DEVELOPMENT OF GENERALIZED INDEX-REMOVAL MODELS,

WITH PARTICULAR ATTENTION TO

CATCHABILITY ISSUES

A Dissertation

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APPROVAL SHEET

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DEDICATION

This dissertation is dedicated to my family: to my wife, Amy, and to my son, Ian. They survived graduate school with me. I survived graduate school because of them.

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ABSTRACT

The index-removal method estimates abundance, exploitation and catchability coefficient, given surveys conducted before and after a known removal. The method assumes a closed population between surveys. Index-removal has seldom been applied due to its strong assumption of constant survey catchabilities. This work generalizes the method to allow multiple years of data to be incorporated, and the assumptions of the original model to be relaxed.

If catchability is constant across years, precision can be improved by analyzing multi-year data simultaneously. Two multiple-year models were developed: the first, 1qIR, assumes constant catchability within and among years; the second, 2qIR, allows catchability to change between surveys within years, but assumes survey-specific catchability constant across years. The new models were tested by Monte Carlo simulation then applied to data from two southern rock lobster (*Jasus edwardsii*) populations. Infeasible exploitation estimates (>1.0) occurred with the original and 1qIR models, but all 2qIR model estimates appeared reasonable. The 2qIR model predicted lower exploitation rates than did the other models, but estimates from the original model demonstrated a different pattern and did not appear to be related to those of either multiple-year model. In one application, a likelihood ratio test found that 1qIR was the most parsimonious model; but diagnostic plots suggested 2qIR provided better estimates than the 1qIR model.

Size- and sex-specific heterogeneity of catchability introduces bias in model estimates. Field experiments were performed to test whether the catchability of small lobster was constant for southern rock lobster during two seasons when fishing occurs. No evidence of heterogeneous catchability was observed during the spring. However, significantly more small lobster were caught in control traps and traps seeded with one large adult male lobster than were caught in traps seeded with one large adult female during the summer, when females are preparing to molt and reproduce in Tasmania. Because heterogeneous catchability occurred during the summer, but not the spring, an index of recruitment based on the catch of lobsters one molt size below legal size might be developed for the spring, however, more sampling is needed to resolve the annual timing of sex- and size-specific catchability changes.

DEVELOPMENT OF GENERALIZED INDEX-REMOVAL MODELS, WITH PARTICULAR ATTENTION TO CATCHABILITY ISSUES

General Introduction

Accommodating for Catchability in Survey Indices

GENERAL INTRODUCTION

Crustacean populations form some of the most valuable fisheries in the world, but they are also some of the most difficult to assess. Assessment is made difficult because crustaceans do not retain hard body parts that accumulate measurable growth increments like most vertebrates do; and so far, a practical method for aging crabs or lobsters has not been developed. Size-structured analyses of many important crustacean fisheries are difficult as well, because these animals often exhibit indeterminate growth, and cohort identification is usually only practical at early ages (Hancock 1980). Consequently, the main focus of this dissertation is to solve problems of abundance and exploitation rate estimation for crustacean fisheries.

Central to abundance estimation problems, is an understanding of catchability. The catchability coefficient, q, is the fraction of the population caught with one unit of randomly placed fishing effort, f:

$$C = qfN \tag{1}$$

where C is the catch, and N is the abundance of the population, provided the fraction caught is small (Chen et al. 1998). The expression for the catchability coefficient followed here was provided by Chen et al.(1998):

$$q = \frac{\rho\phi a}{\phi A} \tag{2}$$

where: ρ is the proportion of animals that encounter the gear that are retained by the gear (gear efficiency), ϕ is the average density of animals (per unit area), a is the area fished by the gear (with one unit of effort), and A is the area inhabited by the population. The catchability coefficient is population specific because it is based on the area inhabited by the population. It is gear specific because it includes efficiency of the gear and the area fished by the gear. Paloheimo and Dickie (1964) described the historical development of the catchability coefficient, and Arreguin-Sanchez (1996) summarized many of the variations in its interpretation over its history.

Heterogeneity in the catchability coefficient among samples presents a problem for abundance estimation that can be hard to overcome. The catchability coefficient is sometimes treated as a nuisance parameter, it is sometimes assumed constant (as discussed in Chapter 2), or at other times estimated together with additional parameters, as in the catch-survey analysis model (Mesnil 2003). However, changes in the catchability coefficient have long been recognized as a potential problem for abundance estimation when using commercial catch per unit effort (CPUE) data (DeLury 1947; Gulland 1964; Paloheimo and Dickie 1964). Though there is less potential for catchability change among carefully-designed survey indices than in commercial CPUE, heterogeneity in survey catchability can still occur (Hilborn and Walters 1992; Ziegler et al. 2002). Catchability change in surveys is often due to a behavioral change of the fished species. The behavioral change may be caused by biological cycles of the animal, behavioral interactions with other animals, environmental (often temperature) change, or, a combination of these. Well-designed surveys will attempt to avoid these potential problems, but some degree of catchability change between surveys may be unavoidable.

This dissertation examines three different fishery situations where knowledge about catchability is critical for making accurate and precise estimates of abundance and exploitation rate. First, an experiment is described which tests for seasonal size- and sex-specific catchability change for small lobster (*Jasus edwardsii*) entering traps occupied by larger animals. Second, a new abundance estimator (1qIR) is described, which can be used if the assumption of constant catchability can be made. The 1qIR model is applied to data from a rock lobster fishery where catchability appears to be relatively constant. Third, another new IR model is introduced (2qIR), which accommodates data collected from fisheries that experience a catchability change over the fishing season. The 2qIR model is then applied to another rock lobster fishery where catchability is thought to change during the fishing season (Ziegler et al. 2003).

Testing for trap inhibition

Managers of the rock lobster fishery in Tasmania, Australia, have had difficulty in developing an index of recruitment based on the catch of animals (pre-recruits) that will recruit to the fishery within the next year (Frusher et al. 2003). The fishery managers found that the catch of pre-recruit lobsters was not related to the abundance of new recruits the following year (Frusher et al. 2003). Recent work has suggested, that small rock lobsters may be inhibited from entering traps that already contain large lobsters (Frusher and Hoenig 2001), so the experiment described herein was designed to determine if such inhibition occurs.

Abundance estimation by the index-removal method

The index-removal (IR) model is a simple abundance estimation model, which bases the parameter estimate on the change observed in the catch rate of a survey index after a relatively large removal takes place. The removal is usually a harvest of the population. The method was first introduced by Petrides (1949) to assess the population size of pheasants. Other wildlife studies have applied the index-removal model to feral horse (Eberhardt 1982) and white-tailed deer (Roseberry and Woolfe 1991) populations. In fisheries, it has been applied to estimate abundance and exploitation rate for snow crab (*Chionoecetes opilio*) (Dawe et al. 1993; Chen et al. 1998), exploitation rate for southern rock lobster (*Jasus edwardsii*) (Frusher et al. 1998; Frusher 2001), and most recently, dredge efficiency for sea scallops (*Placopecten magellanicus*) (Gedamke et al. 2005). Use of the IR model has also been suggested for American shad spawning runs (Olney and Hoenig 2001).

Though known for some time, the basic IR model (which makes estimates annually, hence, hereafter called the "annual model") has received only moderate development (see Hoenig and Pollock (1998) for a detailed review). Routledge (1989) generalized the method to include *i* removals and *i+1* surveys. Chen et al. (1998) pointed out that heterogeneity of capture probabilities among subclasses in the population can be accommodated for by making separate parameter estimates by subclass, provided that removals are known by subclass; and that precision of estimates could be improved by reoccupying the same sampling locations in the second survey.

In Chapter 2, the annual model is generalized to incorporate multiple-years of data. The goal of the multiple-year model (1qIR) is to improve the efficiency of the IR model, and thereby improve the precision of the 1qIR model estimates compared to those of the annual model. The 1qIR model is developed and applied, and its performance is tested by Monte Carlo simulation.

Chapter 3 explores the 2qIR model, a further generalization of the IR method, which allows the assumption of constant catchability to be relaxed. In many fisheries, the assumption of constant catchability over a fishing season is known to be violated (Paloheimo 1963; Morgan 1974; Ziegler et al. 2002). The 2qIR model should be useful in many of these fisheries. The 2qIR model is developed and applied in Chapter 3, and the performance of this new model is tested by simulation.

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Chapter 1

Do Large Rock Lobsters Inhibit Smaller Ones From Entering Traps?
A Field Experiment

ABSTRACT

Indices of recruitment are often derived from trap surveys. If legal-sized lobsters inhibit smaller ones from entering traps, the overall catch rate may depend on population composition and not just overall abundance, and recruitment strength can be overestimated as average length decreases in a population. A controlled field experiment was used to examine whether trapping inhibition of Jasus edwardsii occurred during spring (November) or summer (February) in southeastern Tasmania. Four treatments were applied. Baited traps were seeded with either: one large female lobster, one large male or two sublegal-sized females. Baited traps with no seed were used as a control. Seeded traps always caught fewer sublegal-sized lobsters than control traps. When catches in both seasons were examined by sex of entrants, seeded traps caught fewer small lobsters than control traps in 11 of 12 comparisons. However, a strong inhibitory effect was observed only for female-seeded traps during summer. Our data suggest sublegal-sized indices of recruitment are likely to be influenced in summer by the number of large females present. Spring trials suggest corrections to a sublegal-catch index may be unnecessary then, but more work is needed to better understand the complex, sex-specific and seasonal patterns of interactions in this species.

Keywords: southern rock lobster, trapability, selectivity, trapping behaviour, catchability.

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INTRODUCTION

Frusher and Hoenig (2001) reported strong negative correlations between catches of large and small southern rock lobster (*Jasus edwardsii*), and found that trap selectivity curves differed substantially among areas of Tasmania with differences in the relative abundance of large animals. The catchability of small lobsters (both rock and clawed) appears to increase throughout the fishing season as the larger, more trappable animals are depleted (Smith 1944; Frusher and Hoenig 2001; Tremblay and Smith 2001). If small lobsters are deterred from entering traps by the presence of larger animals, and surveys are conducted when large lobsters are present, 1) size compositions will be biased toward larger animals, and 2) underestimates of the abundance of smaller animals would underestimate the total population size; also, if large animals are depleted over time, 3) the resulting increase in catchability of small lobsters in surveys could deceptively appear as an increase in recruitment; alternatively, if recruitment appears constant over time 4) the perceived relative abundance of new recruits could mask a recruitment decline. Frusher *et al.* (2003) examined the implications of failing to account for temporally changing gear selectivity in the assessment of rock lobster, and found that the biases in parameter estimates could be substantial.

Other studies of the same reserve population studied here suggest that the presence of large rock lobsters influences the catchability of smaller lobsters. Frusher and Hoenig (2001) presented evidence that trap selectivity changed with the size composition of a stock for *Jasus edwardsii*. Ziegler *et al.* (2002) compared animals caught in traps with size distributions estimated by diver surveys. They concluded that the catchability of *J. edwardsii* was size specific and varied by sex and season, and that strong behavioral interactions were likely between large and small lobsters. In an *in situ* video observational study, Green (2002) reported that one of the primary reasons that smaller lobsters failed to enter traps was that larger lobsters inhibited entry.

Numerous studies have concluded that small decapods may be underrepresented in trap catches, and large animals may deter smaller ones from entering traps (see Miller 1990 for review). However, trapping inhibition of small lobsters by large conspecifics has not yet been demonstrated experimentally in the field for rock lobster.

The experiments described here investigate whether small (sublegal) *Jasus edwardsii* are deterred from entering traps that already contain a large lobster, as the results of Frusher and Hoenig (2001) suggest, and whether the hypothesized inhibition varies with season and sex.

MATERIALS AND METHODS

Field experiments were conducted at Crayfish Point Reserve, a small (1.0 km^2) scientific reserve adjacent to the Tasmania Aquaculture and Fisheries Institute (TAFI) (42^o57.2’ S 147^o21.2’ E) near Hobart, Tasmania, Australia. Catch rates were compared among traps that differed in the type of lobster placed in the traps (i.e., the “seed”) prior to setting the traps. Baited traps were seeded with either: one large female lobster (120 - 150 mm carapace length [CL]), one large male (160 - 180 mm CL), or two sexually-mature, sublegal-sized females (90 - 104 mm CL) that were approximately equal in weight to a large female. Baited traps with no seed were used as a control. Different size ranges were defined for large female and large male seeds because sexual dimorphism is pronounced in the study region and females rarely reach the sizes attained by males (Ziegler *et al.* 2002). Throughout the experiment, “small” or “sublegal” lobsters were defined to be those animals 1 - 15 mm below the legal size limit, where minimum legal sizes in the Tasmanian fishery are 105 and 110 mm CL for females and males, respectively. We chose this size range for “small” animals because it includes the size range proposed as an index of future recruitment strength (Frusher 1997), and because animals in this size range are typically sexually mature (MacDiarmid 1989). All experimental animals used as seeds were sexually mature and collected with baited traps. Traps used for this study were the same traps used to collect the data reported by Frusher and Hoenig (2001), and are similar in size (0.6 m x 0.6m x 0.5m – length-width-height;

40mm mesh size) and design to those used by the fishery, but without escape gaps which are designed to release undersized lobster (as described in Frusher *et al.* 1998). On the morning of each trial, 50 traps were set in the reserve areas accessible to trapping and locations were recorded using a Garmin eTrex Legend® differential GPS. An effort was made to use the same locations on each day. Treatments were randomly assigned to new locations for every set. All traps were placed a minimum of 10 m from adjacent traps. Previous work suggests that the limit of influence of a baited lobster trap may be as little as 9 m (Smith and Tremblay 2003), and as much as 120 m (Jernakoff and Phillips 1988). The 10 m minimum distance between traps was chosen to minimize the overlap of area fished between traps while allowing for an adequate sample size. All traps were baited with a standard amount of fish consisting of one barracouta (*Thyrsites atun*) head and one-half mackerel (*Trachurus declivis*), which totaled approximately 1kg. Bait for traps was the standard for TAFI's seasonal scientific surveys. The bait for each trap was placed in a "bait saver," a pocket made of heavy plastic mesh, to prevent easy access to the bait and to prevent immediate consumption of the bait. Traps were set for approximately 22 hours.

Field trials were always performed on 3 consecutive nights. Trials were performed twice in spring during nearly opposite moon phases: November 11 - 13, and November 25 - 27, 2003 (fraction of the moon illuminated ranged between 0.96 - 0.85, and 0.02 - 0.15 respectively; US Naval Observatory, personal communication). Trials were then repeated in summer, February 25 - 27, 2004, to examine potential seasonal changes in catch rates. Frusher and Hoenig (2001) found the strongest negative correlations in survey catches between large females and small females, so catch rates were also examined by sex of the entrants.

Data selection

Traps pulled with zero catches, traps containing dead or injured lobsters, and treatment traps whose seeds escaped were excluded from comparisons among treatments. When a trap was set in poor lobster habitat, or when a trap was improperly set (e.g., if the trap door was open when retrieved), the catch of that trap was typically zero. Also, on occasion, an octopus (*Octopus maorum*) was caught that had injured or killed a trapped lobster, or lobster remains were found in the trap implying consumption by a predator. Moreover, when a seeded lobster escaped a treatment, that trap ceased to be a treatment. Consequently, we excluded these problematic traps from statistical tests and catch rate calculations. To check whether this data-selection procedure was critical, data were also analyzed without the non-zero selection criterion.

Tests of hypotheses

The primary null hypothesis was no difference among treatment and control traps in the mean number of small lobsters that are caught. Significance was tested with a two-way (Model 1) ANOVA (as described by Zar 1996) with interaction. The model was

$$x_{ijk} = \mu + \tau_i + \delta_j + \gamma_{ij} + \varepsilon_{ijk} \quad (1)$$

where: x_{ijk} = a catch observation, i.e. catch in the *k*th replicate of the *ij*th combination of main factors

μ = overall mean number of small lobsters caught

τ_i = ith treatment (or lobster seed) effect

δ_j = jth season effect

γ_{ij} = interaction effect

ε_{ijk} = random error

Subscripts for treatments (*i*) in the model were: 1 = large female seed, 2 = large male seed, 3 = biomass control (2 small female seeds), and 4 = no-seed control. Subscripts for season (*j*) were: 1 = spring, or 2 = summer. If seasonal effects were not significant, the experimental model reduced to a one-way ANOVA:

$$x_{ik} = \mu + \tau_i + \varepsilon_{ik} \tag{2}$$

with symbols as before. If interaction effects were significant, two-way ANOVA for treatment effects was inappropriate (Underwood 1997), and seasons were analyzed separately by one-way ANOVA as described in equation 2. Difference in catch rates between moon phases was also tested for by one-way ANOVA with all catch data pooled for each moon phase.

Count data were transformed prior to ANOVA because variances were heterogeneous among treatments, and treatment variances were proportional to treatment means (Zar 1996). The transformation used was a modified square root transformation, as described in Freeman and Tukey (1950):

$$x' = \sqrt{x} + \sqrt{x+1} \tag{3}$$

where x' = transformed count, and x = observed count. Freeman and Tukey (1950) found that this transformation stabilized variances for Poisson data when the expectation of x was < 2. If transformed counts were found to be significantly different in any ANOVA comparison, Tukey's multiple comparison test was used to determine which treatment means differed significantly. All ANOVA comparisons of transformed counts of small entrants were made overall (sexes combined) and separately by sex.

Differences between treatments in a field experiment were expected to be minimized by the entry of large animals into the control traps. Once a large animal enters a control, the trap is effectively no different from a female- or male-treatment trap. This unavoidable situation in the field weakens the signal of treatment effect in an ANOVA test, so an additional test was applied in case the hypothesized treatment effect was too weak to be significant in ANOVA.

A one-tailed binomial test of significance was used to test the null hypothesis H_o: none of the treatments had an effect on the number of small entrants, against the alternative hypothesis H_a: at least some of the treatments had an effect in reducing the catch of small animals. If none of the treatments affect the number of small animals entering the trap, one should expect to see more small entrants in the control traps than in the treatment traps half of the time. Let X_h equal the difference in mean counts of small animals between control traps and the h^{th} treatment x time (season) combination. When considering the small animals caught in all three treatments and both seasons, there are six possible comparisons. When the small animals caught are divided by sex there are 12 possible comparisons. Let $Y_h = 1$ if X_h is positive (i.e., control catch > treatment catch) and let $Y_h = 0$ if X_h is negative. (Any cases where X is 0 are ignored.) The variable V =

ΣY is approximately binomially distributed. Thus, under the null hypothesis that none of the treatments has an effect, when sexes of entrants are pooled:

$$V \sim B(0.5, 6); \quad E(V) = 3 \qquad (4)$$

and when entrants are separated by sex:

$$V \sim B(0.5, 12); \quad E(V) = 6 \qquad (5)$$

(assuming no $X_h = 0$).

A binomial test is not entirely appropriate in this application because the comparisons of experimental treatments with controls are not completely independent, i.e., three treatments are compared to the same control. A randomization test (see Edgington 1995), i.e., a Monte Carlo random re-assignment of the catches to the treatments to determine the null distribution of V, is more appropriate since a binomial test could be overly sensitive (overstate the significance). However, a comparison of these tests revealed that the distribution of the binomial test statistic under the null hypothesis was similar to the null distribution of the randomization probabilities, regardless of whether 6 or 12 comparisons were made (Figs. 1.3, 1.4). A binomial test offers a useful approximation to the results of the more rigorous randomization test because it is less computationally demanding to perform. We set $\alpha = 0.05$ for all significance tests.

RESULTS

There were 444 traps set in all of the collections combined. Of these, 84% caught lobsters. The percentage of each treatment excluded from significance testing due to zero catch was: controls – 15.3%, biomass controls – 10.0%, large-female treatments – 5.6%, and large-male treatments – 13.5%. Six traps (1.1% of all traps set) were excluded due to death and predation. Of 268 seeds set in traps, about one third (34.3%) escaped and these traps were also excluded. After problematic traps were excluded, 293 traps remained for statistical analyses and catch rates calculations.

Most animals caught were identifiable by sex, and control traps caught a slightly higher sex ratio (male: female) during summer compared to spring, but even higher ratios were observed in female-seeded traps during summer. Of the 1680 animals caught in all traps (n = 375 trap-hauls), 1679 were identifiable by sex. The sex ratio (male: female) in control traps during spring was 1.1: 1 (Fig. 1.1), but a slightly higher proportion of males was observed during summer, when the sex ratio was 1.4:1. Spring sex ratios were generally similar for all treatments, but summer ratios were markedly higher for the large-female treatment and slightly higher for the biomass control (3.0:1 and 1.6:1, respectively) than the other treatments. The presence of any female seed appeared to increase the proportion of males caught during the summer, but not during spring.

