based on the number of fish of all species at a site, together with species-specific catchabilities (probability of being caught given that a fish encounters a hook). The probability of catching a fish increases as the number of fish, which was 0.01 in the base model. The probability of catching a fish of species s in isolation (p_s) increases asymptotically towards one as the number of fish (n_s) and q_s increase:

$$(1) \quad p_s = 1 - \exp(-n_s q_s)$$

which assumes that fish randomly encounter hooks. For m species, the probability of one hook catching a fish (h) is

Table 2. The proportions of fish moving in to (density-dependent habitat selection) or out of survey sites (local depletion).

No. of fish	Relative abundance	Proportion in	Proportion out
20 000	0.1	0.15	0
40 000	0.2	0.13	0
60 000	0.3	0.11	0
80 000	0.4	0.09	0.02
100 000	0.5	0.06	0.04
120 000	0.6	0.04	0.06
140 000	0.7	0.02	0.09
160 000	0.8	0	0.11
180 000	0.9	0	0.13
200 000	1	0	0.15

Note: Numbers of fish moving in to survey sites are calculated by multiplying the proportions and numbers of fish outside survey sites. Numbers of fish moving out of survey sites are calculated by multiplying the proportions and numbers of fish inside survey sites.

$$(2) \quad h = 1 - \prod_{s=1}^m (1 - p_s)$$

For the simulations, in the simplest case where only one species is simulated, for each hook, one Bernoulli trial $B(P = h = p_s)$ determined whether the hook caught a fish. The capture process was repeated for 75 hooks. If a hook caught a fish then n_s was reduced by one, and eqs. 1 and 2 updated the h value. We assumed that each hook had an equal probability of catching fish and did not explore interactions between hook probabilities, as there might be in reality for hooks at different depths on a single line.

For simulations with two species, we assumed that both species had the same site preferences, and that densities of species one and species two were high in the same sites. Specifically, we multiplied the same standardized beta distribution samples by the initial numbers of fish for both species one and species two. This ensured that simulations could test the hook competition effect of one species on another, independent of differences in habitat preferences.

If a hook caught a fish in multispecies simulations, the probability of catching species s (c_s) was calculated from the species-specific abundances n_s and catchabilities q_s :

$$(3) \quad c_s = \frac{n_s q_s}{\sum_{s=1}^m n_s q_s}$$

Table 3. Shape estimates (β) from CPUE values for each initial distribution, sampling type, and number of sites.

Initial distribution	Sampling type	No. of sites							
		5		20		50		100	
Left skew	Density-based	0.67	(0.65–0.69)	0.64	(0.63–0.65)	0.64	(0.63–0.65)	0.65	(0.65–0.66)
	Random	0.67	(0.65–0.70)	0.65	(0.64–0.66)	0.64	(0.63–0.65)	0.66	(0.65–0.66)
Symmetric	Density-based	0.65	(0.57–0.73)	0.62	(0.59–0.65)	0.62	(0.60–0.63)	0.62	(0.61–0.63)
	Random	0.67	(0.60–0.77)	0.64	(0.60–0.67)	0.64	(0.62–0.66)	0.64	(0.63–0.66)
Patchy	Density-based	0.14	(0.05–0.29)	0.16	(0.11–0.22)	0.18	(0.15–0.22)	0.22	(0.20–0.24)
	Random	0.49	(0.12–1.00)	0.40	(0.23–0.64)	0.39	(0.30–0.51)	0.39	(0.32–0.47)
Uniform	Density-based	0.56	(0.49–0.67)	0.55	(0.51–0.59)	0.55	(0.53–0.57)	0.55	(0.54–0.57)
	Random	0.61	(0.52–0.75)	0.60	(0.55–0.66)	0.59	(0.57–0.63)	0.60	(0.58–0.62)

Note: Shape estimates (β) are indicated by median values, with the 5th and 95th percentile values in parentheses. Values less than 1.0 are hyperstable, and values closer to 0 have stronger hyperstability.

Table 4. Catchability (q_{CPUE}) estimates for each initial distribution, sampling type, and number of sites.

Initial distribution	Sampling type	No. of sites							
		5		20		50		100	
Left skew	Density-based	0.89	(0.86–0.91)	0.87	(0.86–0.88)	0.87	(0.86–0.88)	0.88	(0.87–0.88)
	Random	0.89	(0.86–0.91)	0.87	(0.85–0.88)	0.87	(0.85–0.87)	0.87	(0.87–0.88)
Symmetric	Density-based	0.90	(0.81–0.97)	0.88	(0.84–0.92)	0.88	(0.85–0.90)	0.88	(0.86–0.90)
	Random	0.87	(0.75–0.95)	0.85	(0.80–0.89)	0.84	(0.81–0.87)	0.85	(0.82–0.87)
Patchy	Density-based	1.00	(0.86–1.00)	1.00	(0.93–1.00)	0.99	(0.95–1.00)	0.97	(0.94–1.00)
	Random	0.26	(0.02–0.63)	0.28	(0.14–0.43)	0.28	(0.19–0.37)	0.28	(0.22–0.35)
Uniform	Density-based	0.94	(0.78–1.03)	0.93	(0.86–0.98)	0.92	(0.88–0.95)	0.92	(0.89–0.95)
	Random	0.78	(0.54–0.98)	0.77	(0.66–0.87)	0.76	(0.69–0.83)	0.76	(0.72–0.81)

Note: Catchability estimates (q_{CPUE}) are indicated by median values, with the 5th and 95th percentile values in parentheses. Values less than 1.0 are hyperstable, and values closer to 0 have stronger hyperstability.

A single draw from a multinomial distribution $M(1, P = c_1, c_2, \dots, c_m)$ determined which species was caught. Again this process was repeated for 75 hooks.

Competition between species was controlled by the initially specified catchabilities, with three scenarios simulated whether species 1 was either less than ($q_1 = 0.003$, $q_2 = 0.007$), equal to ($q_1 = 0.005$, $q_2 = 0.005$), or more aggressive ($q_1 = 0.007$, $q_2 = 0.003$) than species 2.

Scenarios

We simulated each survey scenario over a range of population levels to evaluate survey performance at different population levels. The population size can change because of natural processes like movement and mortality, which were not explicitly included in the simulations.

For the single-species scenarios, the total number of fish summed over all sites from 20 000 to 200 000 in increments of 20 000 (Table 1). Results are presented in terms of relative abundance where the highest population level (200 000) had a relative abundance of 1.0. We simulated 1000 replicates of each scenario.

Bias may be caused by both site selection (random or density-based) and gear saturation. We ran single-species scenarios with increased numbers of hooks to reduce gear saturation and isolate the bias due to site selection. Surveys with 150 or 600 hooks deployed per site (compared with 75 hooks in other surveys) were conducted with 50 survey sites, patchy initial fish distributions, and random or density-based sampling.

Density-based sampling may be problematic, as survey sites experience local depletion or density-dependent habitat selection (Lindberg et al. 2006). We ran scenarios incorporating each process into the survey simulations and evaluated the associated biases. Survey sites were selected based on the initial numbers of fish, and the numbers of fish in each survey site were increased or decreased depending on the process. With local depletion, a proportion of the fish within each survey site was decreased (Table 2), and this proportion decreased as relative abundance decreased.

Note that despite referring to this scenario as local depletion, there was no fish mortality and only fish movement. With density-dependent habitat selection, a proportion of fish outside survey sites moved in, and this proportion increased as relative abundance decreased (Table 2). As a result of the calculations, the numbers of fish moving into survey sites was much higher than the number of fish moving out of survey sites. We conducted these scenarios with 50 survey sites, patchy initial fish distributions, and density-based sampling.

For the two-species simulations, we simulated a reduced set of scenarios, looking only at surveys with sampling at 50 survey sites with initial fish density distributions that were patchy or symmetric, and with random or density-based sampling. Note that sites with high densities of species one also had high densities of species two.