Size frequency plots appear similar across treatments and sexes during spring catches, but the size range of females caught was reduced in female treatments during summer. The size range of females caught during summer in the large-female treatment was reduced by 50%, and the biomass-control was reduced by 40% compared to those caught during spring. Similar restrictions in the sizes of females caught were not observed for the large-male treatment and the control, though the extremely large and small animals of both sexes caught in these treatments during spring trials were not observed again in summer. Though the large-female treatment and the biomass control also caught fewer males > 160 mm CL in summer, the size distribution of males captured was generally similar across treatments during both seasons. Consequently, female seeds appear to have restricted the entry of other females during the summer, but not males.

Significantly fewer small animals were captured in large-female treatments during summer trials than during spring. The transformed total number of lobsters caught had a significant interaction between seasons and treatments (P = 0.0106), so ANOVA was performed separately by season. Spring catches of small lobsters did not differ significantly among treatments (Table 1.1). However, summer catches did differ significantly between the large-female treatment and control. When small-lobster catches were examined separately by sex, it was found that differences in summer were entirely due to the reduced catch of small females in the large-female treatment compared to the control. Small-male catches did not differ significantly among treatments in either season.

When ANOVAs were done without excluding zero catches (n = 347 trap-hauls), mean transformed catches of small lobsters did not differ significantly among treatments for either season regardless of whether data were separated by sex or pooled. All F-values from ANOVA comparisons of summer catches were smaller when zero catches were included (Table 1.2).

No significant differences were found in the catches of small lobsters, or in the catches of small lobsters by sex, during different moon phases in the spring (Table 1.3).

Direct comparisons of mean catch rates of controls to each treatment, plotted by sex of the entrants (Fig. 1.2) revealed that the strongest seasonal effect of treatment on catch rates occurred in the large-female treatment. While spring mean catch rates of small animals in treatment traps (combined and separated by sex; Table 1.4 and Fig. 1.2) were only slightly lower than those of the control, summer catch rates of small animals was reduced by 71% in large-female treatments and by 44% in biomass-control traps (the other female treatment). The summer mean catch rate of small animals in the large-male treatment was only slightly reduced (6%) when compared to the control. When summer catch rates of small animals were examined separately by sex, both small female and small male entrants were greatly reduced in large-female treatments relative to those in control traps (small female and small male reductions were 87% and 52%, respectively). Correspondingly, catch rates of small animals in the biomass-control traps also decreased in the summer relative to control traps (small female and small male reductions were 37% and 52%, respectively). When catch rate trends in control traps were examined separately by sex, the catch rate of small males increased from 0.50/trap in spring to 0.73/trap in summer, but the catch of small females was relatively constant over the two seasons (spring: 0.82/trap; summer: 0.88/trap).

Catch rates of small animals in the control traps were always greater than those of the other treatments when sexes were combined (Table 1.4), regardless of season (P = 0.0156, P = 0.0368, binomial and randomization tests, respectively; Fig. 1.3). Therefore, the null hypothesis that treatments have no effect on the catch of small animals was rejected. When counts of small animals were separated by sex (Fig. 1.2), the catch in the control traps was still greater than that of the treatments in 11 out of 12 cases (P = 0.0032, P = 0.0103, binomial and randomization tests, respectively; Fig. 1.4). The one instance when the mean of a treatment catch exceeded that of the control was during summer, when the large-male treatment caught more small females. The mean summer catch rate of small females in the large-male treatment also had the largest standard error of the 12 estimates.

When zero catches were included for the binomial and randomization tests, significance was similar to that found when zero catches were excluded. The ranking of treatment mean catch rates remained consistent, but values were reduced, and the control catch rate was then greater than the treatment catch rates in 12 of 12 comparisons of the number of small females and small males captured (P = 0.0002, P = 0.0013, binomial and randomization tests, respectively).

DISCUSSION

We demonstrate a strong inhibition effect of large female lobsters on small lobsters entering traps in summer. Seeding a trap at that time with one large female lobster, or two small female lobsters, reduced the subsequent catch of small lobsters by 71% and 44%, respectively. Though consistent with Frusher and Hoenig (2001), our results suggest that a strong inhibitory effect of a large lobster may be limited to females in summer. Large male seeds in summer, and all seeds in spring, have only a slight negative effect on the subsequent catch of small lobsters.

Other studies have documented that any seed reduces the catch of *Homarus* spp. (Richards *et al.* 1983; Addison 1995; Miller and Addison 1995; Addison and Bannister 1998), and that behavioural interactions both inside and outside the trap can limit the catch of *Homarus* spp. (Karnofsky and Price 1989; Jury *et al.* 2001). However, only one other study has provided evidence of inhibition of *Jasus* spp. from entering traps. Green (2002) noted in video observations that behavioural interactions limit trap entry of "small" *J. edwardsii*. Unfortunately, her observations took place during a five-month period that spanned peak mating and she could not identify animals by sex. Sample size was small so Green drew no quantitative conclusions, but the aggressive behavioural interactions she observed suggest a possible mechanism for the trapping inhibition of small lobsters reported here.

Sex differences

Female seeds reduced the catch of small females and small males during summer, but male seeds may have increased the catch of small females. When catches of small animals were examined by sex, it was clear that seeding a trap with one large female or two small females reduced the subsequent catch of both small females and small males during summer. The strongest inhibitory effect was observed between large female seeds and small female lobsters. The mean summer catch rate of small females was reduced by 87% in the presence of a large female seed. This confirms the observations of Frusher and Hoenig (2001), who saw the strongest negative correlations between the catches of these two subgroups. However, traps seeded with one large male caught more small females than did controls in summer (Fig. 1.2). This difference was slight, and could have been due to small sample size. But, if sexually mature females compete for preferred males, as suggested by MacDiarmid and Butler (1999), males (including the largest that we could catch) might be expected to attract small, but sexually mature females in late February, about 1 ½ months before mating begins (Ziegler *et al.* 2004). Thus, while large females inhibited small lobsters of both sexes from entering traps prior to the onset of the mating season, large males appeared to have the opposite effect on small females during this time.

A male seed inhibitory effect on the catch of small lobsters (males and females combined) may not be strong enough to be detected by our study design at this point in the summer, and further sampling will be necessary to confirm that large males inhibit the entry of small lobster into traps. Frusher and Hoenig (2001) reported that the catch of large males had a strong negative correlation with the catch of small animals, in the same Tasmanian reserve studied here. However, they sampled over much of the year and did not account for seasonality in their study, and this may explain the difference between the studies. MacDiarmid (1989) reported that agonistic behaviour between large male *J. edwardsii* and any other male, in a northeast New Zealand reserve, was highly seasonal and began as early as five months prior to the peak mating period. The aggressive behaviours of males became more common as the mating season approached and were most frequent during the peak mating period. Thus, a male-inhibitory effect on the catch of small lobsters may still be weak in late February in Tasmania, when peak mating occurs at the beginning of May (Ziegler *et al.* 2004). The attractant effect large males may have had on small females would have further weakened any detectable signal of male inhibition. Hence, large-male inhibition of small animals may not have been strong enough to be detected by our study design at the time of our experiment. Lack of a strong large-male inhibitory effect in our data, and the strong negative correlations between large-male lobsters and small animals reported by Frusher and Hoenig (2001) suggest that sampling during more months will be necessary to confirm that large-male southern rock lobsters negatively impact the catch of small animals.

Fishery management implications

Various workers have reported strong inhibitory effects of trap occupants on prospective entrants for a variety of species (Heydorn 1969; Richards *et al.* 1983; Addison 1995). Reports that small animals are underrepresented in traps are common

(Pollock and Beyers 1979; Miller 1989; Tremblay and Smith 2001; Ziegler *et al.* 2002). Winstanley (1977) documented anecdotal reports from fishermen that large *J. edwardsii* prevented the entry of smaller lobster into traps, and Green (2002) documented that larger lobster prevented smaller ones from entering traps.

It was somewhat surprising, therefore, that the strong interactions observed here were limited to females in the summer. However, previous work on *J. edwardsii* has established that aggressive behaviours related to mating are highly seasonal (MacDiarmid 1989). The video documentation of lobster interactions reported by Green (2002) also took place during a period which included the peak mating season. The strong trapping inhibition reported here similarly appears to be related to the mating season. More work is needed to determine whether trapping inhibition occurs at times other than the mating season. However, it seems clear that catch rates of sublegal-sized lobsters observed just before and after the mating season should not be used as an index of recruitment because the index is affected by the abundance of large animals.

Large females inhibit small animals from entering traps in late February in Tasmania, and work by MacDiarmid (1989) and MacDiarmid *et al.* (1991) suggests that large males are also likely to inhibit small animals from April to June in Tasmania during mating. Thus, the consequences of an increasing catch efficiency for small animals as large animals are depleted, as discussed by Frusher *et al.* (2003), must be considered carefully before the catch of sublegal-size animals is used as an index of recruitment to the fishery here. Recruitment indices based on sublegal catches have been useful in predicting the catch of *Panulirus* spp. (Caputi and Brown 1986; Caputi *et al.* 1995; Cruz *et al.* 2001), but application of sublegal catch data for predicting catch of *Jasus* spp. is limited. In recent work, Bentley *et al.* (2005) concluded that sublegal indices based on commercial catch of *J. edwardsii* showed promise in predicting catch per unit of effort (CPUE) the following year. But they found useful results in only half of the areas where indices were available in New Zealand, and their CPUE predictions based on sublegal indices were often underestimated. If small lobsters are inhibited from entering traps by large lobsters during any portion of the year, as our results suggest for *J. edwardsii* in Tasmania, the seasonally-integrated sublegal index described by Bentley *et al.* (2005) may be unreliable because trapping inhibition of sublegal lobsters is not accounted for.

Data selection

The zero catches that were excluded from the analysis did not affect the overall patterns observed in the data, but allowed for greater resolution of biologically important patterns. Even though differences among catch rates were fairly clear for female treatments in the summer (Fig. 1.2), the inclusion of zero catches weakened this signal so that no significant differences in the catch of small animals were found among treatments with ANOVA. Additionally, with the zero catches included, the mean number of small lobster caught was always greater in control traps than in other treatments. This result suggests greater significance in the binomial and randomization tests, and thus, a stronger non-random effect of the treatment seeds. However, the one instance where a treatment caught more small animals than the control (summer: male treatment) was obscured by the inclusion of the zero catches. Documenting an attractant effect of a male seed on the catch of small animals is as important as documenting an inhibitory effect of a female seed. Thus, the exclusion of the zero catches was critical to discern significant differences in ANOVA and to fully appreciate the subtle effects that different treatment seeds may have had in different seasons.

Other considerations

Predation and injury were not important factors affecting the catch of small lobster in our study, as only 1 % of traps were excluded due to these factors.

Moon phase did not have a statistically significant effect on spring catches. Previous work has documented that the catch of multiple *Panulirus* spp. varies with moon phase (reviewed by Srisurichan *et al.* 2005). A similar relationship between catch and moon phase has not yet been demonstrated for *Jasus* spp., though only one other study has considered the potential effect. MacDiarmid *et al.* (1991) reported that moon phase was not correlated with *J. edwardsii* movement in visual tracking of tagged lobsters via SCUBA, though that work was not concerned with the catchability of the animals. Considering the well-documented effect that moon phase has on other palinurids, this effect should be tested further before being considered unimportant for the catchability of *J. edwardsii*. It is unfortunate that only one round of field trials was possible during summer sampling in this study, as this precluded testing for lunar effect during that season.

Our sex-specific treatment design allowed better understanding of observed sex ratios in this study, and those of previous work. The sex ratios reported here are similar to those reported by Ziegler *et al.* (2004) for trap catches in the same reserve during the same months four years earlier. Ziegler *et al.* (2004) reported that male catchability increases strongly during the month of February, and it was interesting that our independent February sampling confirmed this high ratio of males, but only in large-female treatments. Thus, our data suggest that the male-dominated sex ratio observed in both studies was due to large females inhibiting the entry of other females at this time of year. Females may improve their chances of mating with a preferred male and maximizing their clutch size (MacDiarmid and Butler 1999) by excluding other females prior to the onset of the moulting and mating period.

Conclusion

The behavioural effects on the indices of abundance of sublegal animals are complex for *J. edwardsii* and need to be better resolved before sublegal indices can be corrected for in all seasons; however, it may be better to just sample in the spring when behavioural interactions related to mating do not occur. This work establishes that catch rates of small lobsters in traps in summer are influenced by population composition through behavioural interactions involving attraction into traps or inhibition from entering traps, depending on the sex and size of the lobsters already in a trap and the sex and size of the potential trap entrant. Experimental replication is needed over multiple years and at more times each year to confirm these complex seasonal patterns of social interactions, and their effect on the catchability of sublegal *J. edwardsii*. Our study has been limited to examining whether the catchability of sublegal lobsters is affected by the presence of one large lobster already in a trap. Future investigations should also examine whether the inhibitory (or attractant) effect of a trap seed on catch is greater when more lobster seeds are used per trap. The experimental approach used here will be useful to accomplish these tasks, and can lead to insights critical for the accurate interpretation of trap surveys.

APPENDIX

Catch data for all traps set. Counts are totals per trap. Abbreviations: Treatment denotes the lobster seed used: B = biomass control (two sublegal-sized females), C = control, F = large female, or M = large male; Escape denotes whether trap was problematic: N = seed did not escape, Y = seed escaped, S = seed appeared sick, D = a dead lobster was present in the trap; total counts of lobsters caught per trap by subgroup: LF = legal-sized females, SF = sublegal-sized females, LM = legal-sized males, SM = sublegal-sized males, Lg = legal-sized (large) animals, and Sm = sublegal (small) animals; Moon denotes moonphase, either F = full, or N = new.

Date	PotID	Treatment	Escape	LF	SF	LM	SM	Total	Lg	Sm	Moon
11/11/2003	1	C		0	0	0	1	1	0	1	F
11/11/2003	2	C		3	0	3	0	6	6	0	F
11/11/2003	3	C		1	0	4	1	6	5	1	F
11/11/2003	4	B	N	0	0	0	0	0	0	0	F
11/11/2003	5	M	N	1	2	2	0	5	3	2	F
11/11/2003	6	B	N	4	4	1	0	9	5	4	F
11/11/2003	7	F	N	1	0	4	4	9	5	4	F
11/11/2003	8	C		1	0	1	0	2	2	0	F
11/11/2003	9	C		1	0	2	0	3	3	0	F
11/11/2003	10	F	N	2	1	4	0	7	6	1	F
11/11/2003	11	B	N	0	0	2	1	3	2	1	F
11/11/2003	12	M	N	1	0	3	1	5	4	1	F
11/11/2003	13	C		1	1	1	0	3	2	1	F
11/11/2003	14	C		2	1	1	1	5	3	2	F
11/11/2003	15	F	N	1	0	0	1	2	1	1	F
11/11/2003	16	M	N	1	0	3	1	5	4	1	F
11/11/2003	17	B	N	2	0	3	0	5	5	0	F
11/11/2003	18	M	Y	1	1	1	3	6	2	4	F
11/11/2003	19	C		4	0	3	1	8	7	1	F
11/11/2003	20	M	Y	1	0	1	1	3	2	1	F
11/11/2003	21	C		2	0	4	0	6	6	0	F
11/11/2003	22	C		0	0	0	0	0	0	0	F
11/11/2003	23	C		0	1	1	2	4	1	3	F
11/11/2003	24	B	Y	0	0	1	0	1	1	0	F

(continued)

Date	PotID	Treatment	Escape	LF	SF	LM	SM	Total	Lg	Sm	Moon
11/11/2003	25	C		4	2	1	1	8	5	3	F
11/11/2003	26	C		1	1	0	0	2	1	1	F
11/11/2003	27	M	N	2	1	0	1	4	2	2	F
11/11/2003	28	F	N	0	0	3	0	3	3	0	F
11/11/2003	29	C		3	2	0	4	9	3	6	F
11/11/2003	30	B	N	2	0	0	0	2	2	0	F
11/11/2003	31	F	N	4	4	1	2	11	5	6	F
11/11/2003	32	F	N	1	0	3	0	4	4	0	F
11/11/2003	33	B	Z	1	0	0	0	1	1	0	F
11/11/2003	34	C		2	0	3	1	6	5	1	F
11/11/2003	35	C		0	0	1	0	1	1	0	F
11/11/2003	36	C		3	1	3	1	8	6	2	F
11/11/2003	37	M	N	1	0	3	1	5	4	1	F
11/11/2003	39	F	N	3	1	3	0	7	6	1	F
11/11/2003	40	B	N	10	1	0	0	11	10	1	F
11/11/2003	41	B	N	2	0	4	0	6	6	0	F
11/11/2003	42	M	N	0	0	0	0	0	0	0	F
11/11/2003	43	M	N	0	0	1	0	1	1	0	F
11/11/2003	45	C		1	2	0	0	3	1	2	F
11/11/2003	46	C		1	0	2	0	3	3	0	F
11/11/2003	47	C		2	0	0	0	2	2	0	F
11/11/2003	48	F	N	6	3	2	0	11	8	3	F
11/11/2003	49	B	N	0	1	2	0	3	2	1	F
11/11/2003	50	F	N	0	0	6	0	6	6	0	F
11/12/2003	1	C		0	0	2	0	2	2	0	F
11/12/2003	2	M	N	0	0	3	0	3	3	0	F
11/12/2003	3	M	N	0	0	2	1	3	2	1	F
11/12/2003	4	C		0	0	1	0	1	1	0	F
11/12/2003	5	C		0	1	2	0	3	2	1	F
11/12/2003	6	C		2	1	2	0	5	4	1	F
11/12/2003	7	B	Y	0	0	3	0	3	3	0	F
11/12/2003	8	C		0	0	3	0	3	3	0	F
11/12/2003	9	B	N	0	0	0	0	0	0	0	F
11/12/2003	10	F	D	1	0	1	0	2	2	0	F
11/12/2003	11	B	N	0	0	4	0	4	4	0	F
11/12/2003	12	B	Y	3	0	0	0	3	3	0	F
11/12/2003	13	M	Y	0	0	2	0	2	2	0	F
11/12/2003	14	M	N	4	0	4	0	8	8	0	F
11/12/2003	15	B	N	0	1	2	0	3	2	1	F
11/12/2003	16	C		1	0	1	1	3	2	1	F
11/12/2003	17	C		2	0	1	0	3	3	0	F

(continued)

Date	PotID	Treatment	Escape	LF	SF	LM	SM	Total	Lg	Sm	Moon
11/12/2003	18	C		1	1	2	2	6	3	3	F
11/12/2003	19	B	N	0	1	2	1	4	2	2	F
11/12/2003	20	F	Y	2	0	0	0	2	2	0	F
11/12/2003	21	F	Y	4	0	2	0	6	6	0	F
11/12/2003	22	F	N	0	1	0	1	2	0	2	F
11/12/2003	23	C		1	2	0	1	4	1	3	F
11/12/2003	24	F	N	0	0	0	0	0	0	0	F
11/12/2003	25	F	N	5	3	0	1	9	5	4	F
11/12/2003	26	M	N	1	1	2	1	5	3	2	F
11/12/2003	27	B	D	8	3	0	0	11	8	3	F
11/12/2003	28	F	N	1	0	1	1	3	2	1	F
11/12/2003	29	F	N	0	0	0	1	1	0	1	F
11/12/2003	30	M	Y	1	0	2	0	3	3	0	F
11/12/2003	31	M	N	0	0	2	1	3	2	1	F
11/12/2003	32	C		1	1	1	0	3	2	1	F
11/12/2003	33	C		1	1	0	0	2	1	1	F
11/12/2003	34	C		3	0	1	0	4	4	0	F
11/12/2003	35	C		0	0	0	0	0	0	0	F
11/12/2003	36	C		0	1	3	0	4	3	1	F
11/12/2003	37	B	N	0	0	6	0	6	6	0	F
11/12/2003	38	C		0	0	0	0	0	0	0	F
11/12/2003	39	C		5	3	0	1	9	5	4	F
11/12/2003	40	C		1	1	1	0	3	2	1	F
11/12/2003	41	M	N	1	0	1	0	2	2	0	F
11/12/2003	42	B	N	0	0	1	1	2	1	1	F
11/12/2003	43	M	N	0	0	1	0	1	1	0	F
11/12/2003	45	M	Y	0	0	0	0	0	0	0	F
11/12/2003	46	C		0	0	0	0	0	0	0	F
11/12/2003	47	B	Y	2	0	5	1	8	7	1	F
11/12/2003	48	F	N	1	1	3	1	6	4	2	F
11/12/2003	49	F	N	2	1	3	1	7	5	2	F
11/12/2003	50	C		5	0	2	1	8	7	1	F
11/13/2003	1	C		0	0	0	0	0	0	0	F
11/13/2003	2	B	N	0	0	3	0	3	3	0	F
11/13/2003	3	C		0	0	2	0	2	2	0	F
11/13/2003	4	B	N	0	0	0	0	0	0	0	F
11/13/2003	5	F	N	1	0	2	0	3	3	0	F
11/13/2003	6	M	N	0	0	2	0	2	2	0	F
11/13/2003	7	F	Y	3	1	0	1	5	3	2	F
11/13/2003	8	M	N	0	0	2	0	2	2	0	F
11/13/2003	9	C		3	3	3	3	12	6	6	F