Summary values

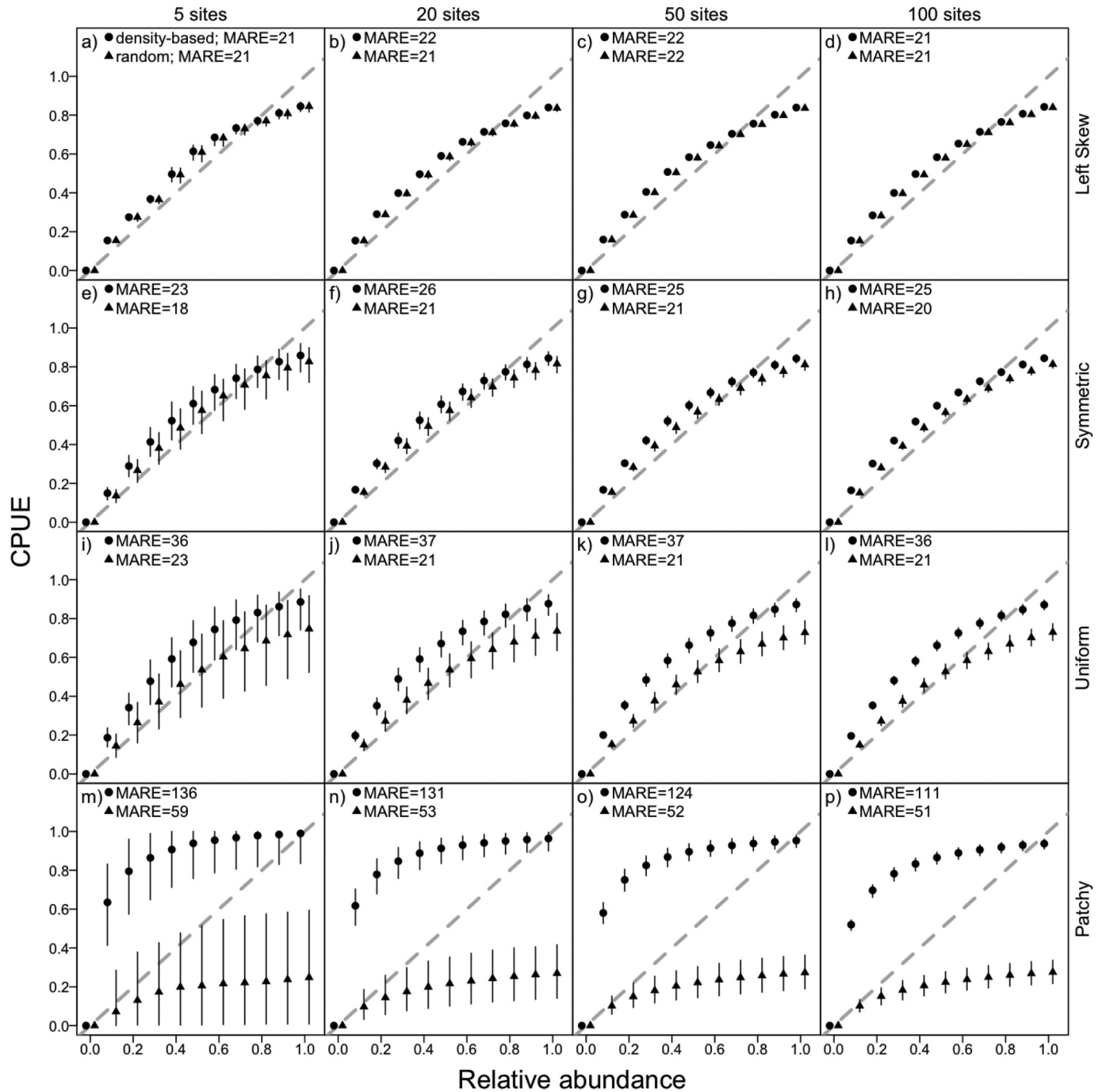
Site-specific CPUE is the number of fish caught divided by the number of hooks. Survey CPUE was the average of site-specific CPUE values and was reported as median and 95th percentiles across 1000 sets of surveys.

To estimate the degree of hyperstability between abundance and CPUE, we fit the power curve equation:

$$(4) \quad \theta = q_{\text{CPUE}} n^\beta$$

to individual abundance (n) and survey CPUE (θ) values using linear regression to estimate survey catchability (q_{CPUE}) and shape (β). Hyperstability, when CPUE declines more slowly than biomass, has shape parameter values of $0 < \beta < 1$. Hyperdepletion, when CPUE declines faster than biomass, has shape parameter values of $\beta > 1$. When $\beta = 1$ there is neither hyperstability nor hyperdepletion, and instead there is a linear relationship between CPUE and abundance (Harley et al. 2001).

Fig. 2. Catch per unit effort (CPUE) and relative abundance for each survey. CPUE is the number of fish caught per 75 hooks, averaged over all sites. Points indicate the median CPUE values for density-based sampling (circles) and random sampling (triangles), with 5th and 95th percentiles (bars) shown for 1000 replicates. Median absolute relative error values (MARE) are shown in the top left of each panel for simulations with density-based and random survey design. Rows show initial distribution types and columns the number of survey sites. The one-to-one line (gray dashed line) represents an unbiased survey and is shown for reference.



Bias and precision were summarized by calculating median absolute relative error (MARE) values for each scenario. Relative error was calculated with the following equations:

$$E = \frac{\theta_r - r}{r}$$

$$A_j = |\bar{E}_i|$$

$$\text{MARE}_j = 100 \times \text{median}(A_j)$$

where relative error E was calculated at each relative abundance level r , where θ_r is the estimated CPUE value. Relative error values were then averaged across 1000 iterations i to obtain average absolute relative error A values for each survey combination j .

Additionally, we relate the change in CPUE values (θ) to the change in true population size, to evaluate the ability of the simulated survey to capture overall population trends. We calculated slopes at each level of relative abundance with eq. 6:

Table 5. Difference in CPUE between 5th and 95th quantiles for each initial distribution, sampling type, and number of sites.

Initial distribution	Sampling type	No. of sites	Relative abundance level									
			0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1
Left skew	Density-based	5	0.02	0.03	0.04	0.07	0.08	0.05	0.05	0.04	0.05	0.05
		20	0.01	0.02	0.02	0.03	0.03	0.03	0.03	0.02	0.02	0.03
		50	0.01	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02
		100	0.00	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
	Random	5	0.02	0.03	0.04	0.08	0.08	0.06	0.05	0.04	0.05	0.05
		20	0.01	0.02	0.02	0.03	0.04	0.03	0.03	0.03	0.03	0.03
		50	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
		100	0.00	0.01	0.01	0.01	0.02	0.01	0.01	0.01	0.01	0.01
Symmetric	Density-based	5	0.06	0.11	0.15	0.19	0.19	0.18	0.18	0.16	0.15	0.15
		20	0.03	0.05	0.08	0.09	0.09	0.08	0.08	0.08	0.08	0.07
		50	0.02	0.03	0.04	0.05	0.05	0.05	0.05	0.05	0.05	0.04
		100	0.01	0.02	0.03	0.04	0.04	0.04	0.04	0.04	0.03	0.03
	Random	5	0.07	0.12	0.16	0.21	0.22	0.21	0.21	0.20	0.19	0.18
		20	0.03	0.05	0.08	0.09	0.09	0.09	0.09	0.09	0.09	0.08
		50	0.02	0.03	0.05	0.06	0.06	0.06	0.06	0.06	0.06	0.05
		100	0.01	0.02	0.03	0.04	0.04	0.04	0.04	0.04	0.04	0.04
Uniform	Density-based	5	0.10	0.16	0.23	0.25	0.27	0.27	0.26	0.24	0.22	0.21
		20	0.05	0.09	0.12	0.12	0.13	0.13	0.12	0.12	0.11	0.11
		50	0.03	0.05	0.06	0.07	0.07	0.08	0.08	0.07	0.07	0.07
		100	0.02	0.04	0.04	0.05	0.05	0.05	0.06	0.05	0.05	0.05
	Random	5	0.12	0.21	0.28	0.34	0.38	0.4	0.41	0.41	0.40	0.39
		20	0.06	0.10	0.14	0.16	0.17	0.19	0.19	0.19	0.19	0.19
		50	0.04	0.07	0.09	0.10	0.11	0.12	0.12	0.12	0.12	0.12
		100	0.03	0.05	0.06	0.07	0.08	0.08	0.09	0.09	0.09	0.09
Patchy	Density-based	5	0.42	0.39	0.34	0.29	0.24	0.21	0.19	0.18	0.17	0.17
		20	0.19	0.18	0.16	0.14	0.13	0.12	0.12	0.11	0.10	0.10
		50	0.11	0.11	0.10	0.10	0.09	0.08	0.08	0.07	0.07	0.06
		100	0.05	0.06	0.07	0.07	0.06	0.06	0.06	0.05	0.05	0.05
	Random	5	0.29	0.38	0.42	0.47	0.51	0.54	0.56	0.57	0.58	0.59
		20	0.15	0.20	0.22	0.24	0.25	0.26	0.27	0.27	0.27	0.28
		50	0.09	0.12	0.14	0.15	0.16	0.17	0.17	0.17	0.18	0.17
		100	0.06	0.09	0.10	0.11	0.11	0.11	0.12	0.12	0.12	0.12

$$(6) \quad L_{i,r} = \frac{\theta_{i,r+0.1} - \theta_{i,r-0.1}}{\theta}$$

where slope L of iteration i at relative abundance level r is calculated with the CPUE values for i and $r + 0.1$ and $r - 0.1$. Slopes were not calculated at relative abundance levels of 0 or 1. The slope calculations were then compared with the true population slope ($=1$).