(continued)

Date	PotID	Treatment	Escape	LF	SF	LM	SM	Total	Lg	Sm	Moon
11/13/2003	10	C		1	0	0	0	1	1	0	F
11/13/2003	11	F	N	3	0	2	0	5	5	0	F
11/13/2003	12	M	Y	0	0	0	0	0	0	0	F
11/13/2003	13	F	N	1	1	2	0	4	3	1	F
11/13/2003	14	B	N	7	1	2	0	10	9	1	F
11/13/2003	15	B	N	4	0	0	1	5	4	1	F
11/13/2003	16	B	Y	7	1	2	0	10	9	1	F
11/13/2003	17	B	Y	3	0	0	0	3	3	0	F
11/13/2003	18	F	N	0	0	1	0	1	1	0	F
11/13/2003	19	M	N	0	0	0	0	0	0	0	F
11/13/2003	20	C		1	3	5	1	10	6	4	F
11/13/2003	21	M	D	1	2	1	0	4	2	2	F
11/13/2003	22	C		0	3	0	1	4	0	4	F
11/13/2003	23	M	N	0	0	1	0	1	1	0	F
11/13/2003	24	B	N	0	0	0	0	0	0	0	F
11/13/2003	25	M	N	0	0	0	0	0	0	0	F
11/13/2003	26	B	N	3	0	0	3	6	3	3	F
11/13/2003	27	F	S	0	0	0	0	0	0	0	F
11/13/2003	28	C		1	0	0	0	1	1	0	F
11/13/2003	29	C		0	0	0	0	0	0	0	F
11/13/2003	30	C		0	0	0	0	0	0	0	F
11/13/2003	31	F	N	0	0	0	0	0	0	0	F
11/13/2003	32	B	N	0	0	2	0	2	2	0	F
11/13/2003	33	B	N	5	0	0	0	5	5	0	F
11/13/2003	34	C		0	1	0	0	1	0	1	F
11/13/2003	35	C		0	1	0	0	1	0	1	F
11/13/2003	36	C		4	1	4	1	10	8	2	F
11/13/2003	37	C		5	4	3	2	14	8	6	F
11/13/2003	38	C		0	0	1	0	1	1	0	F
11/13/2003	39	F	Y	0	0	1	0	1	1	0	F
11/13/2003	40	C		1	1	0	1	3	1	2	F
11/13/2003	41	M	N	6	0	0	0	6	6	0	F
11/13/2003	42	F	N	0	0	0	0	0	0	0	F
11/13/2003	43	M	N	0	0	0	0	0	0	0	F
11/13/2003	45	M	N	0	0	0	0	0	0	0	F
11/13/2003	46	C		0	0	0	0	0	0	0	F
11/13/2003	47	C		1	3	1	2	7	2	5	F
11/13/2003	48	F	N	1	0	0	0	1	1	0	F
11/13/2003	49	C		0	0	0	0	0	0	0	F
11/13/2003	50	C		1	1	4	0	6	5	1	F
11/25/2003	1	F	N	1	0	1	0	2	2	0	N

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Date	PotID	Treatment	Escape	LF	SF	LM	SM	Total	Lg	Sm	Moon
11/25/2003	2	C		1	0	1	1	3	2	1	N
11/25/2003	3	B	Y	0	0	2	0	2	2	0	N
11/25/2003	4	C		0	1	1	0	2	1	1	N
11/25/2003	5	B	Y	1	2	5	1	9	6	3	N
11/25/2003	6	C		0	1	5	0	6	5	1	N
11/25/2003	7	C		1	2	2	1	6	3	3	N
11/25/2003	8	F	N	1	0	6	0	7	7	0	N
11/25/2003	10	M	N	3	3	4	0	10	7	3	N
11/25/2003	11	C		0	0	2	1	3	2	1	N
11/25/2003	12	C		1	1	0	0	2	1	1	N
11/25/2003	13	F	Y	0	1	3	2	6	3	3	N
11/25/2003	14	C		3	2	2	0	7	5	2	N
11/25/2003	15	B	N	0	0	4	0	4	4	0	N
11/25/2003	16	C		2	3	2	2	9	4	5	N
11/25/2003	17	C		1	0	5	0	6	6	0	N
11/25/2003	18	M	N	0	6	4	0	10	4	6	N
11/25/2003	19	M	Y	1	4	0	2	7	1	6	N
11/25/2003	20	M	Y	0	0	0	0	0	0	0	N
11/25/2003	21	B	Y	1	1	3	0	5	4	1	N
11/25/2003	22	B	Y	0	3	0	3	6	0	6	N
11/25/2003	23	M	Y	0	0	2	0	2	2	0	N
11/25/2003	24	F	Y	0	0	1	0	1	1	0	N
11/25/2003	25	B	Y	3	2	5	0	10	8	2	N
11/25/2003	26	C		5	3	2	0	10	7	3	N
11/25/2003	27	M	Y	1	1	3	1	6	4	2	N
11/25/2003	28	M	N	0	0	1	0	1	1	0	N
11/25/2003	29	B	Y	0	1	2	0	3	2	1	N
11/25/2003	30	C		3	2	3	0	8	6	2	N
11/25/2003	31	M	N	1	2	0	2	5	1	4	N
11/25/2003	32	B	N	1	2	1	0	4	2	2	N
11/25/2003	33	C		1	0	1	0	2	2	0	N
11/25/2003	34	C		3	3	4	1	11	7	4	N
11/25/2003	35	C		0	0	0	0	0	0	0	N
11/25/2003	36	C		2	0	3	0	5	5	0	N
11/25/2003	37	B	N	1	1	2	1	5	3	2	N
11/25/2003	38	C		0	1	1	1	3	1	2	N
11/25/2003	39	F	N	11	2	3	0	16	14	2	N
11/25/2003	40	F	N	1	1	1	0	3	2	1	N
11/25/2003	41	F	Y	6	4	3	0	13	9	4	N
11/25/2003	42	F	N	0	0	0	0	0	0	0	N
11/25/2003	43	C		4	2	2	1	9	6	3	N
11/25/2003	44	M	Y	0	0	0	0	0	0	0	N
11/25/2003	45	M	Y	1	0	4	0	5	5	0	N

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Date	PotID	Treatment	Escape	LF	SF	LM	SM	Total	Lg	Sm	Moon
11/25/2003	46	F	Y	0	0	0	0	0	0	0	N
11/25/2003	47	B	Y	4	0	2	0	6	6	0	N
11/25/2003	48	C		1	0	3	0	4	4	0	N
11/25/2003	49	F	N	3	0	1	0	4	4	0	N
11/25/2003	50	C		0	0	1	0	1	1	0	N
11/26/2003	1	C		3	0	2	0	5	5	0	N
11/26/2003	2	F	Y	1	0	3	0	4	4	0	N
11/26/2003	3	C		1	1	1	0	3	2	1	N
11/26/2003	4	B	Y	0	0	0	0	0	0	0	N
11/26/2003	5	M	Y	1	2	1	1	5	2	3	N
11/26/2003	6	F	Y	0	0	2	1	3	2	1	N
11/26/2003	7	C		1	3	3	2	9	4	5	N
11/26/2003	8	C		0	1	1	0	2	1	1	N
11/26/2003	9	C		0	0	1	0	1	1	0	N
11/26/2003	10	M	Y	1	0	0	0	1	1	0	N
11/26/2003	11	C		0	1	2	1	4	2	2	N
11/26/2003	12	B	Y	0	0	2	0	2	2	0	N
11/26/2003	13	M	N	0	0	0	0	0	0	0	N
11/26/2003	14	B	N	1	1	2	0	4	3	1	N
11/26/2003	15	M	N	0	0	0	0	0	0	0	N
11/26/2003	16	F	N	2	0	0	0	2	2	0	N
11/26/2003	17	F	N	0	0	5	0	5	5	0	N
11/26/2003	18	B	N	6	1	6	2	15	12	3	N
11/26/2003	19	M	N	2	0	0	0	2	2	0	N
11/26/2003	20	C		1	0	0	0	1	1	0	N
11/26/2003	21	C		1	1	1	0	3	2	1	N
11/26/2003	22	C		0	0	1	1	2	1	1	N
11/26/2003	23	B	N	0	0	0	0	0	0	0	N
11/26/2003	24	F	Y	0	0	0	0	0	0	0	N
11/26/2003	25	M	N	2	0	2	0	4	4	0	N
11/26/2003	26	F	N	3	1	1	0	5	4	1	N
11/26/2003	27	M	Y	0	0	0	1	1	0	1	N
11/26/2003	28	B	Y	1	1	1	0	3	2	1	N
11/26/2003	29	C		1	0	0	0	1	1	0	N
11/26/2003	30	C		2	2	4	0	8	6	2	N
11/26/2003	31	B	Y	1	0	1	1	3	2	1	N
11/26/2003	32	B	N	1	1	1	1	4	2	2	N
11/26/2003	33	C		2	1	1	0	4	3	1	N
11/26/2003	34	F	N	1	0	0	1	2	1	1	N
11/26/2003	35	F	Y	0	1	2	0	3	2	1	N
11/26/2003	36	F	Y	3	1	4	1	9	7	2	N
11/26/2003	37	C		0	0	2	0	2	2	0	N
11/26/2003	38	C		2	1	1	1	5	3	2	N

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Date	PotID	Treatment	Escape	LF	SF	LM	SM	Total	Lg	Sm	Moon
11/26/2003	39	M	N	0	0	2	0	2	2	0	N
11/26/2003	40	M	N	0	1	1	0	2	1	1	N
11/26/2003	41	B	N	1	0	4	0	5	5	0	N
11/26/2003	42	C		0	0	1	0	1	1	0	N
11/26/2003	43	B	N	0	0	1	0	1	1	0	N
11/26/2003	44	M	Y	0	0	2	0	2	2	0	N
11/26/2003	45	C		1	0	0	0	1	1	0	N
11/26/2003	46	C		0	0	0	0	0	0	0	N
11/26/2003	47	C		2	0	4	0	6	6	0	N
11/26/2003	48	C		0	0	0	0	0	0	0	N
11/26/2003	49	F	N	2	1	2	0	5	4	1	N
11/26/2003	50	C		0	0	6	1	7	6	1	N
11/27/2003	1	C		1	0	1	1	3	2	1	N
11/27/2003	2	C		1	0	6	0	7	7	0	N
11/27/2003	3	B	N	1	1	3	0	5	4	1	N
11/27/2003	4	C		0	0	0	0	0	0	0	N
11/27/2003	5	F	Y	1	1	2	0	4	3	1	N
11/27/2003	6	C		4	0	0	0	4	4	0	N
11/27/2003	7	F	N	0	0	2	2	4	2	2	N
11/27/2003	8	M	N	0	1	0	0	1	0	1	N
11/27/2003	9	F	Y	2	0	3	0	5	5	0	N
11/27/2003	10	C		0	0	0	0	0	0	0	N
11/27/2003	11	C		1	0	3	0	4	4	0	N
11/27/2003	12	C	D	0	0	1	0	1	1	0	N
11/27/2003	13	B	N	1	2	1	0	4	2	2	N
11/27/2003	14	M	Z	0	0	0	0	0	0	0	N
11/27/2003	15	B	D	0	0	1	0	1	1	0	N
11/27/2003	16	C		3	3	0	1	7	3	4	N
11/27/2003	17	C		0	0	1	1	2	1	1	N
11/27/2003	18	B	N	0	1	0	3	4	0	4	N
11/27/2003	19	M	Y	1	0	0	0	1	1	0	N
11/27/2003	20	F	N	1	3	3	0	7	4	3	N
11/27/2003	21	F	N	2	0	1	0	3	3	0	N
11/27/2003	22	C		3	1	5	1	10	8	2	N
11/27/2003	23	C		0	1	4	1	6	4	2	N
11/27/2003	24	C		0	0	0	0	0	0	0	N
11/27/2003	25	B	N	0	1	2	0	3	2	1	N
11/27/2003	26	C		0	0	1	0	1	1	0	N
11/27/2003	27	C		1	1	2	1	5	3	2	N
11/27/2003	28	C		2	0	0	0	2	2	0	N
11/27/2003	29	M	N	1	0	1	0	2	2	0	N
11/27/2003	30	F	Y	0	0	0	0	0	0	0	N
11/27/2003	31	B	N	1	2	0	1	4	1	3	N

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Date	PotID	Treatment	Escape	LF	SF	LM	SM	Total	Lg	Sm	Moon
11/27/2003	32	M	Y	0	0	3	0	3	3	0	N
11/27/2003	33	M	Y	0	0	0	0	0	0	0	N
11/27/2003	34	F	N	2	1	2	0	5	4	1	N
11/27/2003	35	C		0	0	4	0	4	4	0	N
11/27/2003	36	F	Y	0	2	1	2	5	1	4	N
11/27/2003	37	M	N	1	0	2	0	3	3	0	N
11/27/2003	38	C		0	0	1	0	1	1	0	N
11/27/2003	39	M	Y	7	3	1	0	11	8	3	N
11/27/2003	40	M	Z	1	1	1	0	3	2	1	N
11/27/2003	41	C		0	0	0	0	0	0	0	N
11/27/2003	42	B	N	0	0	2	0	2	2	0	N
11/27/2003	43	B	N	0	0	0	0	0	0	0	N
11/27/2003	44	C		0	0	3	0	3	3	0	N
11/27/2003	45	F	Y	0	0	1	0	1	1	0	N
11/27/2003	46	B	Y	2	0	4	0	6	6	0	N
11/27/2003	47	M	Y	1	0	1	1	3	2	1	N
11/27/2003	48	C		1	0	1	0	2	2	0	N
11/27/2003	49	B	Y	2	0	2	1	5	4	1	N
11/27/2003	50	F	Y	1	0	2	0	3	3	0	N
2/25/2004	1	C		0	0	0	0	0	0	0	
2/25/2004	2	C		0	0	2	0	2	2	0	
2/25/2004	3	F	Y	0	0	0	0	0	0	0	
2/25/2004	4	B	N	4	3	1	1	9	5	4	
2/25/2004	6	B	N	0	2	0	0	2	0	2	
2/25/2004	7	B	N	0	0	2	2	4	2	2	
2/25/2004	8	F	Y	3	1	1	1	6	4	2	
2/25/2004	9	B	Y	0	0	1	0	1	1	0	
2/25/2004	10	F	N	2	0	1	0	3	3	0	
2/25/2004	11	C		0	0	0	0	0	0	0	
2/25/2004	12	C		0	0	0	0	0	0	0	
2/25/2004	13	B	Y	0	0	0	0	0	0	0	
2/25/2004	14	B	N	1	0	3	0	4	4	0	
2/25/2004	15	C		1	1	3	0	5	4	1	
2/25/2004	16	F	N	2	0	3	0	5	5	0	
2/25/2004	17	C		1	0	5	0	6	6	0	
2/25/2004	18	C		4	2	4	0	10	8	2	
2/25/2004	19	F	N	1	0	1	0	2	2	0	
2/25/2004	20	C		1	0	0	0	1	1	0	
2/25/2004	21	C		4	1	1	0	6	5	1	
2/25/2004	22	B	Y	2	1	5	2	10	7	3	
2/25/2004	23	M	N	5	1	3	0	9	8	1	
2/25/2004	24	B	N	1	1	2	0	4	3	1	
2/25/2004	25	F	N	1	0	3	1	5	4	1	

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Date	PotID	Treatment	Escape	LF	SF	LM	SM	Total	Lg	Sm	Moon
2/25/2004	26	F	Y	1	0	4	0	5	5	0	
2/25/2004	27	M	N	0	0	1	0	1	1	0	
2/25/2004	28	B	Z	1	0	0	0	1	1	0	
2/25/2004	29	M	Y	0	0	2	2	4	2	2	
2/25/2004	30	B	N	0	0	0	1	1	0	1	
2/25/2004	31	M	N	2	0	2	0	4	4	0	
2/25/2004	32	M	N	3	1	3	2	9	6	3	
2/25/2004	33	F	Y	3	2	1	2	8	4	4	
2/25/2004	34	C		0	0	1	0	1	1	0	
2/25/2004	35	F	N	1	0	1	1	3	2	1	
2/25/2004	36	C		4	3	7	2	16	11	5	
2/25/2004	37	M	N	1	1	1	0	3	2	1	
2/25/2004	38	C		0	1	3	1	5	3	2	
2/25/2004	39	C		3	0	2	0	5	5	0	
2/25/2004	40	F	N	1	0	0	0	1	1	0	
2/25/2004	41	C		2	1	3	1	7	5	2	
2/25/2004	42	M	Y	0	0	1	0	1	1	0	
2/25/2004	43	M	N	4	1	0	1	6	4	2	
2/25/2004	44	C		2	0	3	3	8	5	3	
2/25/2004	45	C		1	0	2	1	4	3	1	
2/25/2004	46	C		3	3	4	2	12	7	5	
2/25/2004	47	C		0	0	0	0	0	0	0	
2/25/2004	48	C		1	0	0	0	1	1	0	
2/25/2004	49	M	N	0	0	2	0	2	2	0	
2/25/2004	50	M	N	2	5	2	3	12	4	8	
2/26/2004	1	M	N	0	0	1	0	1	1	0	
2/26/2004	2	C		0	2	0	0	2	0	2	
2/26/2004	3	B	N	0	0	0	0	0	0	0	
2/26/2004	4	F	Y	3	2	4	0	9	7	2	
2/26/2004	5	B	N	0	0	3	0	3	3	0	
2/26/2004	6	F	Y	0	0	1	0	1	1	0	
2/26/2004	7	M	Y	1	1	2	1	5	3	2	
2/26/2004	8	C		0	1	1	0	2	1	1	
2/26/2004	9	B	N	0	0	4	0	4	4	0	
2/26/2004	10	C		0	0	3	0	3	3	0	
2/26/2004	11	C		0	0	0	0	0	0	0	
2/26/2004	12	M	N	0	0	0	0	0	0	0	
2/26/2004	13	C		0	0	1	0	1	1	0	
2/26/2004	14	F	N	1	0	6	0	7	7	0	
2/26/2004	15	M	Y	0	0	0	0	0	0	0	
2/26/2004	16	C		1	2	3	1	7	4	3	
2/26/2004	17	C		1	0	1	0	2	2	0	
2/26/2004	18	C		2	1	0	0	3	2	1	

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Date	PotID	Treatment	Escape	LF	SF	LM	SM	Total	Lg	Sm	Moon
2/26/2004	19	F	N	0	0	0	0	0	0	0	
2/26/2004	20	C		0	0	0	0	0	0	0	
2/26/2004	21	B	Y	1	0	4	1	6	5	1	
2/26/2004	22	F	Y	2	0	0	0	2	2	0	
2/26/2004	23	C		3	1	7	0	11	10	1	
2/26/2004	24	F	N	0	0	3	0	3	3	0	
2/26/2004	25	C		0	0	0	0	0	0	0	
2/26/2004	26	C		1	0	3	3	7	4	3	
2/26/2004	27	C		0	0	1	1	2	1	1	
2/26/2004	28	M	Y	0	0	3	0	3	3	0	
2/26/2004	29	M	N	0	0	0	0	0	0	0	
2/26/2004	30	C		1	2	1	0	4	2	2	
2/26/2004	31	M	N	0	1	6	1	8	6	2	
2/26/2004	32	C		3	0	2	0	5	5	0	
2/26/2004	33	F	N	1	0	4	0	5	5	0	
2/26/2004	34	M	Y	0	0	1	0	1	1	0	
2/26/2004	35	B	Y	1	3	1	0	5	2	3	
2/26/2004	36	C		3	5	5	3	16	8	8	
2/26/2004	37	B	N	0	1	3	0	4	3	1	
2/26/2004	38	C		1	0	1	1	3	2	1	
2/26/2004	39	F	N	0	0	1	1	2	1	1	
2/26/2004	40	M	Y	0	0	0	0	0	0	0	
2/26/2004	41	B	N	2	2	3	0	7	5	2	
2/26/2004	42	B	N	1	0	0	0	1	1	0	
2/26/2004	43	F	Y	3	1	0	1	5	3	2	
2/26/2004	44	M	N	0	0	0	0	0	0	0	
2/26/2004	45	B	N	0	0	1	0	1	1	0	
2/26/2004	46	C		1	1	3	2	7	4	3	
2/26/2004	47	C		0	0	0	0	0	0	0	
2/26/2004	48	B	N	0	0	0	0	0	0	0	
2/26/2004	49	F	Y	1	2	3	3	9	4	5	
2/26/2004	50	C		3	2	4	0	9	7	2	
2/27/2004	1	C		0	0	0	0	0	0	0	
2/27/2004	2	B	N	0	0	0	0	0	0	0	
2/27/2004	3	C		0	0	0	0	0	0	0	
2/27/2004	4	C		2	2	3	2	9	5	4	
2/27/2004	5	C		0	0	3	0	3	3	0	
2/27/2004	6	C		0	1	1	1	3	1	2	
2/27/2004	7	C		3	1	2	0	6	5	1	
2/27/2004	8	M	Y	2	1	3	1	7	5	2	
2/27/2004	9	C		0	0	1	1	2	1	1	
2/27/2004	10	F	Y	2	0	1	0	3	3	0	
2/27/2004	11	M	N	0	0	0	0	0	0	0	

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Date	PotID	Treatment	Escape	LF	SF	LM	SM	Total	Lg	Sm	Moon
2/27/2004	12	C		0	0	0	1	1	0	1	
2/27/2004	13	F	N	0	0	1	0	1	1	0	
2/27/2004	14	C		0	0	3	0	3	3	0	
2/27/2004	15	M	N	0	0	0	0	0	0	0	
2/27/2004	16	C		2	2	2	0	6	4	2	
2/27/2004	17	B	N	1	1	0	0	2	1	1	
2/27/2004	18	M	N	2	2	2	0	6	4	2	
2/27/2004	19	C		0	0	1	0	1	1	0	
2/27/2004	20	C		0	0	0	0	0	0	0	
2/27/2004	21	C		2	2	2	2	8	4	4	
2/27/2004	22	M	Y	2	0	2	1	5	4	1	
2/27/2004	23	B	N	2	1	3	2	8	5	3	
2/27/2004	24	C		1	0	3	1	5	4	1	
2/27/2004	25	C		3	3	2	3	11	5	6	
2/27/2004	26	B	N	0	0	2	0	2	2	0	
2/27/2004	27	C		2	0	9	2	13	11	2	
2/27/2004	28	M	Y	0	0	1	0	1	1	0	
2/27/2004	29	F	N	0	0	2	0	2	2	0	
2/27/2004	30	F	N	0	0	1	0	1	1	0	
2/27/2004	31	C		0	0	4	0	4	4	0	
2/27/2004	32	F	N	0	0	1	0	1	1	0	
2/27/2004	33	M	N	0	0	1	0	1	1	0	
2/27/2004	34	M	Y	0	0	0	0	0	0	0	
2/27/2004	35	F	Y	2	2	2	0	6	4	2	
2/27/2004	36	B	N	1	0	1	1	3	2	1	
2/27/2004	37	F	N	0	1	0	2	3	0	3	
2/27/2004	38	M	N	0	1	2	1	4	2	2	
2/27/2004	39	B	N	2	0	3	0	5	5	0	
2/27/2004	40	M	N	0	0	1	0	1	1	0	
2/27/2004	41	C		1	1	3	0	5	4	1	
2/27/2004	42	B	N	0	0	1	0	1	1	0	
2/27/2004	43	B	Y	3	1	2	0	6	5	1	
2/27/2004	44	C		3	1	0	0	4	3	1	
2/27/2004	45	B	N	2	0	4	0	6	6	0	
2/27/2004	46	F	Y	0	1	4	0	5	4	1	
2/27/2004	47	F	N	0	0	1	0	1	1	0	
2/27/2004	48	B	N	0	0	1	0	1	1	0	
2/27/2004	49	F	N	0	1	1	1	3	1	2	
2/27/2004	50	C		1	0	1	1	3	2	1	

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TABLE 1.1

One-way ANOVA tables for comparisons of number of small lobsters captured among treatments in spring and summer. Counts were transformed prior to comparison as detailed in the text. (a) Total of all (sexes combined) small animals caught, (b) small females caught, (c) small males caught. When significant differences were found between treatment means in ANOVA, Tukey's multiple comparison test was used to identify which treatments differed significantly.

(a) Sexes pooled	Degrees of freedom	SS	Mean square	F-value	P > F	Treatments that differ
Spring:						
Treatment	3	2.9726	0.9909	0.70	0.5522	NA
Error	190	268.3769	1.4125			
Total	193	271.3494				
Summer:						
Treatment	3	14.5105	4.8368	3.33	0. 0230	Control: Large-female
Error	95	138.1843	1.4546			
Total	98	152.6949				

(b) Small females	Degrees of freedom	SS	Mean square	F-value	P > F	Treatments that differ
Spring:						
Treatment	3	2.3341	0.7780	0.76	0.5161	NA
Error	190	193.7500	1.0197			
Total	193	196.0841				
Summer:						
Treatment	3	9.1668	3.0556	3.28	0.0242	Control: Large-female
Error	95	88.4149	0.9307			
Total	98	97.5817				

(c) Small males	Degrees of freedom	SS	Mean square	F-value	P > F	Treatments that differ
Spring:						
Treatment	3	0.8944	0.2981	0.43	0.7298	NA
Error	190	130.8999	0.6889			
Total	193	131.7943				
Summer:						
Treatment	3	3.0026	1.0009	1.19	0.3180	NA
Error	95	79.9399	0.8415			
Total	98	82.9425				

TABLE 1.2

F-values and P-values from one-way ANOVA comparisons of transformed counts of small lobsters captured among treatments in spring and summer when traps with zero catches were included. (a) Total of all (sexes combined) small animals caught, (b) small females caught, (c) small males caught. All comparisons were not significant.

		F-value	P > F
(a) Sexes pooled			
	Spring	0.93	0.4294
	Summer	1.99	0.1193
(b) Small females			
	Spring	0.94	0.4198
	Summer	2.18	0.0941
(c) Small males			
	Spring	0.57	0.6349
	Summer	0.82	0.4870

TABLE 1.3

Degrees of freedom, F values, and P values from One-way ANOVA comparisons between treatments for: (a) total number of small lobsters captured, (b) number of small females captured, and (c) number of small males captured during different moon phases during spring sampling (November); "*n*" denotes the number of trap-hauls included in the comparison. Counts were transformed prior to comparison as detailed in the text. All comparisons were not significant.

Comparison	*n*	Total degrees of freedom	F value	P > F
(a) Sexes combined	194	193	0.11	0.7350
(b) Small females	194	193	0.65	0.4229
(c) Small males	194	193	2.94	0.0882

TABLE 1.4

Treatment means for counts of small lobsters caught in traps for spring and summer trials; Standard error of the mean (SEM) is in parentheses; "*n*" denotes number of traps in the sample. Sign of the difference of each treatment mean from the control mean; value of the difference in parentheses (i.e., control - treatment).

	Mean counts (SEM)		Sign of difference (value of difference)	
Treatment	Spring	Summer	Spring	Summer
Control	1.320 (0.155)	1.604 (0.254)	NA	NA
	n = 100	*n* = 48		
Biomass	1.156 (0.216)	0.900 (0.261)	+	+
	n = 32	*n* = 20	(0.0645)	(0.7042)
Female	1.206 (0.245)	0.4706 (0.212)	+	+
	n = 34	*n* = 17	(0.1355)	(1.134)
Male	0.9286 (0.272)	1.500 (0.572)	+	+
	n = 28	*n* = 14	(0.3784)	(0.1042)

FIGURE 1.1

Size-frequency distributions and sex ratios (male: female) of lobsters caught by treatment for spring (November) and summer (February) samples. Female size frequencies are gray bars; male size frequencies are black-outlined bars; and overall (sexes combined) size frequencies appear as solid lines. Counts were standardized to 100 successful trap hauls to facilitate comparisons; "*n*" indicates the number of animals each distribution represents, before standardization.

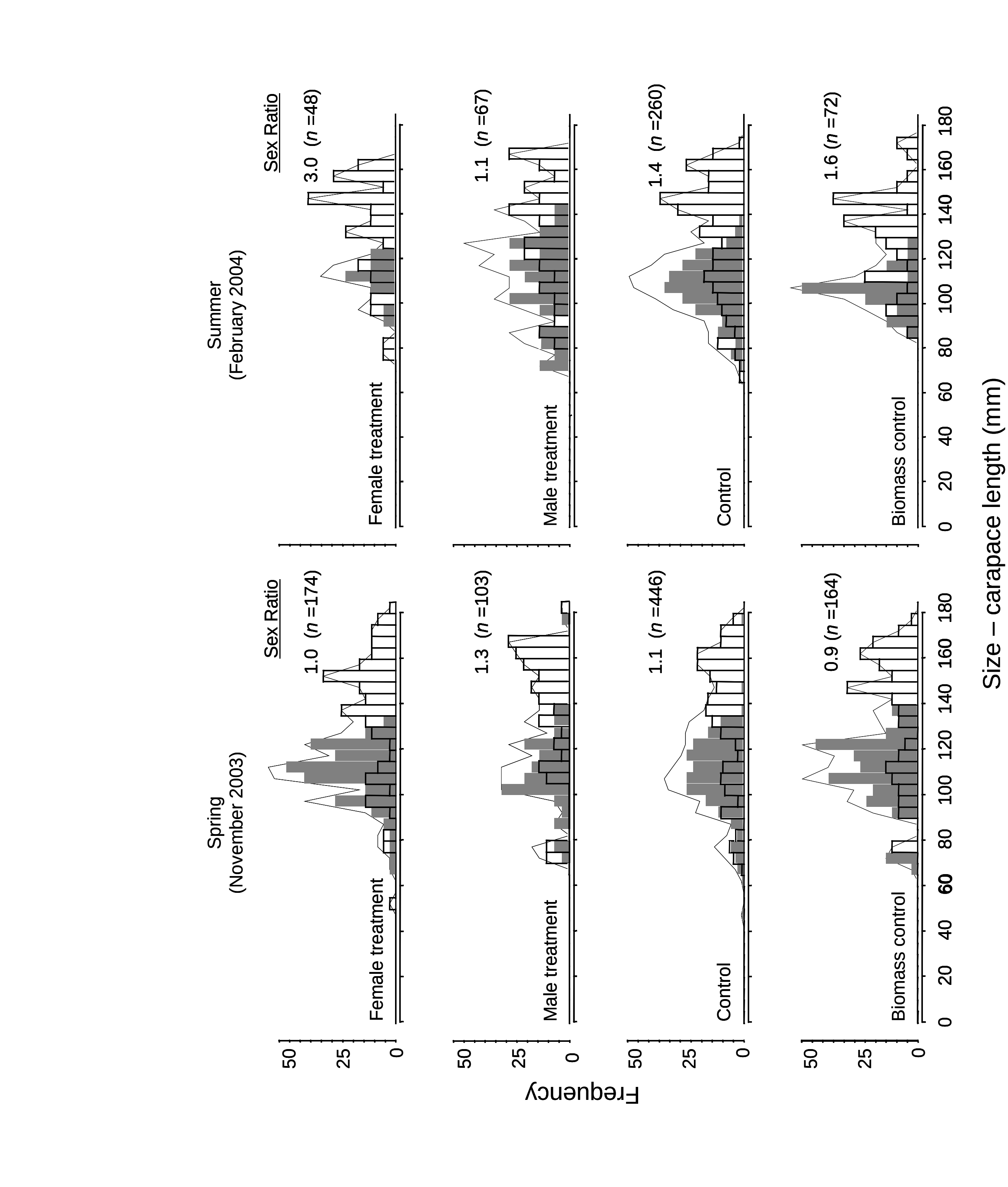

Spring
(November 2003)
Summer
(February 2004)
Sex Ratio
1.0 (n =174)
1.3 (n =103)
1.1 (n =446)
0.9 (n =164)
3.0 (n =48)
1.1 (n =67)
1.4 (n =260)
1.6 (n =72)
Female treatment
Male treatment
Control
Biomass control
Frequency
0
25
50
0
20
40
60
80
100
120
140
160
180
Size – carapace length (mm)

FIGURE 1.2

Untransformed mean catch rates of small lobsters for each treatment compared to those of control traps for spring (November) and summer (February) samples; lobsters caught are separated by sex; error bars are one standard error of the mean. Control catches are repeated for each treatment to facilitate comparisons. The circle indicates the only instance where the mean of a treatment catch was greater than that of the control. Abbreviations above the bars differentiate controls (C) from the other treatments (large female-F, large male-M, biomass control-B). Subgroups are small females (♀), and small males (♂) captured. "*n*" indicates the number of trap-hauls included for each treatment after traps with zero catches, dead or injured lobsters, or escaped seeds were eliminated; total number of trap-hauls performed is given in parentheses. Not shown: controls: spring n = 101 (117), summer n = 48 (59).

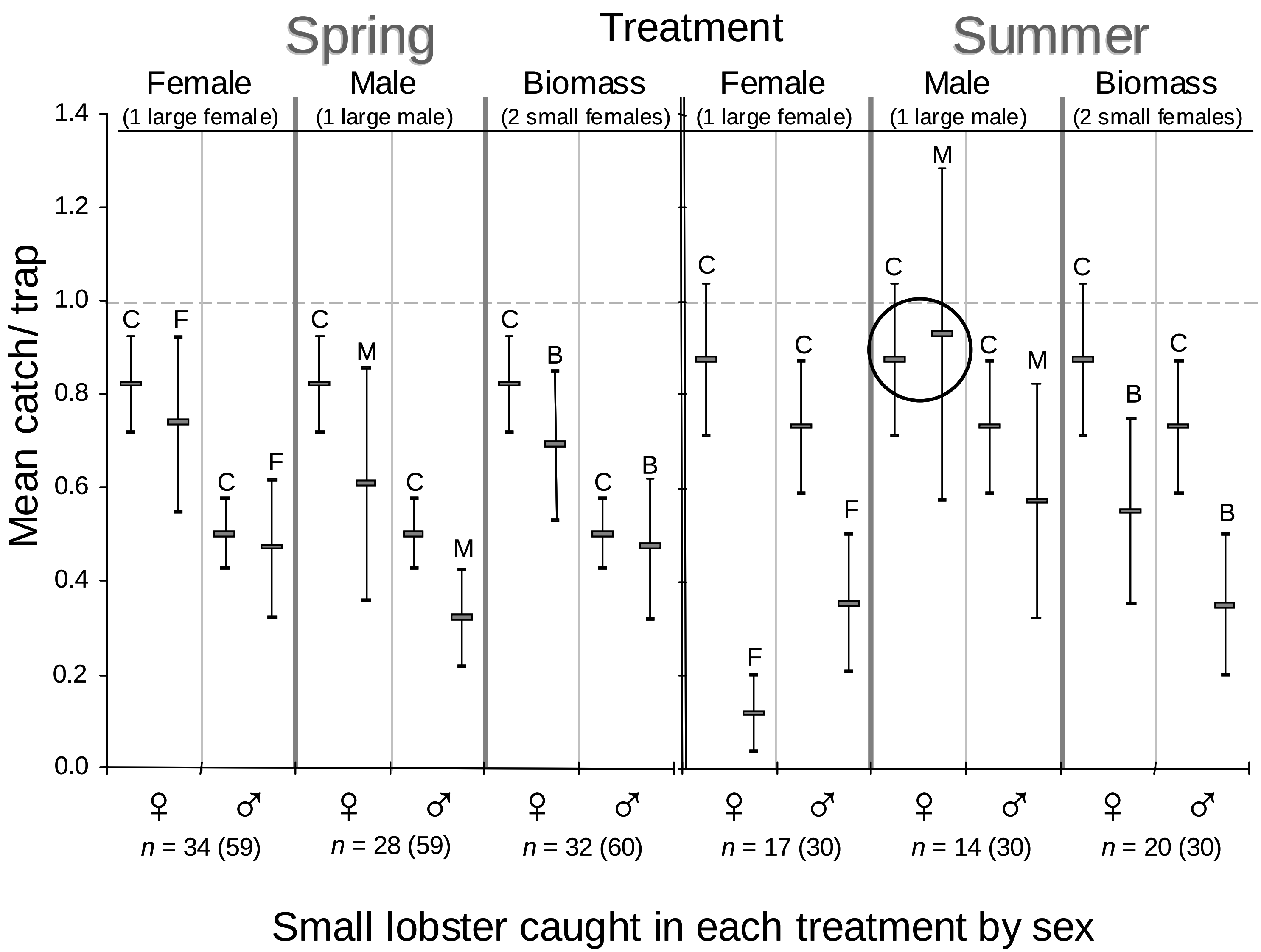

Spring
Treatment
Summer
Female
(1 large female)
Male
(1 large male)
Biomass
(2 small females)
Female
(1 large female)
Male
(1 large male)
Biomass
(2 small females)
Mean catch/ trap
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
C
F
M
B
♀
♂
n = 34 (59)
n = 28 (59)
n = 32 (60)
n = 17 (30)
n = 14 (30)
n = 20 (30)
Small lobster caught in each treatment by sex

FIGURE 1.3

Cumulative distribution of probabilities for a one-tailed test with H_o: control mean catch = treatment mean catch verses the alternative H_a: control mean catch > treatment mean catch (n = 6). Solid line: binomial probabilities; dashed line: probabilities obtained by randomization. Dotted line indicates α = 0.05.

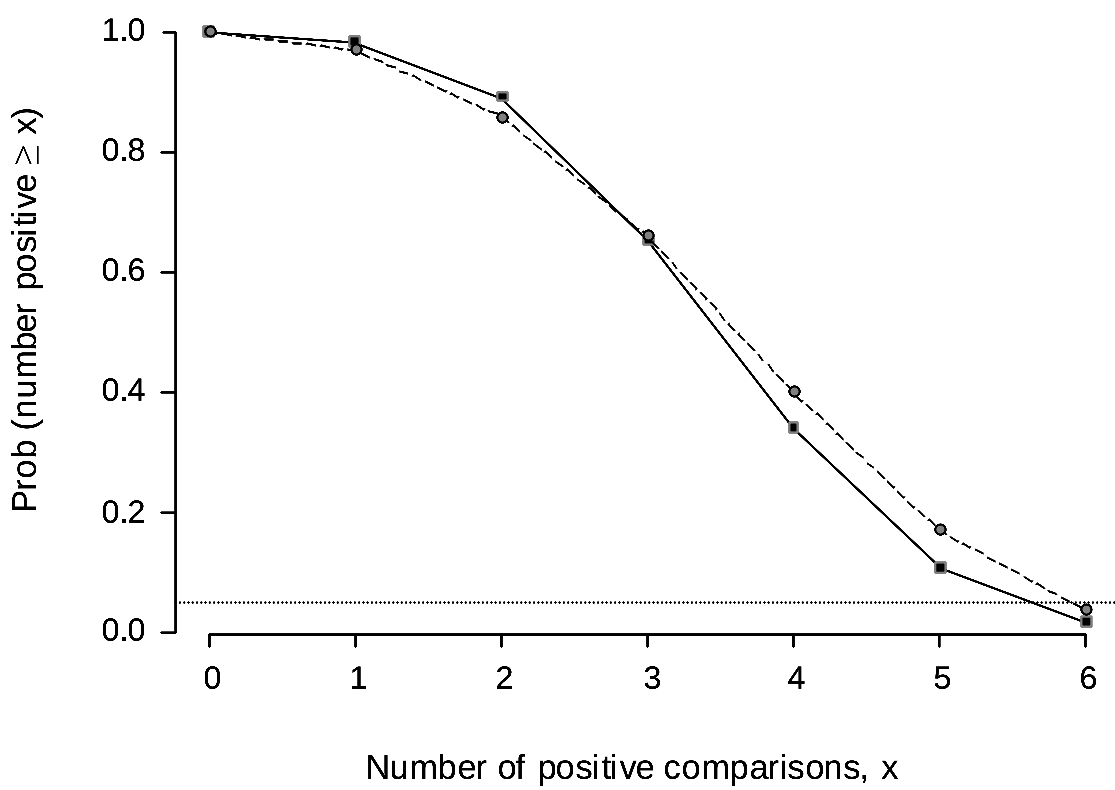
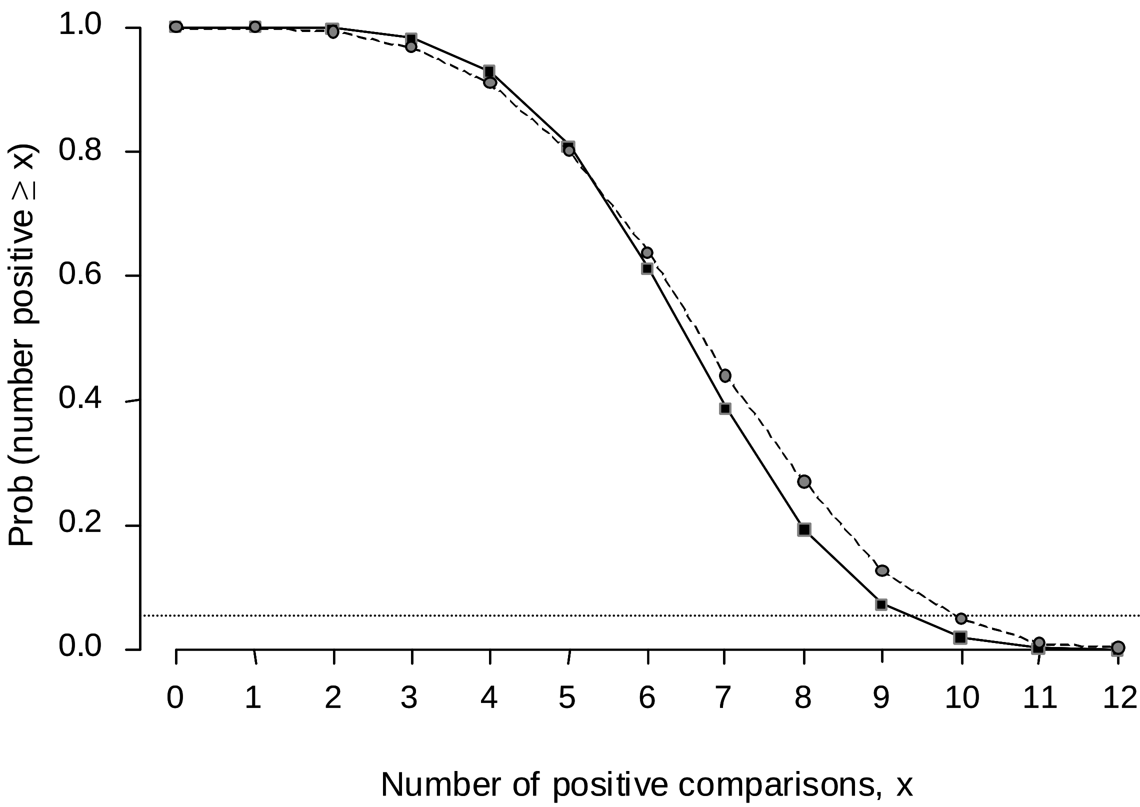


FIGURE 1.4

Cumulative distribution of probabilities for a one-tailed test with H_o: control mean catch = treatment mean catch verses the alternative H_a: control mean catch > treatment mean catch (n = 12). Solid line: binomial probabilities; dashed line: probabilities obtained by randomization. Dotted line indicates α = 0.05.