Power analysis

To test the power of the surveys to detect declines in abundance, we conducted a resampling analysis. The goal was to quantify the ability of the survey to detect a change in population level from an unfished (relative abundance of 1.0) and a half-fished (0.5) state. We sampled CPUE values from the focal relative abundance levels (1.0 or 0.5) and all the other relative abundance levels (e.g., 0.1, 0.2, 0.3, ...). For each relative abundance level, 1000 pairs of CPUE values were sampled, and the difference between the values were calculated. Significant values had 5th and 95th percentile values that did not overlap with 0, indicating that survey CPUE values detected a change. Reported median values are the median differences in paired CPUE values from the replicates. We report the true positive rate as the proportion of sampled CPUE pairs with a difference greater than or equal to the true change.

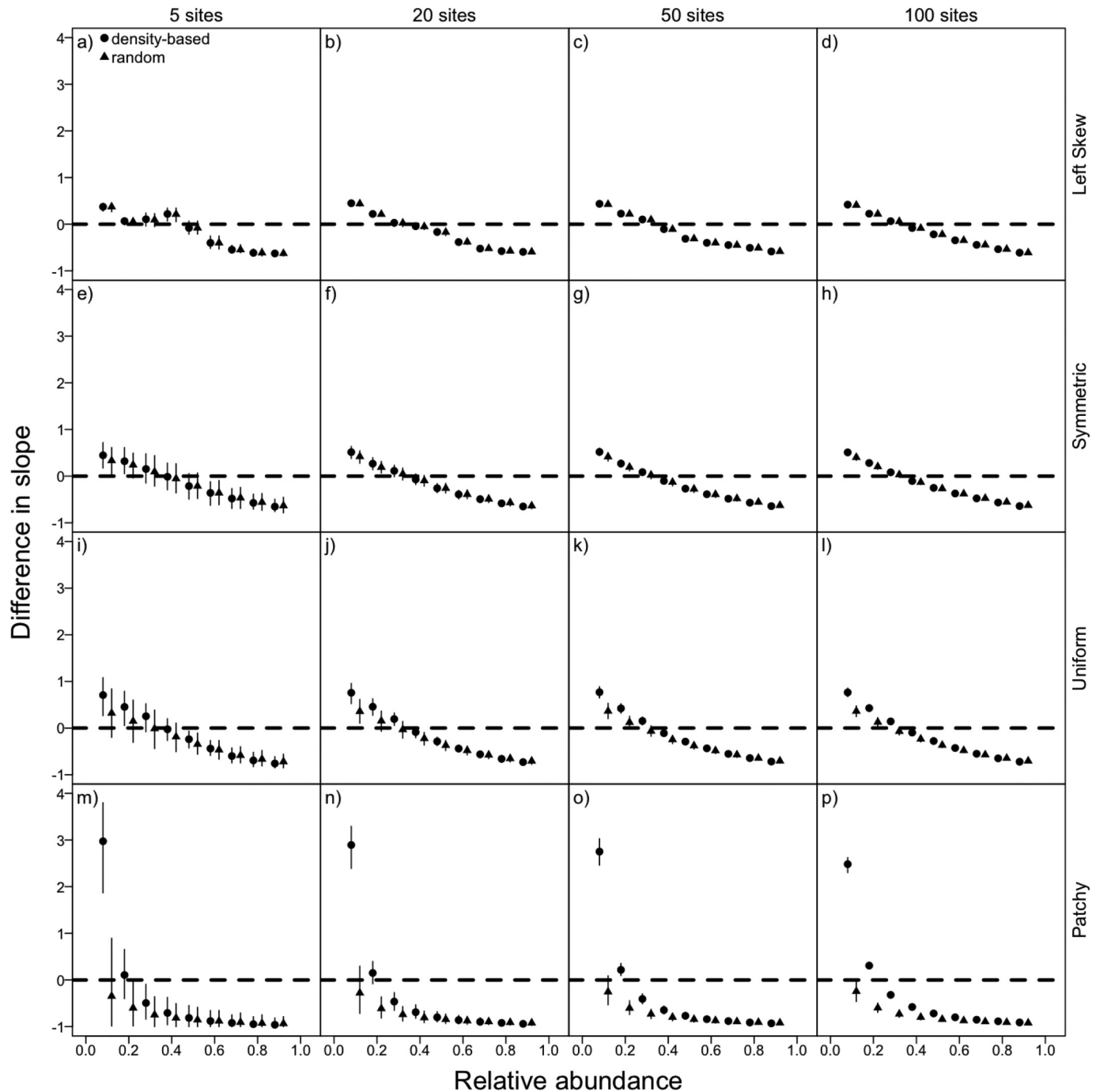
Real-world scenario: California hook-and-line survey

Results from the simulations were related to a real-world example in an effort to determine whether the simulation effectively captures trends and relationships identified in empirical data. Rockfishes (*Sebastes* spp.) are the target species of the California

hook-and-line survey and present significant challenges for research and management in that they are long-lived, slow-growing, late to mature, and slow to recover from sustained overfishing (Punt and Ralston 2007; Clark 2011). There are more than 60 species of rockfish on the US West Coast, most of which are associated with rocky untrawlable habitats (Rooper et al. 2010; Jones et al. 2012). Data from the survey were used in the recent bocaccio (*Sebastes paucispinis*) stock assessment (He et al. 2015) and have been used to quantify spatial density dependence in rockfish abundance estimation (Thorson et al. 2015). As in our simulations, the California hook-and-line survey (Harms et al. 2010) surveys about 100 sites annually. Survey designers worked with recreational fishing captains to select survey sites with high fish densities, similar to density-based site selection in the simulations. Operationally, each vessel has three anglers positioned at the bow, middle, and stern of the boat, and each angler has a line with five hooks. In each of five “drops” from the survey vessel, the anglers drop lines for a maximum of 5 min, for a total of 75 hooks deployed per site.

For comparison with the simulation results, we examined the results of the California hook-and-line survey, focusing on the two most frequently caught species: bocaccio (*S. paucispinis*) and vermilion rockfish (*S. miniatus*). We present site-specific CPUE (number of fish/75 hooks at each site) and unstandardized CPUE for bocaccio and vermilion rockfish (the average of site-specific CPUEs in each year). To quantify species aggression, we calculated the average time to first bite for bocaccio and vermilion rockfish for drops where lines caught only one species.

Fig. 3. Slope bias for each survey. The difference in slope represents the difference between the trend in CPUE values and the true population trend, which has a slope of 1. A difference of 0 is indicated in each plot (black dashed lines). Values for density-based (circles) and random sampling (triangles) are shown with 5th and 95th percentiles (bars) shown for 1000 replicates. Rows show initial distribution types and columns the number of survey sites.