Chapter 2

Evaluation of a multi-year index-removal abundance estimator, with application to a Tasmanian rock lobster fishery

ABSTRACT

The index-removal (IR) method provides estimates of abundance, exploitation rate and survey catchability based on the change in catch rate between pre- and post-harvest surveys. However, model estimates often demonstrate poor precision. A multiple-year IR model (1qIR) was developed to improve the precision of single-year IR estimates. Both models were applied to simulated data to compare model performance over a range of exploitation rates, and to test 1qIR model robustness to failure of the assumption of constant catchability over all years. Both models were then applied to data from a southern rock lobster fishery in Tasmania, Australia. The 1qIR model consistently outperformed the single-year model in all chosen performance criteria using simulated data and data from the rock lobster fishery. Bias, standard deviation, and the square-root of the mean squared error were lower for the new model compared to the single-year model, and the 1qIR model produced useful results a greater proportion of the time than did the annual model. The performance of the 1qIR model continued to improve as additional years were added to the dataset. When the survey catchability coefficient varied in 1 of 5 years, the 1qIR model was robust to failure of the assumption of constant catchability among years until a 50% change in catchabilities occurred. When applied to rock lobster fishery data, 1qIR estimates were less variable than single-year model estimates and provided reasonable estimates of population abundance, survey catchability coefficient, and exploitation rate. Diagnostic tests to evaluate model estimates of exploitation rate were described and applied to model estimates for parameters of the rock lobster fishery. The 1qIR model estimates performed well in diagnostic plots, but results for single-year model were poor. The commercial catchability coefficient was also estimated based on model exploitation rate estimates and known fishing effort; 1qIR estimates appeared reasonable, and ranged from 3.708×10^{-5} to 3.791×10^{-5}. The 1qIR model offers a useful method to estimate abundance and exploitation rate in many situations when estimates from the single-year model prove too variable to be useful.

Keywords: Abundance estimation; Exploitation rate; Catchability coefficient; Southern rock lobster; *Jasus edwardsii*

1. INTRODUCTION

The index-removal (IR) method is a simple model that estimates abundance based on the decline in catch rate of a survey index due to the removal of a relatively large portion of the population. It requires a survey index of the population before and after a known removal, and assumes a closed population except for the known removal (i.e., no recruitment, immigration or emigration occurs, and the time between surveys is short enough to assume that no natural mortality takes place). In fishery applications (snow crab: Dawe et al. 1993, Chen et al. 1998b; sea scallops: southern rock lobster: Frusher et al. 1998; Gedamke et al. 2005) a commercial fishery is usually the source of the removal. The method is attractive because it does not require tagging, it can produce an abundance (or exploitation rate) estimate in only one season, and it does not require a differential in harvest rates among identified groups (e.g., by sex or life stage), as does the closely-related change-in-ratio method.

The IR method was first introduced by Petrides (1949), and it remains a potentially important estimation method because it requires data that may be already collected by management agencies (Dawe et al., 1993). Use of the method has been suggested as a cross-check of estimates from other methods (Eberhardt, 1982; Dawe et al., 1993).

Index-removal has seldom been applied because model estimates often have poor precision, but recent work has demonstrated that careful survey design can substantially improve the precision of model estimates. Dawe et al. (1993) speculated that the model has not received much use in fisheries either because of the cost of the required surveys or because of a lack of awareness of the method among fisheries scientists. Others, however, have pointed out that model estimates suffer from a lack of precision (Routledge, 1989; Roseberry and Woolfe, 1991). Routledge (1989) suggested that wide confidence intervals were due to low trap efficiency. Eberhardt (1982) found that precision was poor when removals or survey samples were small, but that model performance was poorest when removals were small. Chen et al. (1998b) also reported poor performance of the model when sampling locations were randomized independently for each survey. However, they found substantial improvement in the precision of IR estimates with both simulated data and actual survey data when the same sampling locations were used for both surveys. By occupying the same stations, they introduced a positive correlation between the pre- and post-harvest survey catches, and subsequently accounted for more of the variation in their survey indices than if both surveys had been randomized independently. Chen et al. (1998b) concluded that with careful survey design, the model may be very useful for assessing invertebrate stocks.

The goal of this work was to further improve the precision of the IR method by generalizing the approach to include multiple years of data. We investigated the performance of both the single-year model and the new, multiple-year model (hereafter, the “annual” and “1qIR” models, respectively) by Monte Carlo simulation over a range of exploitation rates, and examined the robustness of the 1qIR model to a violation of the model assumption of constant catchability. We then applied the annual and 1qIR models to data from a southern rock lobster (*Jasus edwardsii*) fishery in Tasmania, Australia.

2. MODEL DEVELOPMENT AND EVALUATION

2.1 The annual index-removal method

The annual model requires that an index of the population size be obtained from a survey before and after the removal and assumes that the survey index is proportional to abundance (Hoenig and Pollock, 1998). Thus,

$$E(I) = qfN \tag{1}$$

where E denotes expectation, I = survey catch (obtained from f units of randomly-placed sampling effort), N = population size, and q, the "catchability coefficient," is the constant of proportionality that relates the survey catch to N. It is assumed that the survey does not deplete the population, i.e., the change in abundance due to survey activities is negligible.

In the annual model, the ratio of the expected values of the survey catches per unit effort before and after the removal, R, is equal to the ratio of population sizes before, N, and after, N-R, the removal (Hoenig and Pollock, 1998):

$$\frac{E(I_1)/f_1}{E(I_2)/f_2} = \frac{qN}{q(N-R)} = \frac{N}{N-R} \tag{2}$$

where the subscripts denote time (*1* = before the fishery removal, *2* = after). The pre- and post-fishery *q*'s are assumed equal, and drop out of the equation. Likewise, if $f_1 = f_2$, the survey effort drops out. Eq. (2) can be solved for the population size:

$$\hat{N} = \frac{RI_1 / f_1}{I_1 / f_1 - I_2 / f_2} = \frac{RI_1}{I_1 - I_2(f_1 / f_2)} \tag{3}$$

where "^" denotes an estimate. Estimates can also be made of the survey catchability coefficient, *q*, and exploitation rate (fraction of the population harvested), *u*:

$$\hat{q} = \frac{I_1}{\hat{N} f_1} \tag{4}$$

$$\hat{u} = \frac{R}{\hat{N}} = \frac{I_1 / f_1 - I_2 / f_2}{I_1 / f_1} = \frac{I_1 - I_2(f_1 / f_2)}{I_1} \tag{5}$$

Note that *q* is population and gear specific and is not directly comparable among stocks (Dawe et al., 1993). Also, it is not necessary to know the magnitude of the removal to estimate *u*. When the data come from the exponential family of distributions, the estimates from (3), (4) and (5) can be shown to be maximum likelihood estimates (Davidson and Solomon (1974), as referenced by Brownie et al. (1985)). Estimates are made separately for each year of data collected. Assume that the catch in survey *j*, is a Poisson random variable, $I_j \sim P(qN_jf_j)$, where $j = 1$ or 2. The likelihood, Λ, for one year of pre- and post-harvest survey data is represented as:

$$\Lambda = \prod_{j=1}^{2} \frac{(qN_j f_j)^{I_j} e^{-qN_j f_j}}{I_j!} \tag{6}$$

where $N_2 = N_1 - R$, with other symbols as before. Note that the choice of the most appropriate probability density distribution should be made by an examination of the catch data. The Poisson distribution is used here for demonstration, and because it has been used in earlier work.

2.2 The multiple-year index-removal model ("1qIR")

Assume the catchability coefficient is a constant from survey to survey and from year to year. Again assume the survey catch is a Poisson random variable, I_{ij}, where i = year for i = 1, 2,…, n, and j = 1, 2. We can analyze all data simultaneously. The likelihood, Λ, is:

$$\Lambda = \prod_{i=1}^{n}\prod_{j=1}^{2}\frac{(qN_{ij}f_{ij})^{I_{ij}}e^{-qN_{ij}f_{ij}}}{I_{ij}!} \qquad (7)$$

with $N_{i2} = N_{i1} - R_i$, and R_i = removal in year i.

2.3 Simulation design

2.3.1. Model performance when catchability is constant

To compare the performance of the two models, survey data were generated by Monte Carlo simulation at three levels of exploitation rate, where 10%, 30% or 50% of the initial population was harvested each year. Conditions were ideal for this comparison, i.e., the assumption of constant catchability was met and $q_1 = q_2 = \ldots = q_n$ for all n years. Yearly abundance was constant for all simulations, and yearly removals were constant for all years within each exploitation rate scenario. Survey effort (f) was assumed constant over all surveys in all years and, for convenience, set equal to 1. For each survey, random catch data were generated with the assumption that catches are distributed according to a Poisson distribution:

I_{ij} ~ Poisson($q_i N_{ij}$) , $i = 1, 2, \ldots, n$, $j = 1, 2$, and $N_{i2} = N_{i1} - R_i$. (8)

The simulation parameters were:

1) population size prior to removals: $N_{11} = N_{21} = \ldots = N_{n1} = 1{,}000{,}000$ animals

2) catchability: $q_1 = q_2 = \ldots = q_n = 0.0001$

3) removals: $R_1 = R_2 = \ldots = R_n = uN_{i1}$, for $u = 0.1$, 0.3, 0.5

4) survey effort: $f = 1$

5) number of years of data, n, took on the values 2, 3, or 5.

Survey data were simulated at least 2000 times for each level of u. Each model was applied to the simulated data and model estimates were compared in terms of bias, standard deviation, and square root of the mean squared error (RMSE) as measures of model performance.

When the change in catch rate between surveys is small, unreasonably large estimates are expected. In fact, when the catch is equal in both surveys, the abundance estimate of the annual model becomes infinite. Additionally, if post-harvest survey catch rate is greater than that of the pre-harvest survey, the population estimates of the annual model will be infeasible (negative). Similarly, the estimates of the 1qIR model may be infinite or negative. Additionally, 1qIR estimates are made by non-linear maximization and may fail to converge. Consequently, simulations with unreasonably large estimates ($\hat{N}_i > 100 * N_i$, for any I), infeasible (negative) estimates, and convergence failures were counted and removed prior to calculating statistics from the estimates. Patterns of model estimates were examined in bivariate plots of all feasible abundance estimates against corresponding catchability coefficient estimates.

All survey data were generated in S-PLUS, and maximum likelihood estimates for 1qIR were made with the 'nlminb' function (MathSoft, 2000). The use of reasonable starting values appeared to be helpful in stabilizing model convergence. For an initial value of $\hat{q}$ for all years, we used the maximal estimate based on Eq. (1):

$$\hat{q}_o = \max_i \{ \frac{I_{i1}}{R_i} \} \quad , \tag{9}$$

where the subscript $_o$ indicates an initial guess. For initial abundance for all years estimated, the mean minimum feasible estimate of abundance was used:

$$\hat{N}_{i1_o} = \frac{\sum_{i=1}^{n} (R_i + \sum_{j=1}^{2} I_{ij})}{n} \quad . \tag{10}$$

2.3.2. Varying catchability-ratio comparison

To compare the performance of the models when the assumption of constant catchability over all years is violated for 1qIR, survey data were again generated by Monte Carlo simulation as described above except that, in one year, the catchability coefficient was greater than that of the other years. The catchability ratio ($q_{high\ year}/q_{other\ years}$; hereafter "*q*-ratio") scenarios examined were: 1.2, 1.3, 1.4, 1.5, 1.7, and 2.0; exploitation rate was held constant at 0.1, 0.3, or 0.5. The number of years in each simulated dataset was 2, 3 or 5. In each simulation, survey data were simulated at least 1,000 times for each *q*-ratio.

Note that this simulation study favors the annual model because the violation of assumption only applies to the 1qIR model.

2.4 Example: southern rock lobster fishery

2.4.1. Data collection

The data used here originated from a rock lobster (*Jasus edwardsii*) population in southern Tasmania, Australia. Data were collected from two study sites near Maatsuyker Island (43.679 ^{o}S 146.267 ^{o}E ; 43.671 ^{o}S 146.205 ^{o}E) from 1992 to 2002. Survey and fishery-removal data were collected by, and provided courtesy of, the Tasmanian Aquaculture and Fisheries Institute (TAFI), in Taroona, Tasmania, Australia. Both survey and fishery data were collected at similar depths (40 to 80 m), similar locations (the 7F3 management area) and over the same time period (1992 to 2001).

Three fishery-independent surveys were performed each year and commercial harvest and effort data were documented for the time periods between the surveys. Surveys were performed during the first week of the fishing season (mid-October to early November), in mid-season (mid-March), and again during the final weeks of the season (mid-July to early September). The timing of the post-harvest survey varied the most because of irregular, early closures of the fishery or to bad weather (Frusher, 1997). Analyses were restricted to data that included only the first two surveys each year (and the fishery removal that occurred between these surveys), because of concerns the catchability of rock lobsters may change towards the end of the season (Ziegler et al., 2003; Ihde et al., 2006).

2.4.2. Model diagnostics

Model performance was evaluated on the strength of the relationship between estimated exploitation rate ($\hat{u}$) and the amount of effort (f_c; measured by the number of trap hauls) expended by the fishery. Exploitation rate is not directly proportional to fishery effort because $\hat{u}$ has an asymptote at 1.0 (100% removal). With no natural mortality,

$$u = 1 - e^{-F} \qquad (11)$$

where F is the instantaneous mortality per year due to fishing (based on the Baranov catch equation as described by Ricker, 1975). Natural mortality, M, for *Jasus edwardsii* is believed to be small, as estimates from tagging studies in Tasmania range from 0.10 – 0.12 yr^{-1} (Punt and Kennedy, 1997; Frusher and Hoenig, 2003). Therefore, ignoring M appears to be a reasonable approximation. F can be modeled as $q_c f_c$, where q_c is the catchability coefficient of the commercial fishing gear. The relationship between commercial effort and $\hat{u}$ can be linearized as:

$$-\log_e(1-\hat{u}) = \hat{F} = q_c f_c \quad . \qquad (12)$$

The relationship in Eq. (12), was evaluated by plotting transformed exploitation rate estimates against effort for each model. The y-intercept of the regression line should be near the origin, the slope should estimate q_c and the R-squared value should be close to unity. Model estimates were evaluated by these criteria. The estimated y-intercept of each model was tested with a t-test (as described in Zar 1996) to determine if each differed significantly from zero. Additionally, model estimates of q_c were compared to that predicted from the Baranov continuous catch equation (modified from Ricker, 1975), which includes natural mortality:

$$\hat{u} = \frac{q_c f_c}{q_c f_c + M}(1 - e^{(-M - q_c f_c)}) \ . \qquad (13)$$

For these computations, M was assumed to be 0.12 yr^{-1} (Frusher and Hoenig, 2003). The catch equation estimate of q_c, (Eq. 13), was calculated by minimizing the sum of squares using the Excel 'solver' function (Microsoft, 1999).

2.4.3. Accommodating problematic data

The annual model produces problematic results if pre- and post-harvest survey indices of abundance are close, or if the post-harvest survey index exceeds the pre-harvest index. However, the 1qIR method can be used to obtain a more reasonable estimate. A two-step process can be used. First, obtain an estimate of q from the 1qIR model fitted to the other years. Then, an estimate for the problem year can be obtained as either:

$$\hat{N} = \begin{cases} I_1 /(\hat{q} f_1) & \text{(14a)} \\ R + I_2 /(\hat{q} f_2) & \text{(14b)} \\ \dfrac{I_1 / f_1 + I_2 / f_2}{\hat{q}(f_1 + f_2)} & \text{(14c)} \end{cases}$$

Eq. (14a) or (14b) might be used if one suspects that survey 1 or 2 is valid, respectively, and the other survey is invalid due to a change in catchability. Eq. (14c) might be used if both surveys are believed valid, with the small or positive change in catch rate being due solely to sampling error. We suggest Eq. (14c) be used in any multiyear study to make estimates for any year in which the change in catch rate is small. Additionally, a large increase (or decrease) in estimated abundance from one year to the next ought to reflect strong (or weak) recruitment; if size composition data are available, this hypothesis may be evaluated. If the change in abundance does not appear consistent with recruitment information from size composition data, then Eq. (14) might be used.

3. RESULTS AND DISCUSSION

3.1 Simulation results

3.1.1. Model performance when catchability is constant

When there was no violation of the assumption of constant catchability, 1qIR estimates always had lower bias, greater precision, and lower root mean squared error than annual model estimates, and 1qIR could use a greater percentage of the data than could the annual method (Fig. 2.1). As more years were added to the dataset, 1qIR model results continued to improve in all performance measures.

Biases for abundance estimates of both models were always positive, but were consistently lower for 1qIR model estimates than for those of the annual model (Fig. 2.1a). Biases for catchability coefficient estimates of both models followed those of abundance closely (though without an increase at $u = 0.2$) (Fig. 2.2). These results were partly a result of our exclusion criteria, because negative abundance (and catchability coefficient) estimates were excluded from analysis. Bias was most severe for both models when exploitation rate was low, as would be expected if the removal were not large enough to cause a distinct change in the survey catch rate. Annual model bias for abundance increased sharply from exploitation rates of 0.1 to 0.2, and began to drop again when exploitation rate reached 0.3. Although bias was reduced for both models when 30% or more of the population was removed, the performance of the annual model remained poor relative to that of the 1qIR model. Biases of the abundance estimates of the annual model remained at least a third of the true abundance or more until 40% of the population was removed. Biases of 1qIR abundance estimates were consistently less than half that for the annual model at exploitation rates of 20% or more, with only 2 years of data. Further improvements in bias can be expected if survey q or f is increased, because maximum likelihood estimates are asymptotically unbiased. This expectation was verified in simulation (Fig. 2.3). When two years of survey data were simulated with a catchability coefficient ten times that of all other simulations (q = 0.001), bias was 5% or less at an exploitation rate of only 0.20.

Standard deviation and root mean squared error were always lower for 1qIR estimates than for annual model estimates. The percent standard deviation and percent RMSE of 1qIR estimates were 43% to 70% lower than annual model estimates when 20% or more of the population was removed, with only 2 years of data (Fig. 2.1b-c).

The 1qIR model estimates improved in all performance measures as more years of data were added, but annual model performance was unchanged, because annual model estimates are made separately for each year of data, and all years are simulated with the same parameters. With 3 years of data, the improvement of 1qIR estimates over that of the annual method was evident for all performance measures even when only 10% of the population was removed (Fig. 2.1). The greatest improvements in performance for the 1qIR model over that of the annual model were seen with 5 years of data at moderate exploitation rate (30%), when 1qIR estimates of bias, standard deviation, and RMSE were 10%, 13% and 13% of the corresponding annual model estimates, respectively.

The 1qIR model produced useful estimates more often than the annual model did (Fig. 2.1d). The relatively low estimates of bias, standard deviation, and RMSE of the annual model at $u = 0.1$, was an artifact of excluding a quarter of the estimates. All other performance indicators for the annual model deteriorated at higher exploitation rates ($u = 0.2$ or 0.3) as more estimates were included.

Our findings that the annual model performed poorly at low levels of exploitation are not new. Eberhardt (1982) predicted poor precision at low exploitation rate when he examined the properties of the annual IR model. Routledge (1989) also reported discouragingly wide confidence intervals when removals were low.

The imprecision of the annual model is due to a few, very large estimates that result when the post-season survey catch is similar to the pre-season survey catch. These infrequent, but very large estimates result in a skewed frequency distribution with an extremely long right tail (Chen et al., 1995). It was because of this extremely long right tail that Chen et al. (1998a) found the mean and variance to be unreliable indicators of the reliability of the model estimates. In this study, we avoided the frequency distributions of $\hat{N}$ with extremely long right tails reported by Chen et al. (1998a) by excluding simulations that produced estimates in excess of 100 times the known abundance. Consequently, we were able to employ statistics based on the mean estimate rather than the median. The problems with the IR methods were not hidden by the exclusion of extremely high estimates, however, because problems were accounted for in the statistics on the number of rejected estimates. Also, the exclusion criterion was applied to both the annual and the 1qIR model results. The 1qIR model performed better than the annual model, both because model estimates had lower bias and mean squared error and because 1qIR was able to accommodate more simulated data sets.

The mean abundance estimate was plotted against the mean catchability estimate for each five-year simulation performed, for both models (Fig. 2.4). The resulting bivariate plots demonstrated a substantial improvement in the precision of 1qIR estimates (n = 10,000) compared to those of the annual model (n = 9,673). Though some 1qIR model estimates of abundance were unreasonably large, all the estimates of this model were positive, while a large portion of annual model estimates were negative (infeasible), and more than 3% of annual estimates were infinite and had to be removed before calculating the mean estimate for each simulation. Though the precision of the estimates of both models improved substantially in simulations that had higher exploitation rates (Fig 2.4), mean abundance estimates of the 1qIR model were substantially less variable, and catchability coefficient estimates were moderately less variable than were similar estimates of the annual model at all exploitation rates tested.

3.1.2. Violations of the constant catchability assumption

The 1qIR model generally performed much better than the annual model when the catchability differed in one of the years analyzed (Figs. 2.5, 2.6, and 2.7). Relative patterns of abundance estimates for annual and 1qIR models were similar whether two (Fig. 2.5), three (Fig. 2.6) or five (Fig. 2.7) years were simulated. However, the most clearly defined trends are seen with five years of simulated data. Consequently, the five-year simulation comparison is discussed here. With five years of data, the estimates for the 1qIR model appeared robust to the violation until a 50% difference between catchabilities occurred, and 1qIR could always use a greater portion of the simulated data than could the annual model. In the four years with the same catchability (solid lines in Fig. 2.7), bias, standard deviation and root mean squared error in the 1qIR model were smaller than those of the annual model. Predictions for the 1qIR model suffered a penalty in bias, standard deviation and RMSE for the year that the catchability coefficient differed, but the penalty was generally moderate until the difference in catchabilities was 50% or more. The increased bias and variability in 1qIR estimates for the high-*q* year was expected because the catchability coefficient estimated for all years was wrong for the year catchability differed. Even so, the 1qIR model generally outperformed the annual model. With five years of data, the percent standard deviation of the annual model was less than that of the 1qIR model only once, at the highest level of exploitation rate simulated, when high-*q* year estimates were compared and catchabilities differed by a factor of 2 (Fig. 2.7 Cb).

Neither model performed well when exploitation level was low (u = 10%; Fig. 2.7A). The 1qIR model bias for the four constant-*q* years never exceeded 18%, and was less than half that of annual model bias. However, the 1qIR model bias of the high-*q* year estimates exceeded that of the annual model when there was a 50% difference in catchabilities. Annual model estimates for the high-*q* year trended toward worse performance as catchability increases at this low exploitation rate, whereas the opposite trend was observed for exploitation rates of 30% and 50%. We suspect the behavior at low exploitation rate is due to the extreme nature of the estimates when survey catches are similar in magnitude. With only 10% of the original population removed, there was much overlap in the frequency distributions of the survey catches. Though this resulted in about ¼ of annual estimates being excluded (Fig. 2.7Ad), fewer estimates were excluded as catchability increased in the high-*q* year. Accordingly, when fewer estimates were excluded, a greater number of very high estimates were retained with our exclusion criteria. Thus, the increasing trend in bias coincident with the increasing *q*-ratio for the annual model high-*q* year is likely an artifact of our exclusion criteria.

At a moderate exploitation rate (30%) with five years of data (Fig. 2.7B), the 1qIR model outperformed the annual model until there was a 50% difference in catchabilities. The percent bias of the 1qIR model was always less than 10% of the known abundance for the 4 years with the same catchability coefficient (Fig. 2.7Ba). Though the bias for the high-*q* year increased as the *q*-ratio violation grew more severe, the 1qIR model continued to outperform most annual model estimates until there was a 50% difference in catchabilities. The 1qIR percent standard deviation was low, and always less than half that of the annual model (Fig. 2.7Bb). 1qIR percent RMSE was much lower than that of the annual model, until catchability in the high-*q* year doubled the catchability of the other years. Even then, the only annual model RMSE to approximate that of the 1qIR model was from the high-*q* year (Fig. 2.7Bc).

When half the population was removed (Fig. 2.7C) both models generally performed well overall. Both models generally had low bias, while precision and root mean squared error improved relative to those estimates made with a 30% exploitation rate. These results were expected, as Eberhardt (1982) predicted satisfactory annual model performance when removals were large. Note that when catchability (and subsequently, when *qf*) was higher, the annual model results improved. In fact, when *q* was doubled, annual model percent RMSE was reduced by more than half. Eberhardt (1982) predicted that annual model performance would be unsatisfactory unless the proportion of the population seen in the survey (*qf*) was relatively large. Accordingly, at high exploitation rate, with high *q*, annual model performance sometimes surpassed that of the 1qIR model for the high-*q* year.

In all scenarios (Fig. 2.7 A,B,C), the 1qIR model estimates were usable more often than were annual model estimates. The 1qIR model excluded data about two-thirds less often than did the annual model when only 10% of the population was removed (percentages averaged over all years and all *q*-ratio scenarios were 8.5% and 23.6%, respectively). Moreover, the 1qIR model never excluded data when exploitation rate was 30% or greater, but the annual model continued to fail a small percentage of the time until half of the population was removed (Fig. 2.7d).

3.1.3. Evaluating the Poisson assumption

The Poisson assumption could result in overly optimistic simulated survey variances when survey catches are large (Table 2.1). Since survey catches were Poisson random variables, the coefficient of variation (cv) of the survey catch decreases as the mean catch of the surveys increase, and *vice versa*:

$$\text{cv} = \frac{\sigma_P}{\mu_P} = \frac{\sqrt{\mu_P}}{\mu_P} = \frac{1}{\sqrt{\mu_P}} \qquad (15)$$

where σ_P = standard deviation of survey catch, and μ_P = mean survey catch. Consequently, the variation of simulated surveys could have been unreasonably low for data modeled on a potentially aggregated fisheries resource like that of rock lobster.

A model that assumes a normal distribution can have any cv without regard to the size of the mean, but use of a normal assumption introduces at least one more parameter to estimate (depending on the assumptions made about the σ parameter). The choice of the best distribution for the model depends on the distribution of the data.

3.2 Results for southern rock lobster example

3.2.1. Comparison of model performance

1qIR model predictions were less variable than those of the annual model and appeared more reasonable (Fig. 2.8). The abundance estimate of the annual model for 1996 was unreasonably high, with abundance seemingly increasing by a factor of six in one year and then declining the next year back to the usual level. The high abundance estimate was accompanied by an extremely low estimate of catchability, and an exploitation rate less than 10%. The low exploitation rate is not credible because fishing effort in 1996 was not unusually low. These extreme annual model predictions were the result of a relatively poor catch in the pre-harvest survey of similar magnitude to the post-harvest survey (Table 2.2). Though the pre-harvest catch rate of 1996 was the lowest observed in the 9-year dataset, similar catch rates were seen in two other years (1993, 2000). Annual model estimates were more reasonable in those years because those years also had low post-harvest catch rates. Extreme estimates are expected when pre- and post-harvest survey catch rates are similar in magnitude, and this example illustrates the instability of annual model estimates when this situation arises. In contrast, 1qIR model estimates were less variable overall (Fig. 2.8), and the 1996 estimate appears reasonable compared to estimates of surrounding years.

We assumed that the pre-harvest catch rate in 1996 was problematic for use with the annual model. Accordingly, we used 1qIR to estimate a common q for all years except 1996, and then applied Eq. 14b to attain replacement estimates for the problematic year. The overall q estimated without the problematic year was slightly higher than that estimated using all years with the 1qIR model (Fig. 2.8). Estimates of abundance and exploitation rate, however, were similar to those estimated with 1qIR, and appear reasonable.

Estimates for the 1qIR model suggest that this population was relatively stable, and that exploitation rate was very high from 1992 to 1994, but has generally been declining since 1994 when the statewide catch was reported to be at its lowest level (Frusher et al., 2003). Similar trends were hard to detect in annual model estimates because they were so variable; however, the trends predicted by 1qIR appear reasonable. In 1997, Frusher described this stock as highly exploited, with a biomass of only 5% of the virgin biomass, and nearly 90% of the exploited stock composed of new recruits. The next year (1998), the fishery adopted an individual transferable quota (ITQ) management system to reduce high exploitation rates statewide. Frusher et al. (2003) report that even before the ITQ system was established, a trend had begun for fishers to fish more in winter (after the mid-March survey), in shallower water, and away from home ports, to target higher-priced, premium-quality lobsters. They further suggest that the ITQ system has amplified these trends. If these trends are real and continue until 1998, one would expect the gradual decline described by 1qIR estimates from 1994 to 1997 because, as increasingly more effort was being expended after the mid-March survey, less exploitation would be accounted for in the model estimates. Exploitation rate estimates of the 1qIR model also support the notion that these trends have been amplified since ITQ was established. Exploitation rate estimates of the multiple-year model were consistently under 50% from 1998 to 2000, 42% lower than the mean exploitation rate of the first 6 years (1992 – 1997).

T-tests of the intercepts of the regression lines did not differ significantly from zero for either model, but diagnostic plots of the regression lines, and the magnitude of R^2 values revealed that the 1qIR model performed better than the annual model (Fig. 2.9). No significant difference was found between the y-intercept and 0 for either model (1qIR: $P > |t| = 0.6593$; annual: $P > |t| = 0.2459$), so a model could not be chosen based on these test statistics. However, the 1qIR model had a y-intercept for the regression line closer to the origin (-0.08) than did the annual model estimate (-0.47). And commercial fishing effort explained much more of the variation of 1qIR estimates ($R^2 = 0.8345$) than it did for annual model estimates ($R^2 = 0.6602$). The slope estimate of the commercial catchability coefficient for the 1qIR model ($\hat{q}_c = 3.791 \times 10^{-5}$) was similar to that derived from the catch equation ($\hat{q}_c = 3.708 \times 10^{-5}$). The 1qIR estimate of q_c only differed from the catch equation estimate by 2%, whereas the slope estimate of q_c from the annual model (5.166×10^{-5}) differed by 39%.

3.2.2. The assumption of constant catchability for rock lobster data

Recent work has suggested that the catchability of *Jasus edwardsii* is complex and varies seasonally with both sex and size of the lobster (Ziegler et al., 2002; Ihde et al., 2006), and that changes in catchability are important to take into account when modeling life history parameters of this species (Frusher and Hoenig, 2003). Those studies, however, all concerned more temperate populations of this species. Ziegler *et al.* (2003) presented evidence that the catchability for the southern population described here is typically stable from November to March. Thus, our use of IR models, which assume constant catchability between the first (November) and second (March) surveys, appears justified in this region of Tasmania.

4. CONCLUSION

The 1qIR model consistently outperformed the annual method when all assumptions were met, and was robust to violations of the assumption that the catchability coefficient remains constant among years until a 50% change in catchabilities occurred. Model performance of the 1qIR model consistently improved as more years were added to the dataset. Estimates of the 1qIR model were much less variable than annual model estimates, both in simulation and in application to data from a southern rock lobster fishery in Tasmania, Australia. The 1qIR model offers a useful method to estimate abundance and exploitation rate in many situations where annual model estimates prove too variable to be useful. However, if the constant catchability assumption is thought to be violated and the difference between catchabilities is thought to exceed 50%, or if both exploitation rate and *qf* are high, simulation results suggest that use of the annual model may be preferable.

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TABLE 2.1

Ranges of the coefficient of variation observed for the pre-harvest survey and the post-harvest survey for each simulation performed, and the number of simulations (*n*) performed for each scenario. (Section numbers) correspond to descriptions of survey parameters on which each simulation was based.

Simulation	*n*	Pre-harvest survey cv	Post-harvest survey cv
Exploitation rate variation			
(*Section 2.3.1.)*			
1qIR model: 2 years	2,000	9.9% - 10.0%	10.4% - 13.9%
3 years	2,000	9.9% - 10.1%	10.4% - 14.1%
Both models: 5 years	2,000	9.8% - 10.1%	10.4% - 14.4%
Catchability varies			
(*Section 2.3.2.*)			
1qIR model: $u = 0.1$	1,000	9.8% - 22.7%	10.3% - 23.0%
$u = 0.3$	1,000	9.8% - 22.7%	11.6% - 23.4%
$u = 0.5$	1,000	9.8% - 22.7%	13.8% - 24.0%
Annual model: $u = 0.1$	10,000	10.0% - 22.8%	10.5% - 22.9%
$u = 0.3$	10,000	10.0% - 22.8%	11.9% - 23.4%
$u = 0.5$	10,000	10.0% - 22.8%	14.1% - 24.2%

TABLE 2.2

Survey catch rates, commercial removals, and commercial effort (number of pot-lifts) for a southern rock lobster fishery in Tasmania, Australia (management area 7F3), near Maatsuyker Island. The fishing season runs from mid or late October to August or September, so the "fished year" spans 2 calendar years. Scientific surveys were conducted the first week of commercial harvest, and again in mid-season (mid March). Commercial removal and effort data correspond to time periods between the first 2 surveys.

	Fished year								
	1992-1993	1993-1994	1994-1995	1995-1996	1996-1997	1997-1998	1998-1999	2000-2001	2001-2002
Pre-harvest survey	1.55	0.86	1.84	1.87	0.85	1.73	2.35	0.90	2.1
Post-harvest survey	0.39	0.40	0.33	0.90	0.79	0.37	1.48	0.56	1.58
Removals (kg)	34095	22770	39238	40311	20277	30497	26052	15284	16968
Effort	38859	25726	34599	31252	20815	29487	18134	15507	11572

FIGURE 2.1

Comparisons of model performance between the annual and 1qIR models when the assumption of constant catchability is not violated. Performance indicators are (a) bias, (b) standard deviation, (c) square root of mean squared error (RMSE) of model estimates and (d) the percentage of unusable simulations over all years simulated. Performance indicators are expressed as a percentage of the known abundance (1,000,000), except (d). Scenarios differ in the exploitation rate (u = 0.1, 0.2, 0.3, 0.4, 0.5) on the simulated population. Annual model plots are solid lines with open circles. Each annual model scenario represents a weighted mean of usable data from 5 years of 2000 simulated datasets, because the annual model estimates are made separately for each year of data, and all years are simulations generated with the same parameters. 1qIR plots are for 2 years (dash-dot lines), 3 years (dashed lines), and 5 years (solid line). Each scenario for the 1qIR model represents the mean of usable estimates from 2000 sets of simulated data. Dotted lines indicate 10% of actual abundance, and are included for reference.

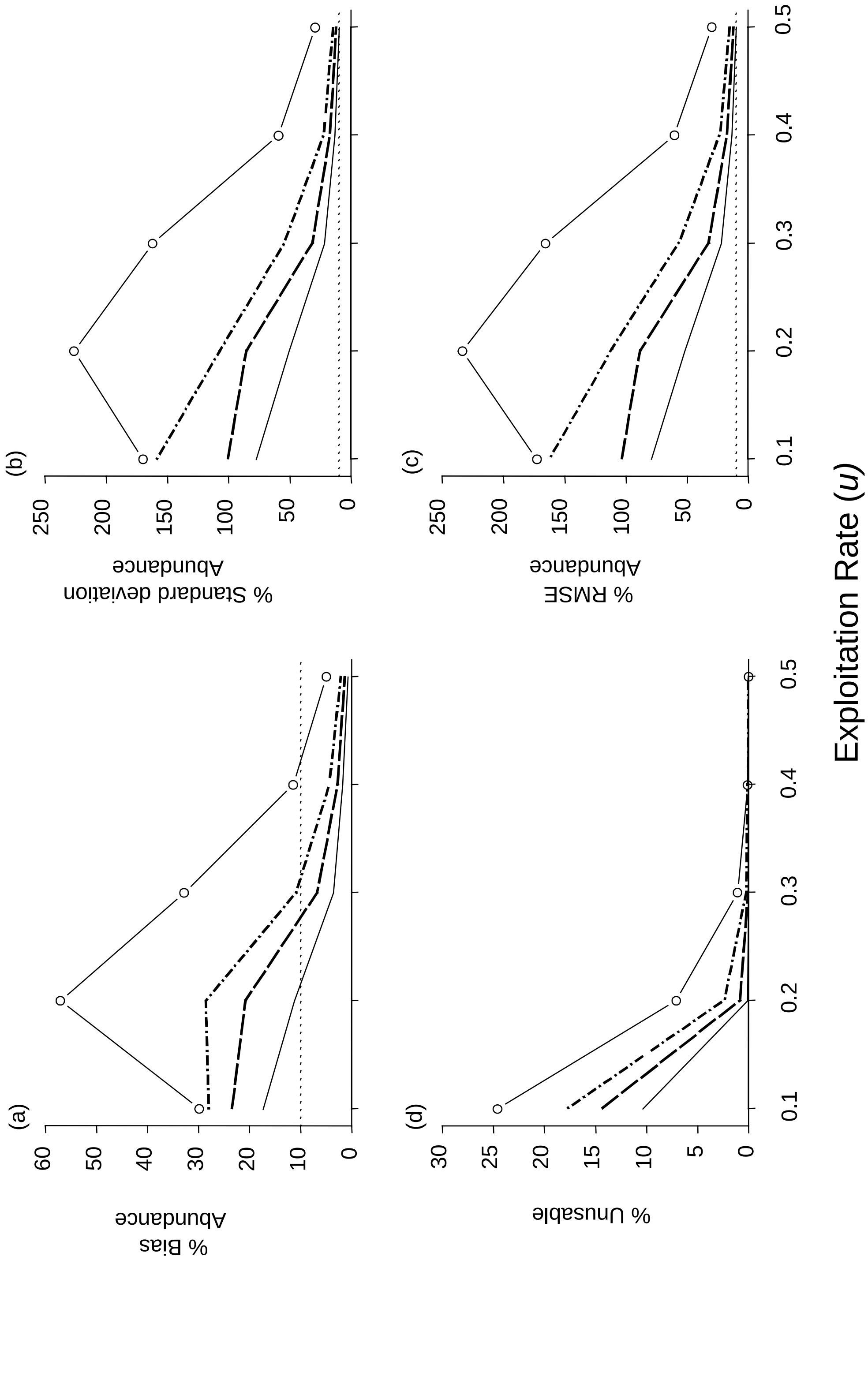
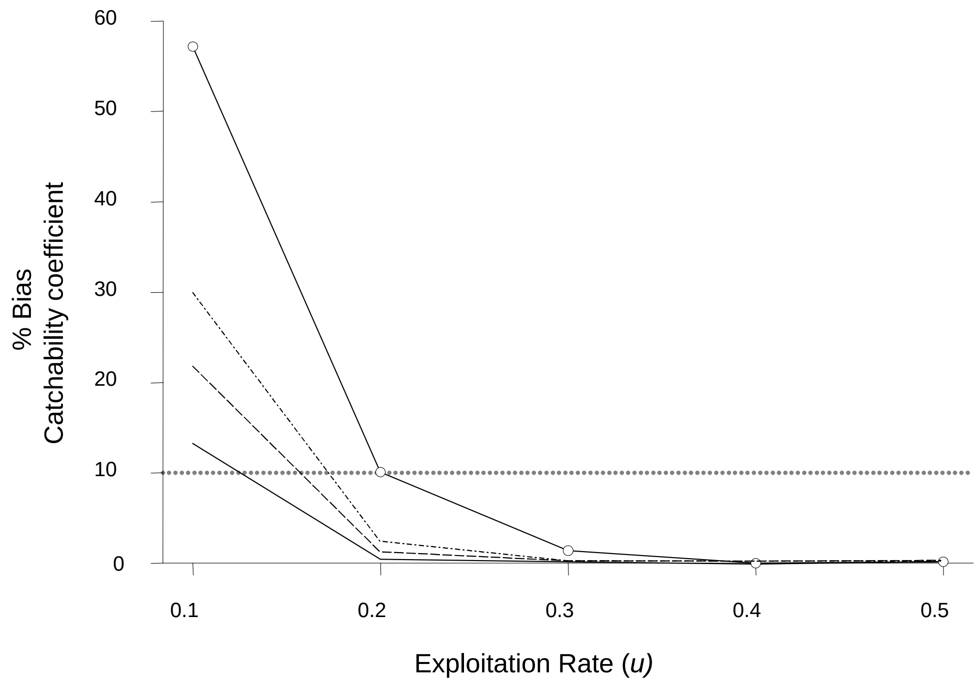
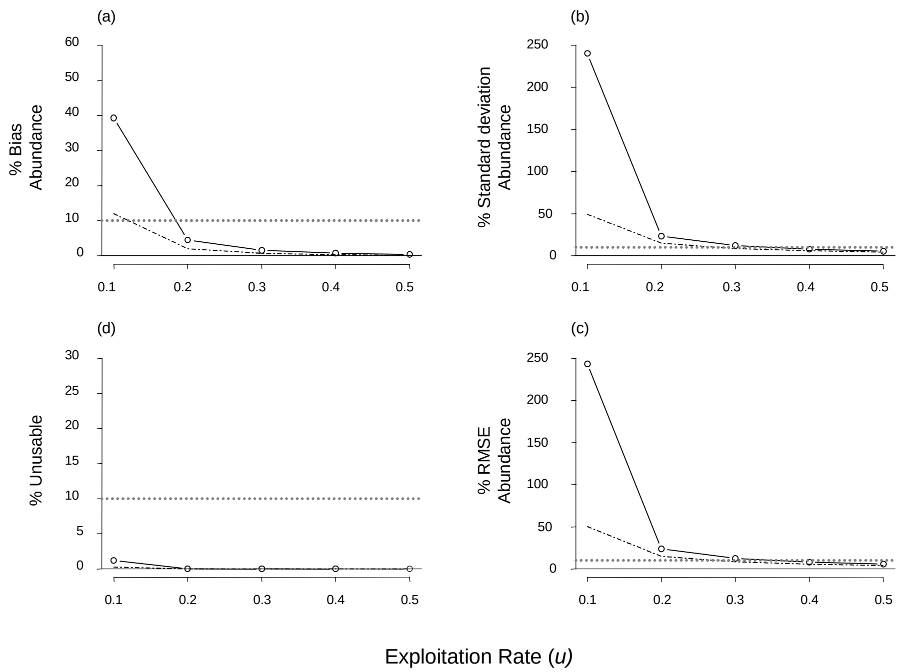