Results

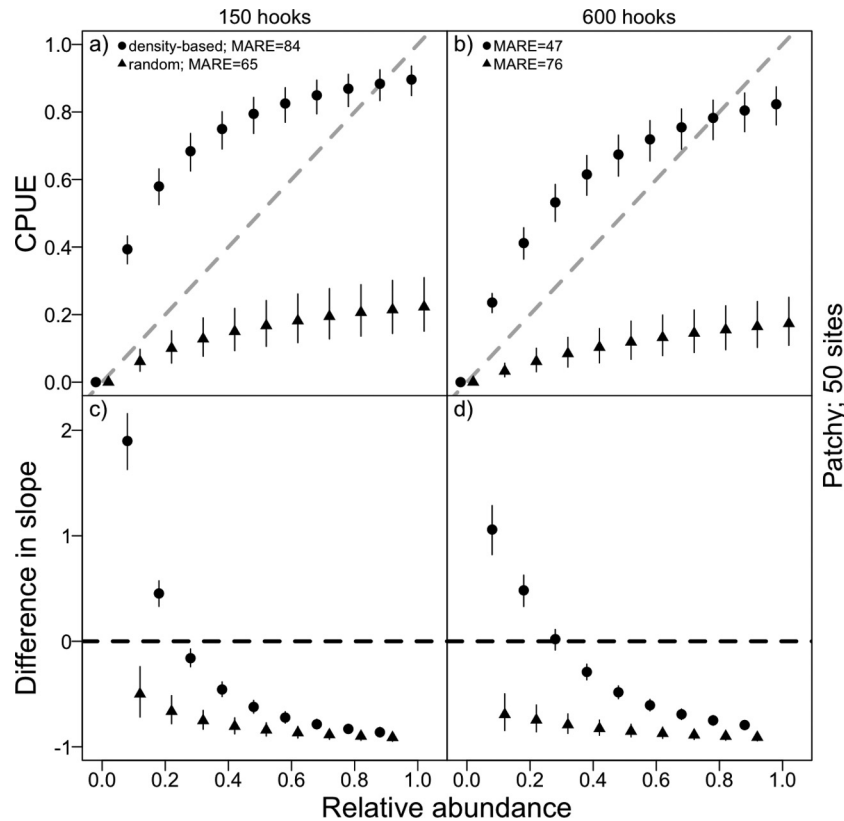
Single-species CPUE

Simulated surveys across all initial fish distributions showed evidence of hyperstability, where CPUE declined more slowly than population levels. Surveys on patchy initial fish distributions had the highest degree of hyperstability, evidenced by β values closer to zero than to one (Table 3; see Table 4 for catchability estimates). For patchy initial distributions, hyperstability is more marked with density-based site selection (median $\beta = 0.14$ – 0.22 ; Table 3) than for random site selection (median $\beta = 0.39$ – 0.49 ;

Table 3). Surveys with left-skew, symmetric, and uniform initial distributions have much lower hyperstability (median $\beta = 0.55$ – 0.67 ; Table 3) and display less difference between density-based and random site selection (Figs. 2a–2l). Generally, density-based site selection results in greater hyperstability than that found with random site selection (Table 3).

In our simulations, density-based sampling nearly always resulted in more biased indices than random sampling. When fish had patchy initial distributions, MARE values from density-based sampling were more than double those from random sampling

Fig. 4. The influence of increasing the number of hooks from 150 (left column) to 600 (right column) on CPUE (a–b) and difference in slope (c–d). The surveys had patchy initial fish distributions and were conducted in 50 sites. Median absolute relative error values (MARE) are shown in the top left of CPUE panels. The one-to-one line (gray lines; a–b) and difference of 0 values (black lines; c–d) are indicated in each plot. Values for density-based (circles) and random sampling (triangles) are shown with 5th and 95th percentiles (bars) shown for 1000 replicates.



(Figs. 2m–2p). However precision was higher with density-based sampling compared with random sampling (Table 5). The rate of change in CPUE values was greater than that in the true population at low population levels (relative abundance <0.3), and above these low population levels, the CPUE slopes were less than 1 (Fig. 3). Density-based surveys that tend to sample in areas with more fish will also have higher levels of bias.

Surveys with density-based sampling were most affected by gear saturation. MARE values for surveys decreased by roughly 30% with 150 hooks and 60% with 600 hooks (Figs. 4a–4b) compared with the same surveys with 75 hooks. The differences in slopes for density-based sampling surveys moved closer to 0 as the number of hooks increased (Figs. 4c–4d). Note that these results only apply to surveys with patchy initial fish distributions and sampling in 50 survey sites. The addition of more hooks to the survey reduced but did not eliminate bias.

Surveys with local depletion and density-dependent habitat selection had less and more bias, respectively, than surveys without these processes. Surveys without processes (Fig. 2o) had MARE values that were roughly 10% higher than those from surveys with local depletion (Fig. 5a) and roughly 10% lower than those from surveys with density-dependent habitat selection (Fig. 5b). Hyperstability appeared to remain at lower relative abundance levels, and the calculated slopes at 0.1 and 0.2 relative abundance levels had the greatest difference from the true slope of 1 (Figs. 5c–5d). We ran two additional scenarios with proportions of moving fish that were two and roughly four times higher (see online Supplementary data, Table S1¹), and the results showed similar patterns (Fig. S1¹).

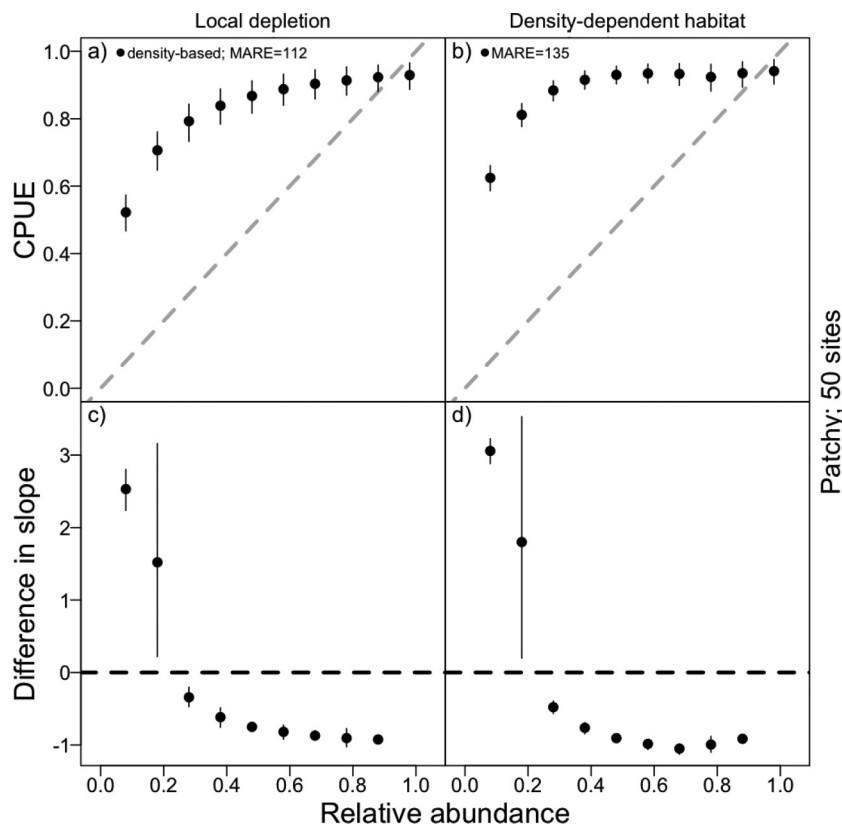
Single-species power analysis

Surveys with density-based sampling had more bias but a better ability to detect changes than surveys with random site selection. Variability was lowest in surveys with density-based sampling, particularly with patchy initial fish distributions, which resulted in a stronger ability to detect change. Specifically, surveys with density-based sampling were better able to detect smaller changes in population levels than surveys with random sampling. For example, simulated surveys with patchy initial fish distributions and 20 site samples detected a significant decline at 30% of the unfished level with density-based sampling and 10% with random sampling (Fig. 6n). Increasing sample size increased the ability to detect change in CPUE values. For the same simulated surveys with 100 survey sites, significant decreases were detected at 60% of unfished levels with density-based sampling and 70% with random sampling (Fig. 6p). Overall, increasing sample sizes led to a greater ability to detect change, and the improved ability was greatest with patchy initial distributions. However, because of hyperstability, even when a change is detected, the magnitude of change detected in CPUE was nearly always less than the true magnitude of change in abundance (Fig. 6).

Similar general patterns were found when detecting increases and decreases from a relative abundance of 0.5 (Fig. 7). Again, density-based site selection resulted in a greater ability to detect changes, and this ability was improved with greater numbers of sites (Figs. 7m–7p). Notably, surveys were better able to detect decreases than increases in median CPUE values. This was because with hyperstability, CPUE declined more for each unit of abun-

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2017-0286>.

Fig. 5. The influence of incorporating local depletion (left column) and density-dependent habitat selection (right column) on CPUE (a – b) and difference in slope (c – d). The surveys had patchy initial fish distributions and were conducted in 50 sites. The one-to-one line (gray lines; a – b) and difference of 0 values (black lines; c – d) are indicated in each plot. Values for density-based (circles) sampling are shown with 5th and 95th percentiles (bars) shown for 1000 replicates.



dance change at lower abundance than CPUE increased for each unit of abundance increase at higher abundance.

The true positive rate, the proportion of resampled pairs with CPUE differences greater than or equal to the true change, was highest when the population had a relative abundance less than 0.5. From unfished levels, the true positive rate was highest for surveys conducted in few sites and with small decreases from unfished levels. Surveys of populations with patchy initial distributions in five sites had the highest true positive rate — nearly 40% — at relative abundance levels of 0.4 and 0.6. Full results are shown in Supplementary data (Figs. S2 and S3¹).

Two species

Indices of abundance for one species were affected by the relative abundance and catchability (or aggressiveness) of two species when both were simulated as competing for hooks. The CPUE for one species can increase because of an increase in its own relative abundance (Fig. 8) or a decrease in relative abundance of its competitor for baited hooks. This pattern was consistent for species distributions that were symmetric or patchy and survey sampling that was random or density-based. The magnitude of the effect depended on the relative aggression (catchability) of the species: aggression increased the degree of positive bias (Fig. 8; if unbiased, the points would track the dotted lines). Additionally, surveys with patchy initial distributions have median CPUE values ranges of 0.04–0.93 with density-based site selection (Figs. 9m–9r) and 0.01–0.26 with random site selection (Figs. 9s–9x).

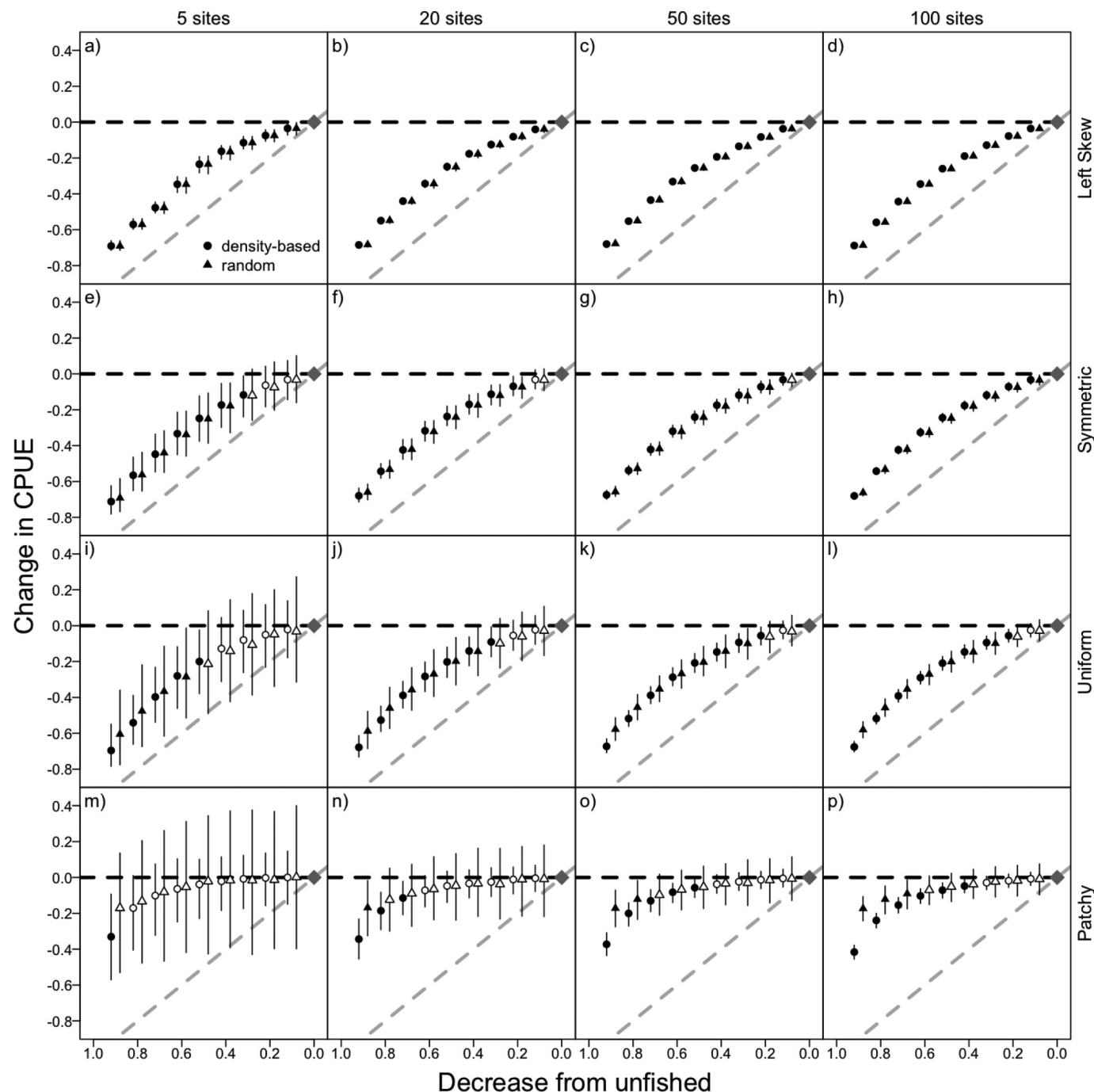
Applicability of simulation results to the California hook-and-line survey

Results from the California hook-and-line survey suggest that the sampled fish (predominantly bocaccio and vermilion rockfish) are patchily distributed with CPUE most often less than 0.5 in the surveyed sites (Fig. 10), which are selected by density-based sampling. The two most-caught species in the survey, bocaccio and vermilion rockfish, account for 52% of fish caught in the survey from 2004 to 2014. Unstandardized CPUE shows bocaccio declining and then increasing (and indeed it has recently been declared rebuilt (June 2017 Council Meeting Decision Summary Document 2017), while vermilion rockfish shows a fairly consistent increasing trend over time (Fig. 11). The survey also provides valuable information on relative aggression of the two species that could be used to correct for the impacts of interspecies competition on CPUE. In this survey, vermilion rockfish is somewhat more aggressive (higher catchability) than bocaccio, on average having a shorter time to first bite when comparing bite times for gangions that only caught a single species, although the ranges were large (Fig. 12).

Discussion

Our simulations show that over a wide range of scenarios, hyperstability is expected to occur in hook-and-line surveys because of gear saturation. Nevertheless, these surveys are able to detect changes in abundance, particularly to or from low stock sizes. Although density-based sampling results in more hyperstability in CPUE, it is also more precise than random sampling and hence has a greater ability to detect changes in populations. Both hyper-

Fig. 6. Change in estimated median catch per unit effort (CPUE) as populations decline from unfished levels (gray diamonds; values are 1 – relative abundance levels) given for density-based sampling (circles) and random sampling (triangles). Bars indicate the 5th and 95th percentiles of 1000 resampled differences from unfished relative abundance. Filled symbols are those that detected changes in CPUE more than 95% of the time. Rows show initial pattern of distribution of fish, and columns show the number of sites that were surveyed. No change in CPUE (black dashed lines), and the true change in the population (gray dashed lines) are shown. Median values are the median differences in paired CPUE values from 1000 replicates at each population level.