(a)
% Bias
Abundance
(b)
% Standard deviation
Abundance
(c)
% RMSE
Abundance
(d)
% Unusable
Exploitation Rate (u)

FIGURE 2.2



Comparison of bias in catchability coefficient estimates of the annual and 1qIR models when the assumption of constant catchability is not violated. Bias is expressed as a percentage of the known survey catchability coefficient (0.0001). Scenarios differ in the exploitation rate (*u* = 0.1, 0.2, 0.3, 0.4, 0.5) on the simulated population. Annual model plots are solid lines with open circles. Each annual model scenario represents a weighted mean of usable data from 5 years of 2000 simulated datasets, because the annual model estimates are made separately for each year of data, and all years are simulations generated with the same parameters. 1qIR plots are for 2 years (dash-dot lines), 3 years (dashed lines), and 5 years (solid line). Each scenario for the 1qIR model represents the mean of usable estimates from 2000 sets of simulated data. Dotted line indicates 10% of actual abundance, and is included for reference.

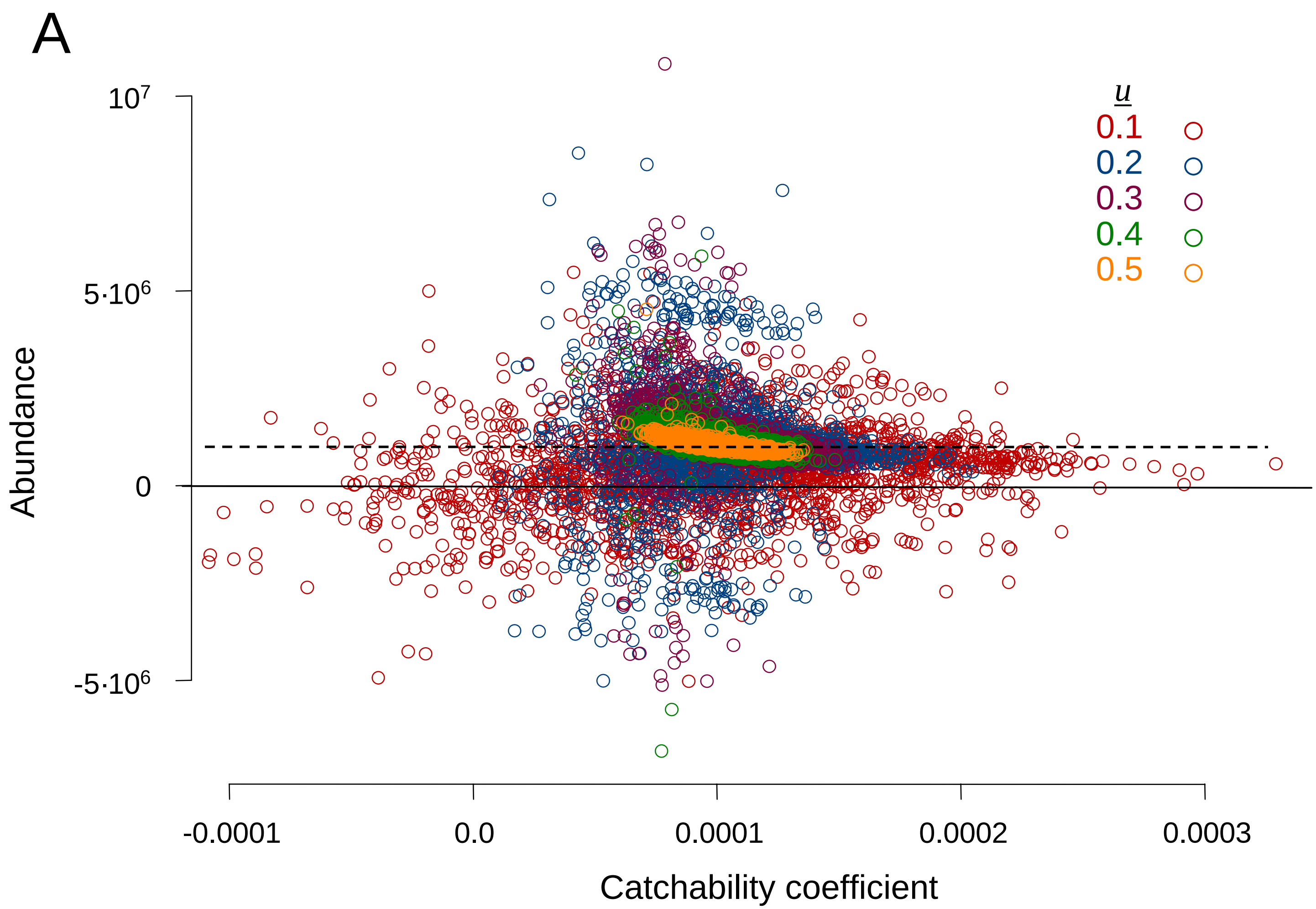
FIGURE 2.3

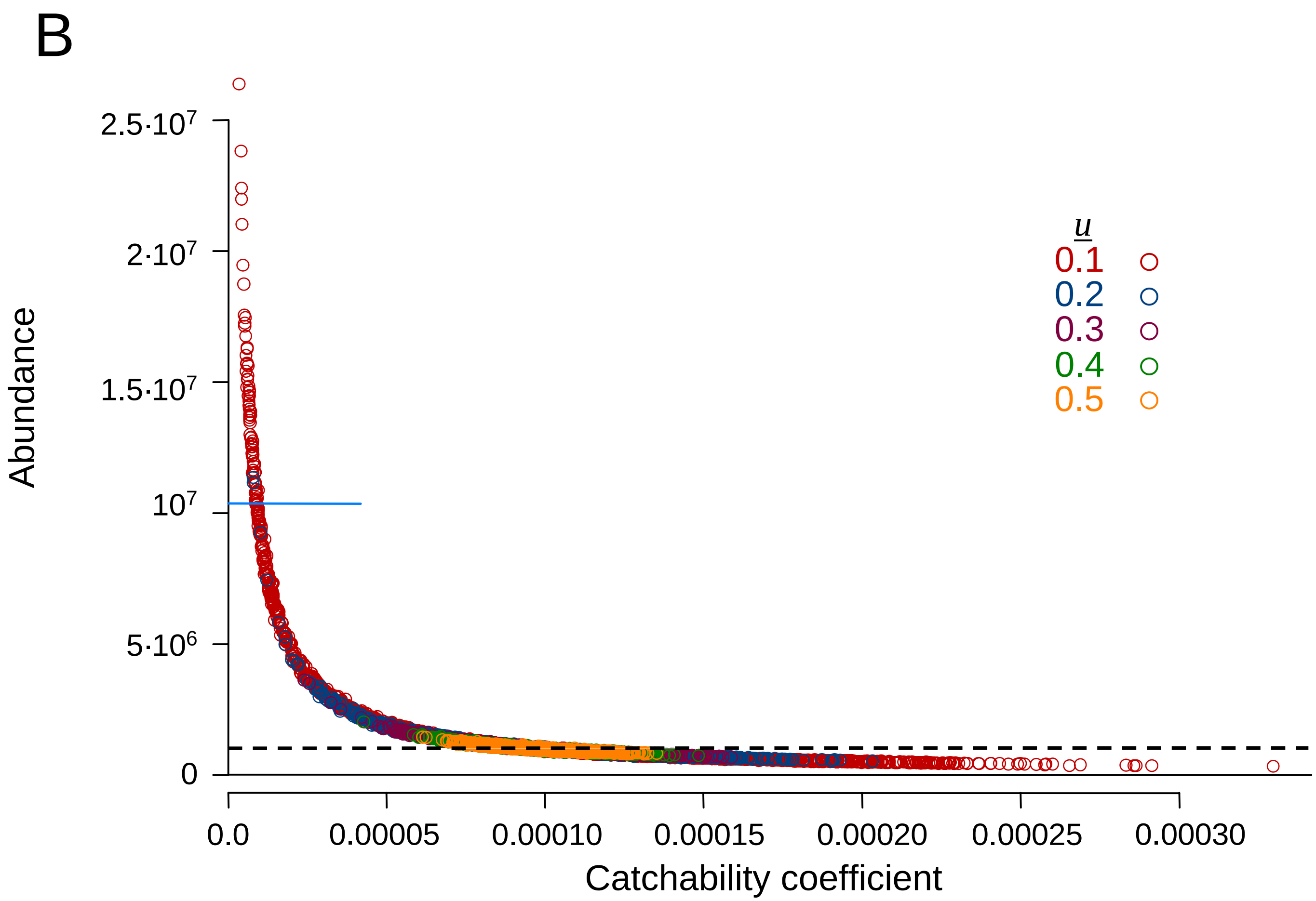


Improvement of model performance when *qf* product is higher (*qf* = 0.001) than that of other simulations discussed in text. Comparisons of model performance between the annual and 1qIR models when the assumption of constant catchability is not violated. Plots are based on two years of simulated data. Performance indicators are (a) bias, (b) standard deviation, (c) root mean squared error (RMSE) of model estimates and (d) the percentage of unusable simulations over all years simulated. Scenarios differ in the exploitation rate (*u* = 0.1, 0.2, 0.3, 0.4, 0.5) on the simulated population. Each annual model scenario (solid lines, open circles) represents a weighted mean of usable data from 2000 simulated datasets, because the annual model estimates are made separately for each year of data, and all years are simulations generated with the same parameters. Each scenario for the 1qIR model (dash-dot lines) represents the mean of usable estimates from 2000 sets of simulated data. Dotted lines indicate 10% of actual abundance, and are included for reference.

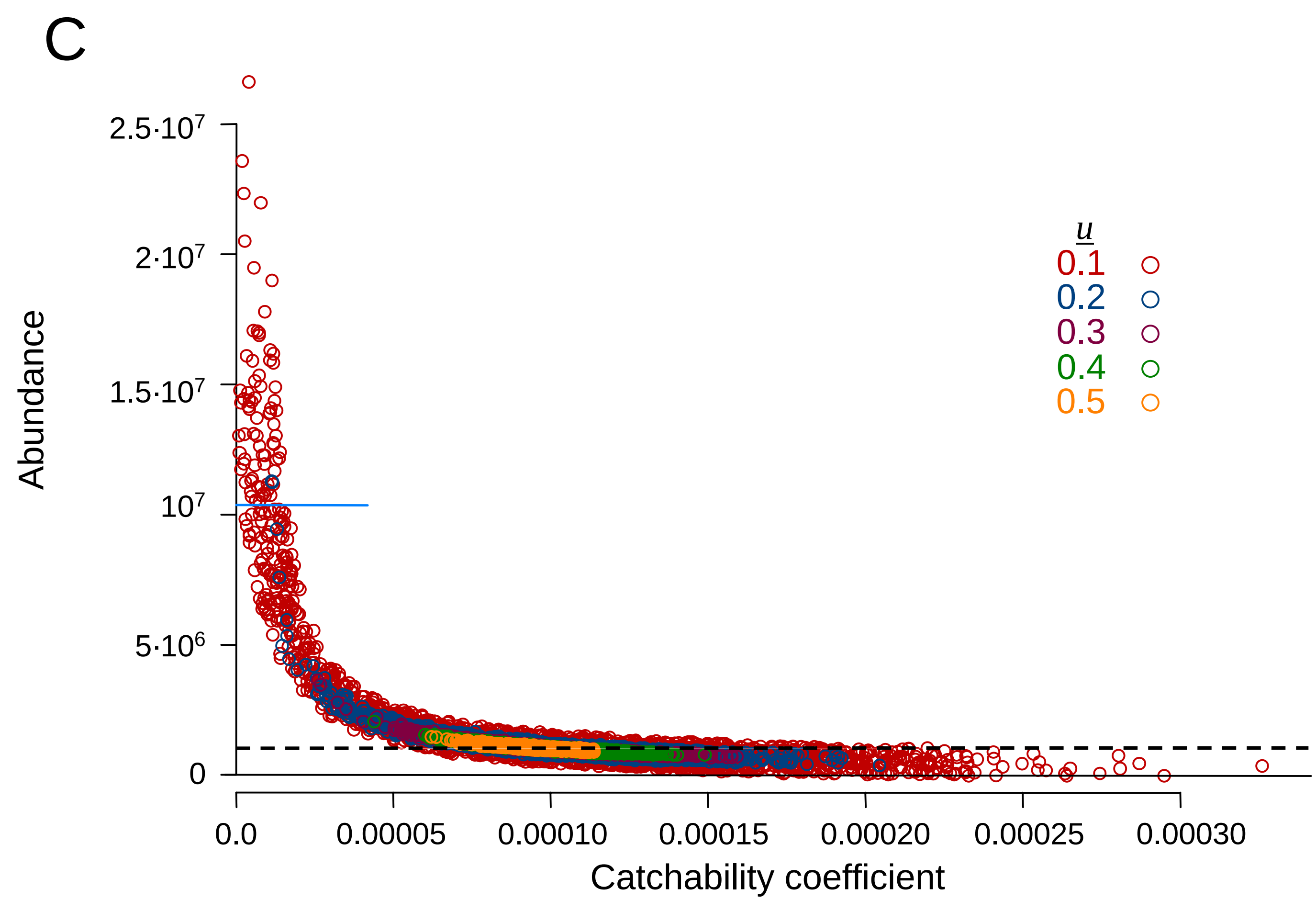
FIGURE 2.4

Bivariate plots for (A) annual model and (B, C) 1qIR model estimates of abundance and catchability coefficient. Catchability coefficient was constant between surveys and among years for the simulated survey data fit to both models. Each open circle represents the mean of five years of data from one simulation (A and C are jittered). Infinite estimates were removed prior to the calculation of the mean (necessary only for annual model estimates). 2,000 simulations were performed at each exploitation rate (*u*); and, estimates from each exploitation rate simulation are plotted in a separate color. The 1qIR model mean estimates were all restricted to the quadrant I (both variables were positive), but annual model estimates occurred in all four quadrants. Dashed line is true abundance. The light blue line in (B) and (C) represents the maximum 1qIR estimate made without a convergence error.


A
Abundance
10^7
$5\cdot10^6$
0
$-5\cdot10^6$
-0.0001
0.0
0.0001
0.0002
0.0003
Catchability coefficient
u
0.1
0.2
0.3
0.4
0.5



B
Abundance
2.5·10^7
2·10^7
1.5·10^7
10^7
5·10^6
0
u
0.1
0.2
0.3
0.4
0.5
0.0
0.00005
0.00010
0.00015
0.00020
0.00025
0.00030
Catchability coefficient



C
Abundance
2.5·10^7
2·10^7
1.5·10^7
10^7
5·10^6
0
0.0
0.00005
0.00010
0.00015
0.00020
0.00025
0.00030
Catchability coefficient
u
0.1
0.2
0.3
0.4
0.5

FIGURE 2.5

Comparisons of model performance between the annual and 1qIR models with 2 years of simulated data. Performance indicators are abundance estimate: (a) bias, (b) standard deviation, (c) square root of mean squared error (RMSE) and (d) the percentage of unusable simulations over all years simulated (dash-dot lines). Performance indicators are expressed as a percentage of the known abundance (1,000,000), except (d). Model comparisons are made at three exploitation rates: (A) 10%, (B) 30%, and (C) 50%. The catchability coefficient (q) of one year is higher (dashed line) than that of the other year (solid line) in each scenario of simulated data. The 7 scenarios differed by the ratio of catchability coefficients ($q_{high\ year}/q_{other\ year}$ = 1.0, 1.2, 1.3, 1.4, 1.5, 1.7, 2.0). Each 1qIR model scenario represents the usable data from 1,000 sets of simulations. Each line in annual model plots represents usable data from 1,000 simulations for each scenario simulated. Dotted lines indicate 0 abundance.

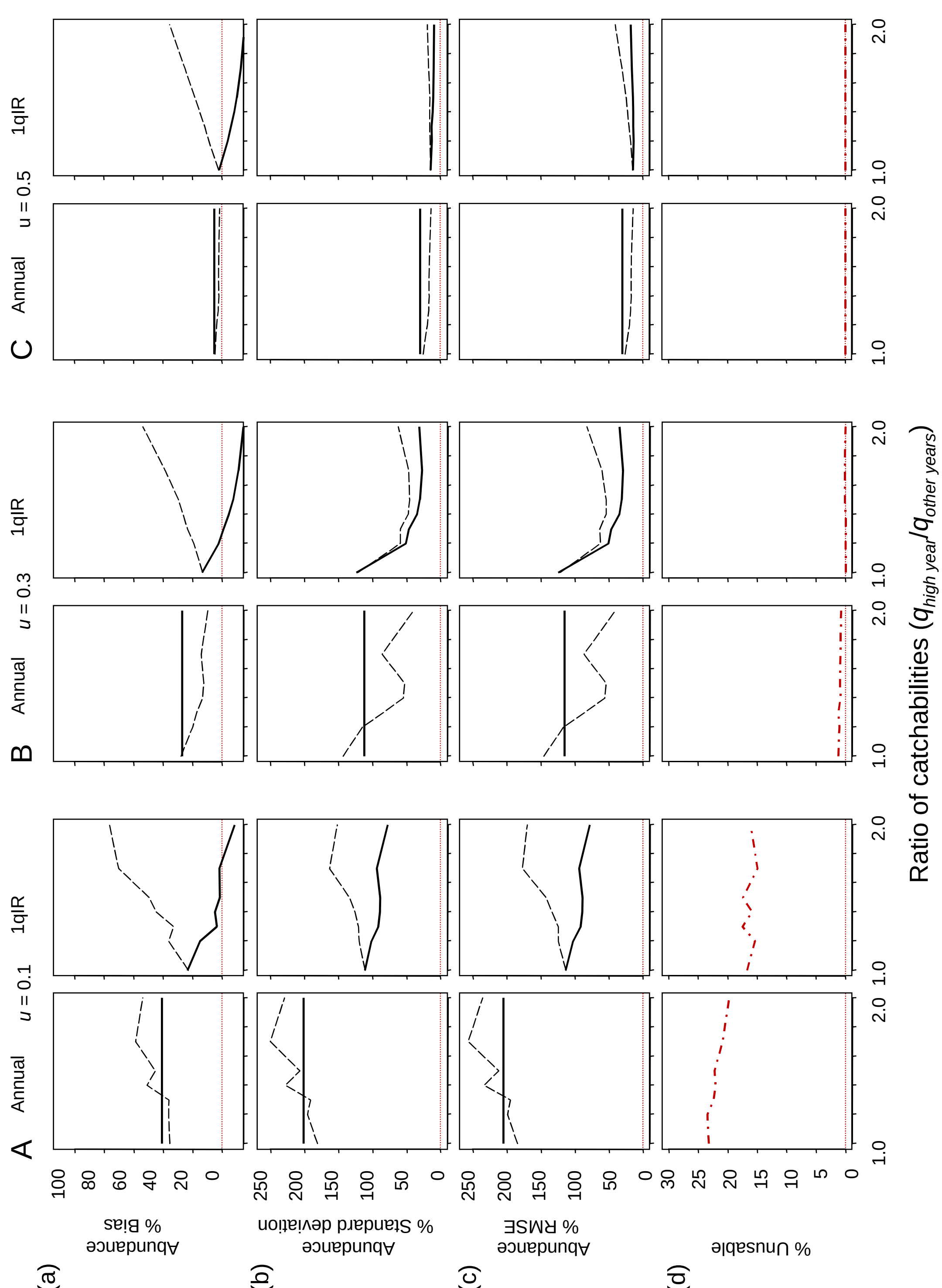

A
B
C
Annual
1qIR
u = 0.1
u = 0.3
u = 0.5
(a)
(b)
(c)
(d)
Abundance
% Bias
Abundance
% Standard deviation
Abundance
% RMSE
% Unusable
Ratio of catchabilities ($q_{high\ year}/q_{other\ years}$)

FIGURE 2.6

Comparisons of model performance between the annual and 1qIR models with 3 years of simulated data. Performance indicators are abundance estimate: (a) bias, (b) standard deviation, (c) square root of mean squared error (RMSE) and (d) the percentage of unusable simulations over all years simulated (dash-dot lines). Performance indicators are expressed as a percentage of the known abundance (1,000,000), except (d). Model comparisons are made at three exploitation rates: (A) 10%, (B) 30%, and (C) 50%. The catchability coefficient (q) of one year is higher (dashed line) than that of the other 2 years (solid line) in each scenario of simulated data. The 7 scenarios differed by the ratio of catchability coefficients ($q_{high\ year}/q_{other\ years}$ = 1.0, 1.2, 1.3, 1.4, 1.5, 1.7, 2.0). Each 1qIR model scenario represents the usable data from 1,000 sets of simulations. The solid line in 1qIR model plots represents the mean of 2 years of estimates, and the dashed line represents one year in which q is higher than in other years. Annual model plots represent usable data from 3,000 simulations for each scenario simulated: solid lines are weighted means of up to 2,000 simulations; dashed lines represent up to 1,000 simulations for each scenario plotted. Dotted lines indicate 0 abundance.