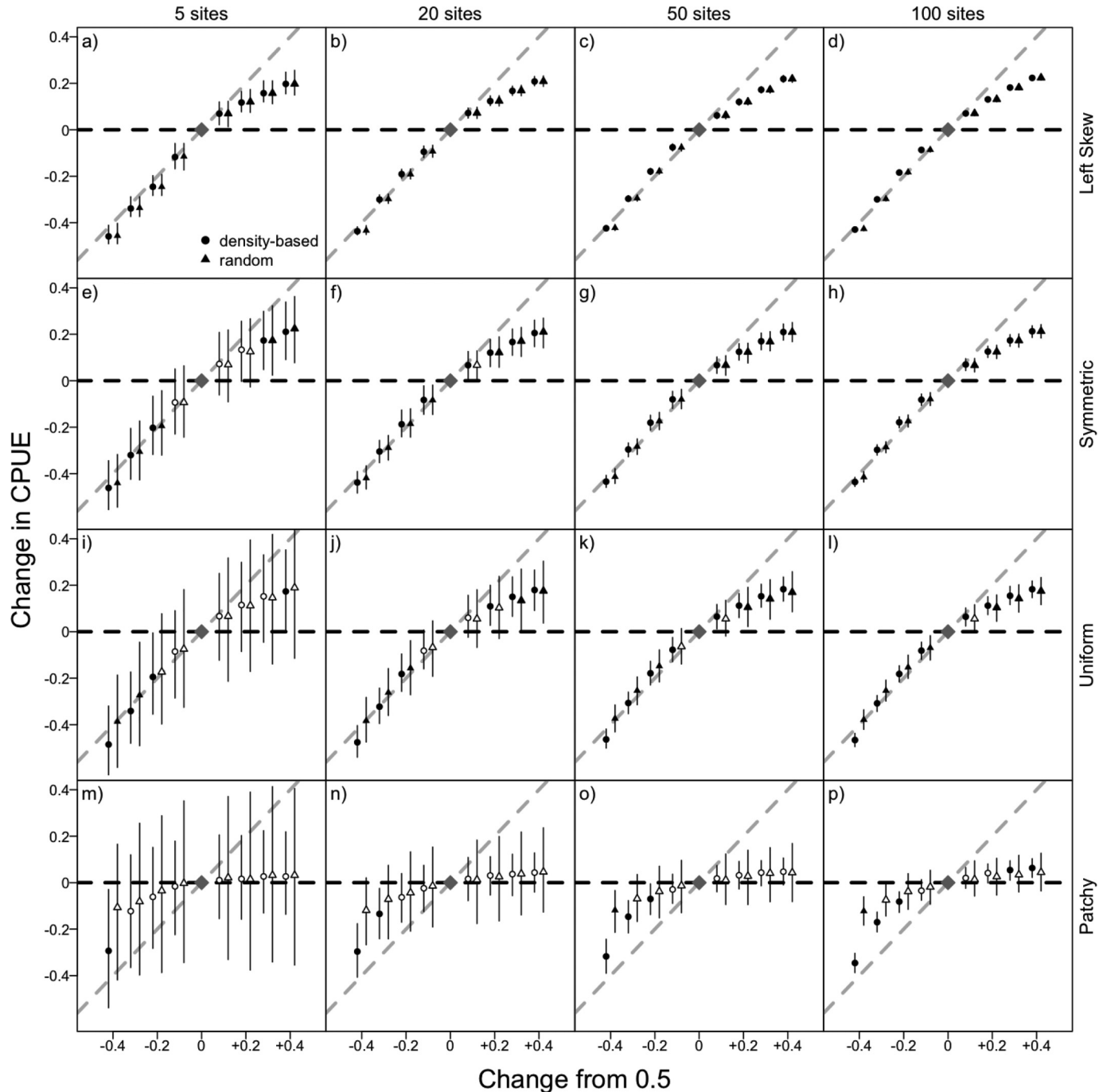


stability and the effects of density-based sampling are magnified when fish are patchily distributed.

Our results indicate that hyperstability should be assumed by default when using CPUE indices from hook-and-line surveys, and this is likely true for any survey prone to gear saturation. Hyperstability in this case arises from gear saturation: too few hooks and too many fish. The direction of bias is generally consistent (e.g., CPUE values from density-based sampling in patchy initial fish distributions are positively biased), suggesting that future

studies may develop standardization models to account for the bias. Real-world cases can have many other sources of hyperstability, such as targeting spawning aggregations (Erisman et al. 2011) or contractions in spatial survey or fishing grounds (Walters 2003). While hyperstability is most common (Harley et al. 2001), there are also cases where hyperdepletion might occur. Notably, hyperdepletion could occur in a density-based sampling design if localized depletion of small high-density sites occurred, but most fish were at lower densities in lightly fished areas (Hilborn and

Fig. 7. Change in estimated catch per unit effort (CPUE) versus change from a population at 50% of unfished abundance (gray diamonds; values are $0.5 \pm$ relative abundance levels) given for density-based sampling (circles) and random sampling (triangles). Bars indicate the 5th and 95th percentiles of 1000 resampled differences from relative abundance of 0.5. Filled symbols are those that detected changes in CPUE more than 95% of the time. Rows show initial pattern of distribution of fish, and columns show the number of sites that were surveyed. No change in CPUE (black dashed lines) and the true change in the population (gray dashed lines) are shown. Median values are the median differences in paired CPUE values from 1000 replicates at each population level.

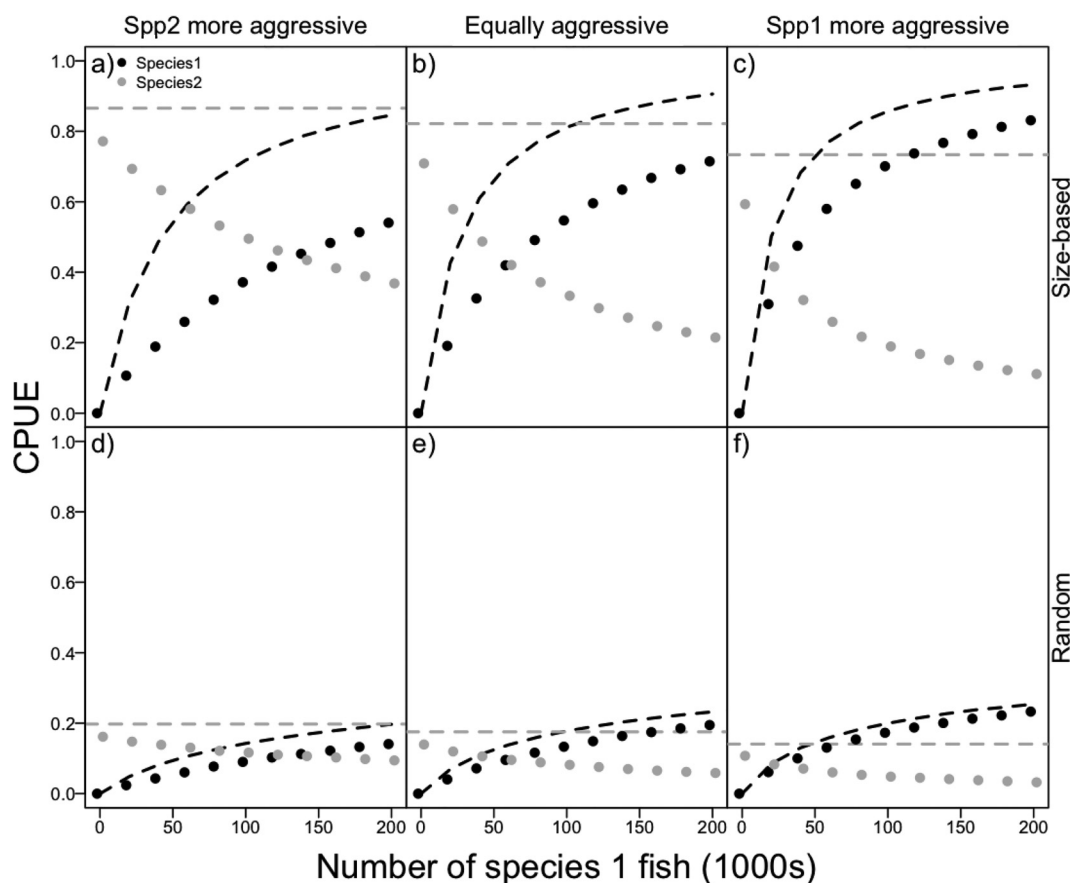


Walters 1992). Here we show that hyperstability is a common occurrence in hook-and-line surveys, and that future research might develop methods to correct the resulting bias.

Hook saturation leading to hyperstability is not the only potential bias in hook-and-line surveys, since many factors can bias fish catchability and in turn bias the relationship between CPUE and population size. Fish catchability is affected by factors at many scales, ranging from the state of an individual fish to a vessel

captain's fishing style (Lennox et al. 2017). An individual fish must make a decision to bite a hook (Løkkeborg and Bjordal 1992), which depends partly on the internal state of a fish (Lennox et al. 2017) and environmental conditions like temperature and dissolved oxygen levels (Stoner 2004). Larger pieces of bait or different types of bait attract larger or different fish (Garner et al. 2016; Ingólfsson et al. 2017), and fishing gear selects for certain sizes or traits of fish (Ricker 1969; Götz et al. 2007). These relationships may

Fig. 8. Number of species 1 versus median CPUE values for species 1 (black) and species 2 (gray). Surveys were conducted with one species (dashed lines) or two species (dots) present. The number of species 1 fish varied, and the number of species 2 fish was constant at 60 000 (gray dashed CPUE line constant as well). The difference between the dashed lines and dots indicates the difference in CPUE values between one-species and two-species surveys. The three competition scenarios (columns) are species 2 more aggressive than species 1, both species equally aggressive, and species 1 more aggressive than species 2. Rows indicate sampling type. Points at each value of species 1 fish are slightly offset to prevent overplotting.



be density-dependent and would result in patterns similar to those from the two-species simulation results. Self-reportedly skilled anglers catch more fish in a lake system (Monk and Arlinghaus 2018), and this skill likely translates to marine systems. Additionally, successive surveys could lead to avoidance behavior, and vessels might have individual fishing styles that could bias results.

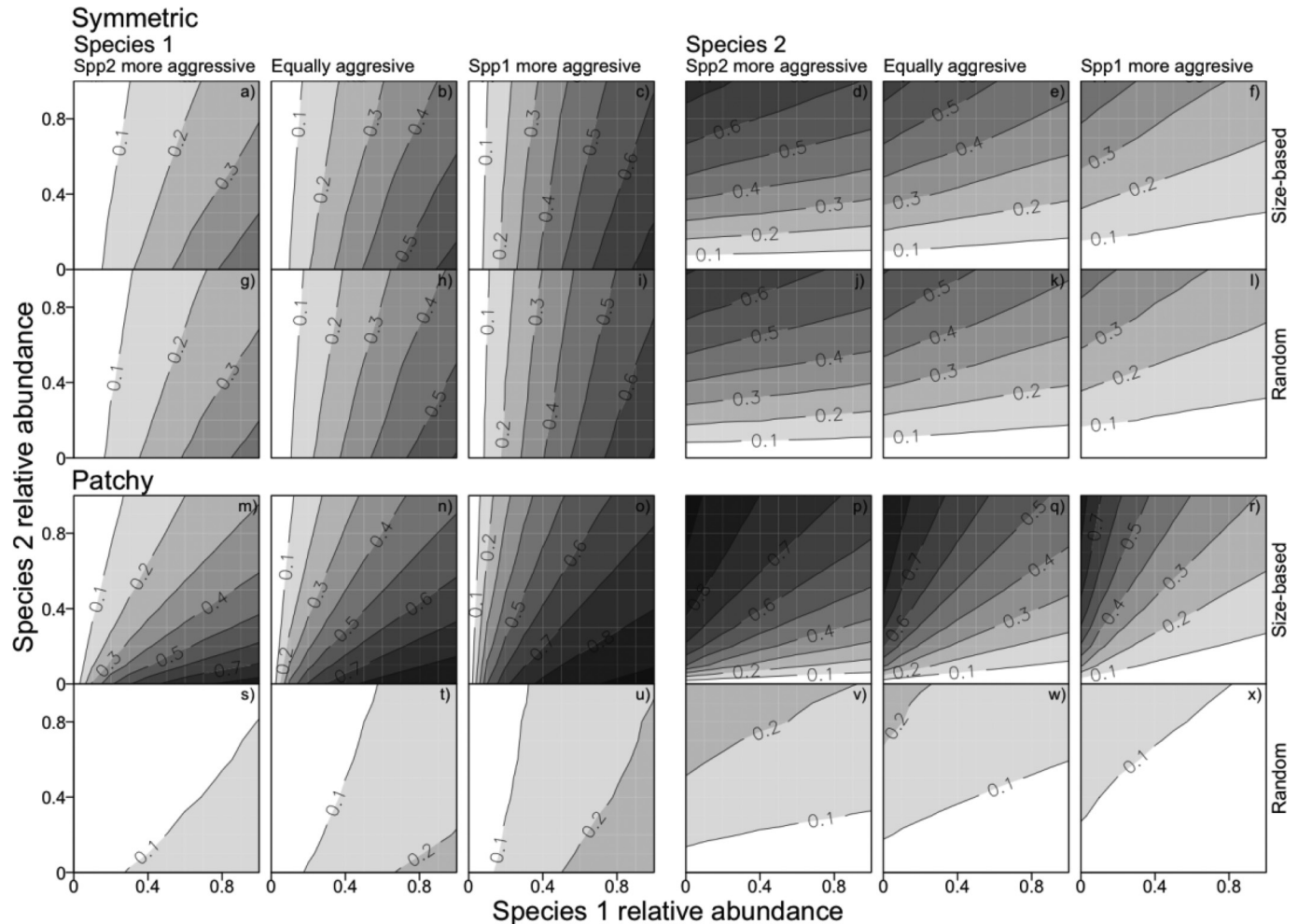
The trade-off between bias and precision is a key part of the design of fisheries-independent surveys. Obviously, increasing sample size always improves precision. In addition, as found in our simulations, randomly selected sites are less biased but result in lower precision (Kimura and Somerton 2007), while density-based sampling with surveys generally are more biased and more precise when tracking population changes (Van der Meer 1997). For the cases that we simulated, density-based sampling is better at detecting abundance changes because the increase in precision outweighs the additional bias (although this might not always be the case). Where density-based sampling is problematic to interpret, methods have been developed to account for this bias. For example, groundfish surveys in the Bering Sea (Alaska, USA) conduct density-based trawl surveys in areas with fish aggregations that are identified with acoustic methods (Hanselman et al. 2012). In that case, simulations of the sampling process were used to correct for bias and improve precision in abundance indices (Spencer et al. 2012). Wildlife surveys are another arena where density-based sampling is common, and hierarchical models that account for fixed and random effects can reduce the associated bias (Conn et al. 2017). Our simulation model could be used to

inform the development of a mixed-effects model incorporating site, vessel, and angler effects, to reduce bias in a similar manner to these other studies.

Bias in CPUE can also result from competition between species. Our simulations show that with two species, even if the true abundance of one species is constant over time, CPUE can decline as the abundance of a competitor species increases. Trends in CPUE are also affected by relative catchability between species: when one species is more aggressive than another, the CPUE of the less aggressive species will be lower when its competitor is abundant. Similar findings have been reported for other types of surveys where species competition can affect catch rates, notably for longlines (Godø et al. 1997; Rodgveller et al. 2008) and traps (Richards et al. 1983). Competition between species affects survey results but is difficult to quantify. Although relative catchability (aggressiveness) is generally hard to measure, the California hook-and-line survey data did mildly suggest that vermilion rockfish are more aggressive than bocaccio in the analyses of time-to-first-bite data. Despite the potential difference in behaviors, both vermilion rockfish and bocaccio have relatively constant CPUE values over time, suggesting that the simulations may not capture the full range of species interactions present in nature.

This simulation study is motivated by many aspects of the California hook-and-line survey, but there are many real-world factors that were not accounted for. In the actual survey, sites were selected based on historical catch knowledge in conjunction with recreational charter vessel captains, and CPUE was standardized

Fig. 9. Contour plots of median CPUE values at relative levels of abundance for species 1 (x axis) and species 2 (y axis). Darker shades indicate higher CPUE values. Symmetric and patchy initial distribution results are shown here. Left-skew and uniform initial distribution results look similar to those of the symmetric distribution. Columns 1–3 show species 1 results and columns 4–6 show species 2 results. The first and third rows show density-based site selection, and the second and fourth rows show random site selection.



using a generalized linear model that incorporates explanatory variables like soak time, angler, vessel, and site (Harms et al. 2010). Our simulations highlight the bias caused by gear saturation, density-based sampling design, and two competing species. The real-world survey is conducted in areas with more than two species present and may be affected by many ecological processes. Additionally, captains use sonar to position survey vessels near fish aggregations, which may be a source of bias in hook-and-line surveys. The California hook-and-line survey has some sites with consistently low catches, suggesting that the simulated surveys with density-based sampling might exaggerate the degree to which surveys target sites with abundant fish.

The California hook-and-line survey CPUE index is currently used to inform management. The survey provides one of seven indices of abundance that have been used in recent assessments for bocaccio (He et al. 2015), and the unstandardized CPUE indices we presented here for bocaccio have similar trends and comparable changes to the standardized CPUE indices used in recent stock assessments (He et al. 2015). Additionally, the real-world survey provides biological data such as age, sex and maturity information for many different species, including genetic data, otoliths for ageing, and lengths and mass to track cohorts and measure length-mass and age-length relationships.

Future studies may incorporate more complexity and account for ecological processes such as recruitment, environmental

change, and fish movement. Additionally, possible sources of bias may have a different temporal effect, which were not addressed in these simulations that conducted surveys at different population levels. More broadly, the simulations may be expanded as part of a broader management strategy evaluation that more mechanistically accounts for responses to climate change, which were beyond the scope of this study.

Additional research might investigate the benefits of coupling with additional survey methods or develop methods of incorporating space and time into CPUE calculations. Concerns regarding gear saturation and interspecific behaviors might be addressed by combining hook-and-line surveys with video surveys. For example, video surveys conducted at a subset of the California hook-and-line survey sites provide information on site-specific species compositions and abundances that may explain trends in CPUE. Hook-and-line surveys sample a wide range of sizes (Millar and Fryer 1999; Starr et al. 2016), although for certain species video surveys might observe both the smaller and larger fish than those captured using hook-and-line methods (Starr et al. 2016). Indeed, hook-and-line gear selectivity has been estimated to be dome-shaped (Garner et al. 2014), although this varies by species and hook size. Additionally, future studies might continue development of standardization methods (e.g., Harms et al. 2010) to better incorporate the fine-scale information collected from hook-and-line surveys into integrated stock assessment analyses. One direc-

Fig. 10. Histograms of site-specific catch per unit effort (CPUE; number of fish/75 hooks) in each year.

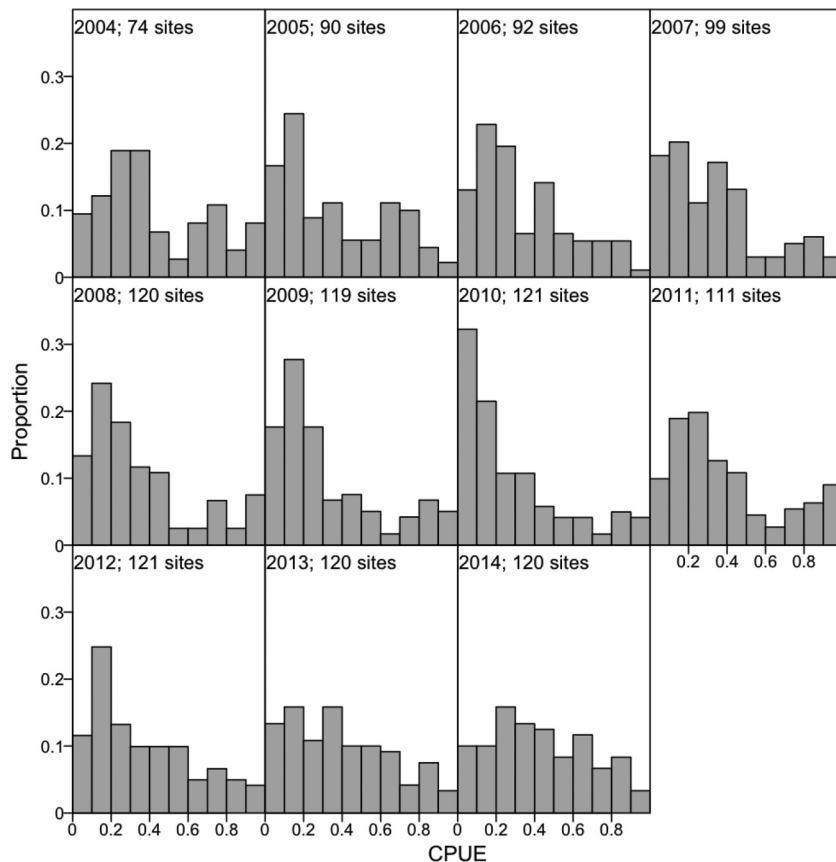


Fig. 11. Unstandardized CPUE (average of site-specific CPUE in each year) for bocaccio and vermillion rockfish from 2004 to 2014.

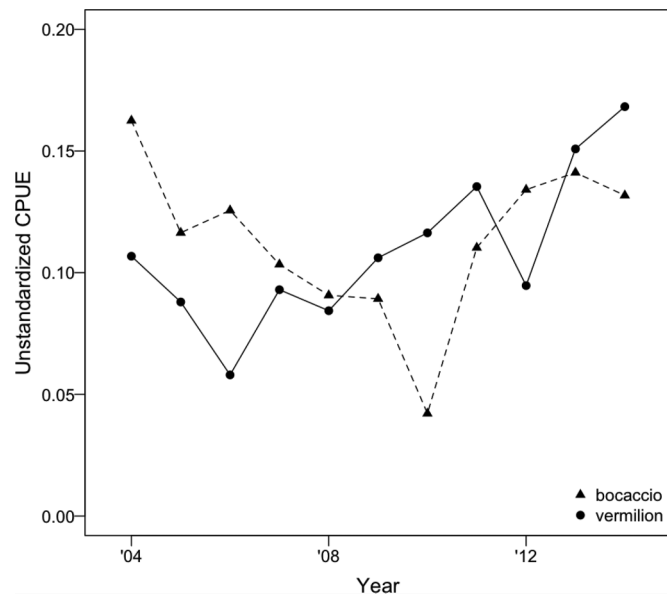
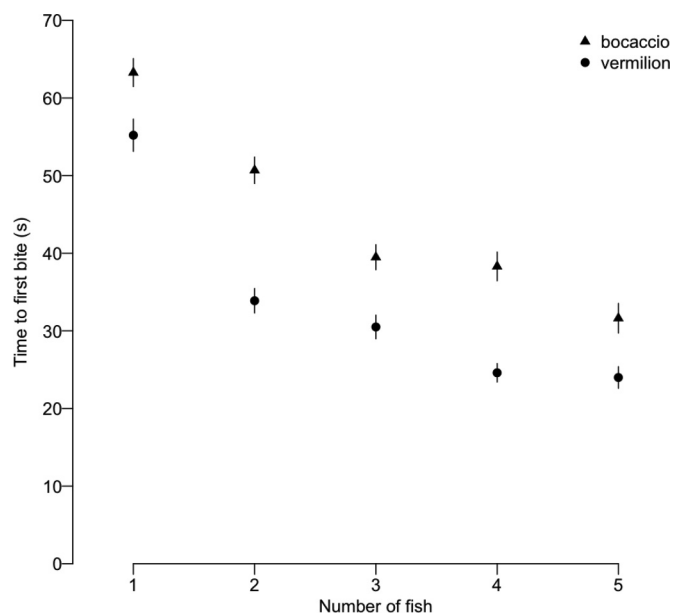


Fig. 12. Mean (point) and standard error (bars) values of time to first bite (seconds). The values here come from gangions (lines with five hooks) with only bocaccio or only vermillion rockfish.



tion would be estimation of spatiotemporal indices of abundance from hook-and-line survey data. Assessment of shrimp in the Gulf of Maine was improved by accounting for temporal variability, which was biased with the design-based estimator (Cao et al. 2017).

Our results investigate several of the potential biases in hook-and-line surveys, which are useful for tracking life histories and species in habitats that cannot otherwise be surveyed. Ideally, fish

surveys will have stratified random designs that allow meet many statistical assumptions. However in practice such designs may not be logistically possible or desirable, as for species with strong habitat preferences as in the California hook-and-line survey, thus the results are applicable to any region that relies on fishery-

dependent hook-and-line surveys. More generally, these results are applicable to any survey that has some degree of density-based sampling and is prone to gear saturation. Both of these factors result in hyperstability although seem to be able to detect population changes, particularly at low relative population levels. Hook-and-line surveys offer considerable promise, since they are able to detect changes in abundance at low population levels, despite important biases such as hyperstability from hook saturation and multispecies competition.

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