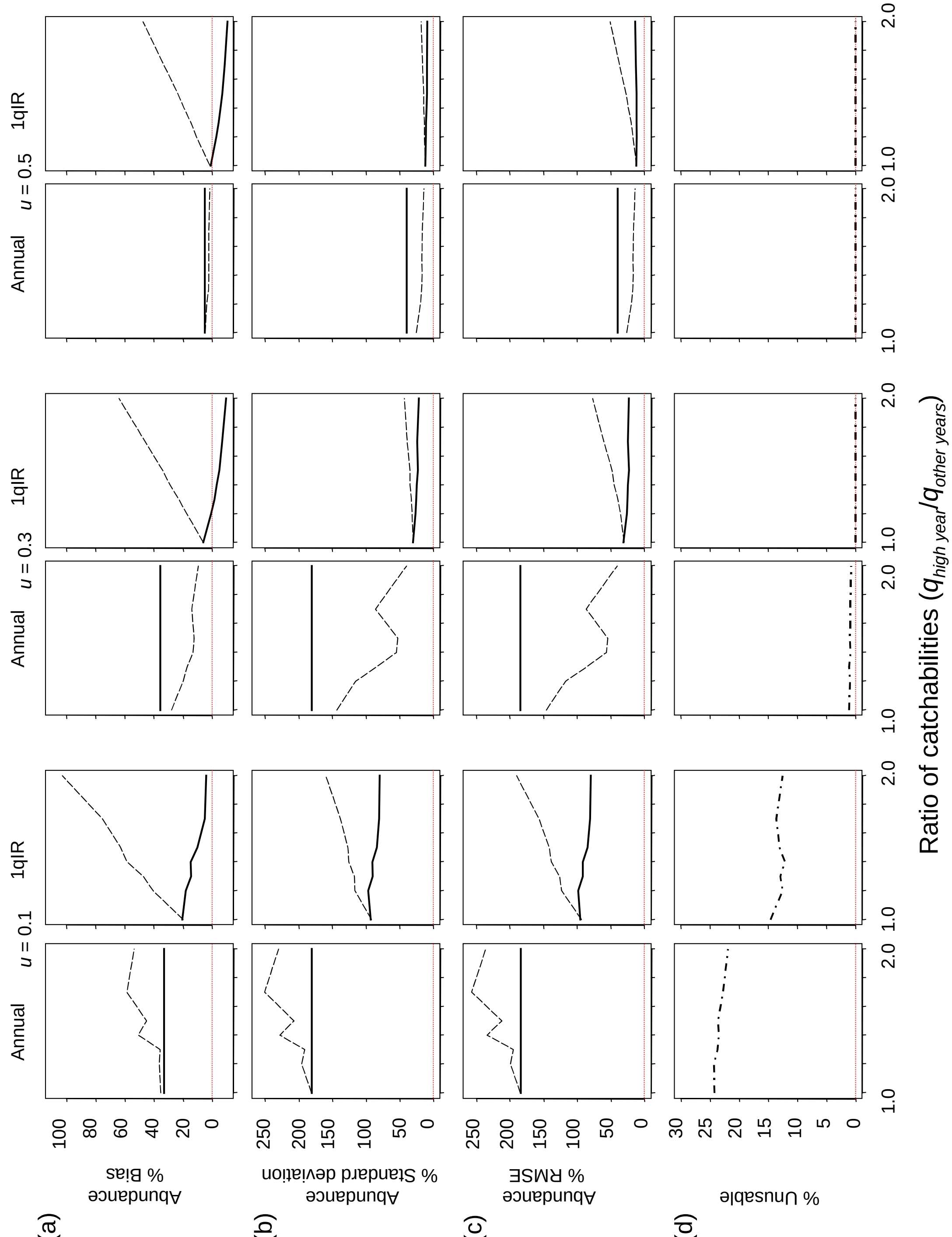

Annual
u = 0.1
1qIR
Annual
u = 0.3
1qIR
Annual
u = 0.5
1qIR
(a)
Abundance
% Bias
(b)
Abundance
% Standard deviation
(c)
Abundance
% RMSE
(d)
% Unusable
Ratio of catchabilities (q high year/q other years)

FIGURE 2.7

Comparisons of model performance between the annual and 1qIR models with 5 years of simulated data. Performance indicators are abundance estimate: (a) bias, (b) standard deviation, (c) square root of mean squared error (RMSE) and (d) the percentage of unusable simulations over all years simulated (dash-dot lines). Performance indicators are expressed as a percentage of the known abundance (1,000,000), except (d). Model comparisons are made at three exploitation rates: (A) 10%, (B) 30%, and (C) 50%. The catchability coefficient (*q*) of one year is higher (dashed line) than that of the other 4 years (solid line) in each scenario of simulated data. The 7 scenarios differed by the ratio of catchability coefficients ($q_{high\ year}/q_{other\ years}$ = 1.0, 1.2, 1.3, 1.4, 1.5, 1.7, 2.0). Each 1qIR model scenario represents the usable data from 1,000 sets of simulations. The solid line in 1qIR model plots represents the mean of 4 years of estimates, and the dashed line represents one year in which *q* is higher than in other years. Annual model plots represent usable data from 50,000 simulations for each scenario simulated: solid lines are weighted means of up to 40,000 simulations; dashed lines represent up to 10,000 simulations for each scenario plotted. Dotted lines indicate 0 abundance.

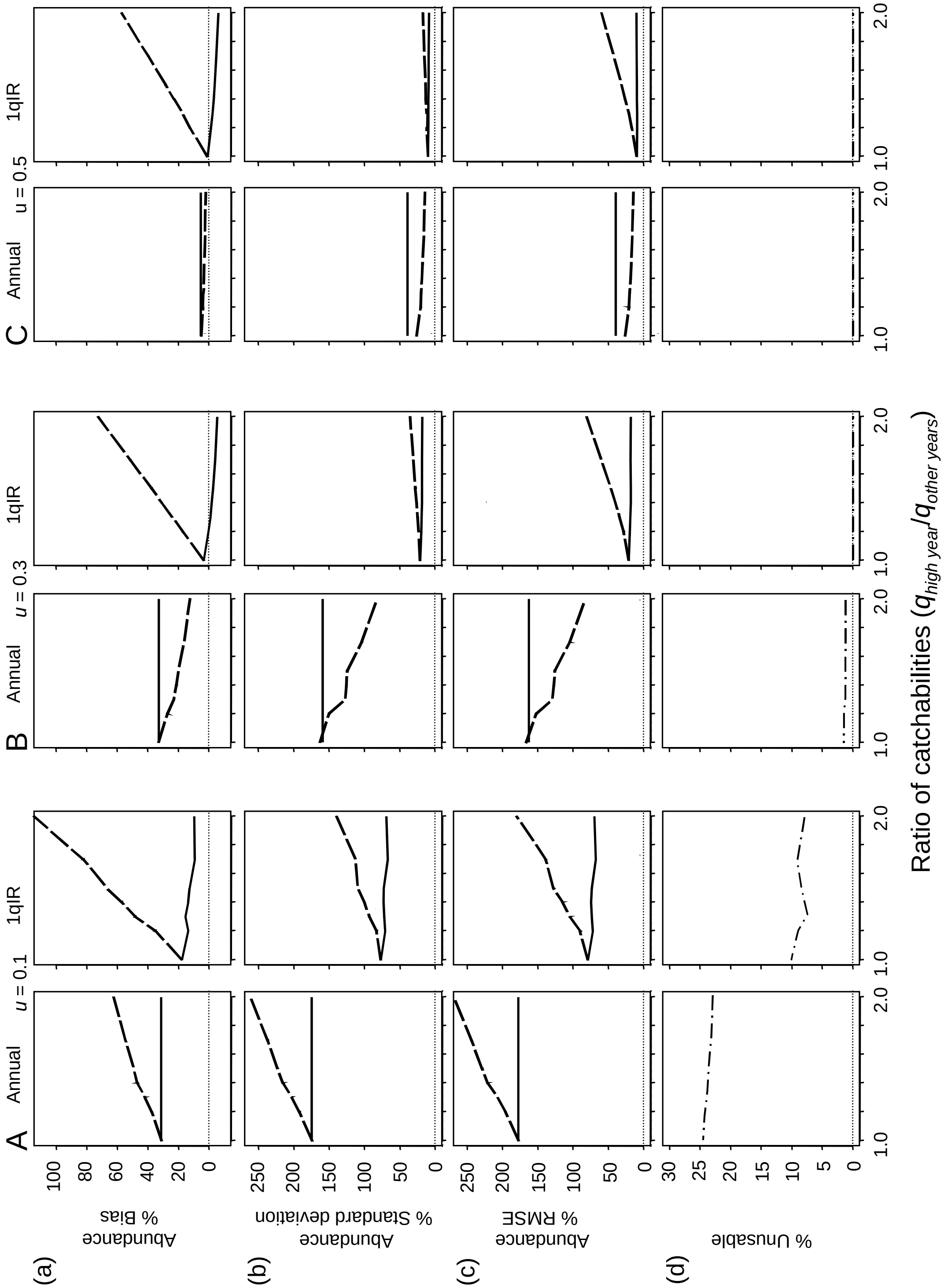
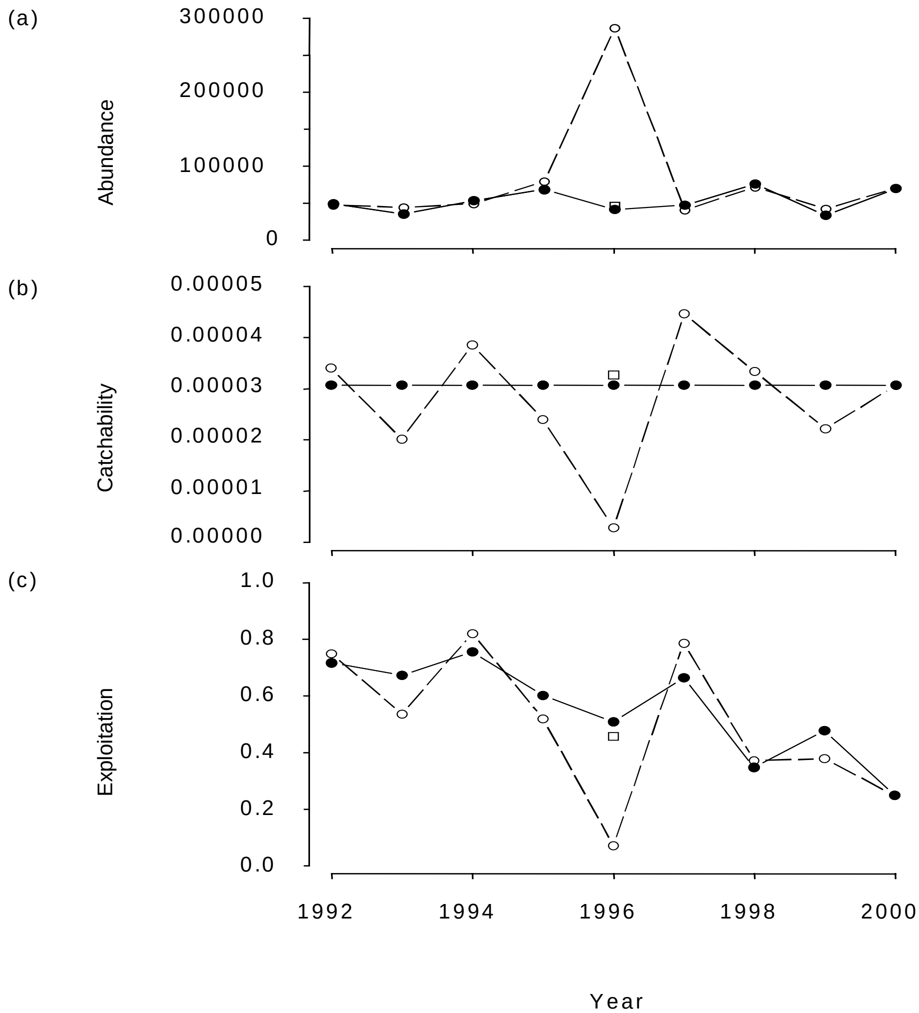
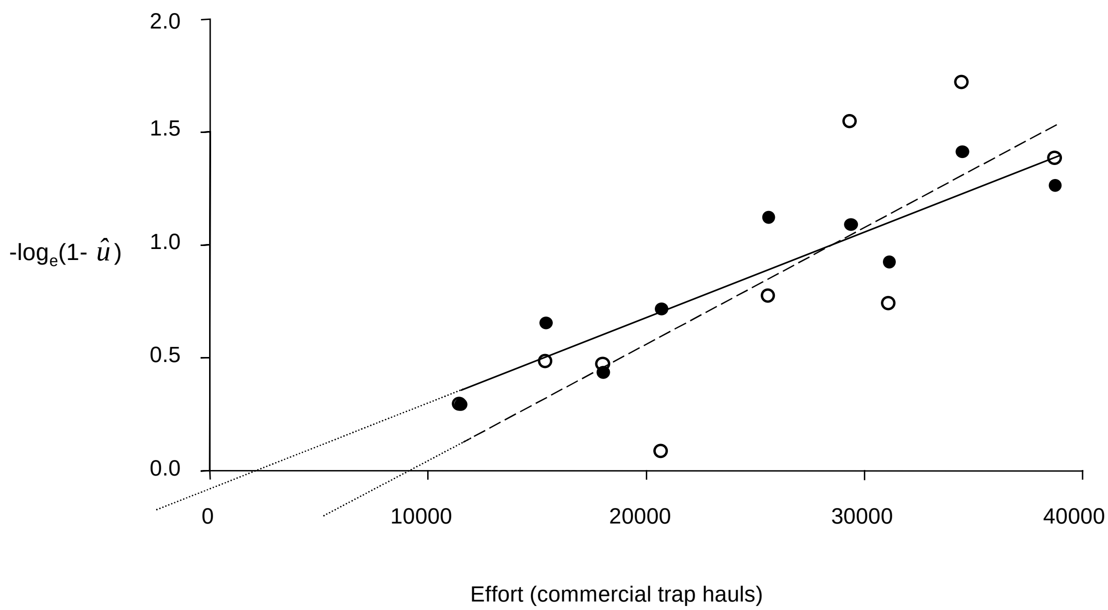

A
B
C
u = 0.1
u = 0.3
u = 0.5
Annual
1qIR
(a)
Abundance
% Bias
(b)
Abundance
% Standard deviation
(c)
Abundance
% RMSE
(d)
% Unusable
Ratio of catchabilities ($q_{high\ year}/q_{other\ years}$)

FIGURE 2.8



A comparison of model estimates of (a) abundance, (b) survey gear catchability, and (c) exploitation rate for southern rock lobster in southern Tasmania, Australia. Open circles denote the annual model estimates; filled circles are the 1qIR estimates. The open squares indicate replacement estimates from the application of Eq. (14b) to the data for 1996.

FIGURE 2.9



Diagnostic plots exploring the relationship between estimated exploitation rate and fishing effort in the annual model (open circles, dashed line), and 1qIR model (filled circles, solid line). Y-axis is the quantity that relates exploitation rate (*u*) to commercial effort (measured in the number of trap hauls performed). The equations for the regression lines, and associated R-squared values are annual model: $-\log_e(1-\hat{u}) =$ 5.166 x 10^{-5} x effort - 0.4713 (R^2 = 0.66); 1qIR model: $-\log_e(1-\hat{u})$ = 3.791 x 10^{-5} x effort - 0.07801 (R^2 = 0.83). Dotted line extensions to the regression lines are included for reference. Model estimates of commercial catchability coefficient correspond to the slopes of the regression lines.

Chapter 3

An index-removal abundance estimator that allows for seasonal change in catchability, with application to rock lobster

ABSTRACT

The index-removal method provides estimates of abundance, exploitation rate and catchability coefficient. Estimates of the original method had suffered from poor precision. Recent work has improved the precision of model estimates; however, the method still includes the strong assumption of constant survey catchability. This assumption is not tenable in many fisheries. This work introduces a new model, 2qIR, that allows catchability to differ between surveys of the same year. The 2qIR model requires that at least two years of data be collected, and that there is some contrast in exploitation rates between at least two years of the dataset. The model also assumes that survey-specific catchabilities remain constant among years. The 2qIR model was tested by Monte Carlo simulation, and then applied to fishery data from a southern rock lobster (*Jasus edwardsii*) population in Tasmania.

Three types of simulations were performed. First, the effect of exploitation rate (u) on model performance was tested. Second, performance was tested over a range of contrasts in survey catchability. Third, the effect of increasing the number of years in a dataset was examined.

The 2qIR model estimates were always accurate and precise when there was moderate contrast in exploitation rates between two years of data (i.e., $|u_1 - u_2|$ was at least 0.3), regardless of the degree of contrast between survey catchability coefficients. Annual model estimates, however, were only accurate and precise when catchability coefficients were the same, or when u was extreme (0.7 or more). The 2qIR model worked well within the tested range of contrasts between survey catchabilities. Catchability ratios (q_2/q_1) tested ranged from 0.1 to 10, but the model worked best at catchability ratios greater than 0.3. In comparison, annual model estimates were only accurate and precise in a narrow range of catchability ratios from 0.9 to 1.1. The 2qIR model performance improved slightly when a third year was added to the dataset, but performance was similar with three or five years of data. In all types of simulations, 2qIR model estimates were useful a greater proportion of the time than were annual model estimates. The 2qIR model produced reasonable results when applied to data from a southern rock lobster population in Tasmania. Parameter estimates of the 2qIR model were similar whether model estimates were made using data from surveys indices with similar catchabilities, or data from surveys whose survey catchabilities are thought to differ. Both simulation and application results to rock lobster data from Tasmania suggest that the 2qIR model can be reliably applied in more situations than can the 1qIR or annual models.

Keywords: Abundance estimation; Exploitation rate; Catchability coefficient; Southern rock lobster; *Jasus edwardsii*

INTRODUCTION

Index-removal (IR) models estimate abundance and survey catchability coefficient in a population that experiences a relatively large, known removal. The method requires that a survey index be obtained before and after the removal and assumes that the population is closed except for the known removals (i.e., there is no recruitment, immigration, or emigration between surveys, and the time between surveys is short enough that no natural mortality occurs). Though the original method (hereafter, the "annual model") is attractive (Dawe et al. 1993), and has been known for some time (Petrides 1949), it has received only moderate development (Hoenig and Pollock 1998). This may be because annual model estimates often have poor precision (Routledge 1989; Roseberry and Woolfe 1991; Chen et al. 1998a). Chapter 2 demonstrated that precision could be improved by simultaneously estimating parameters for multiple years of data. The multiple-year index-removal ("1qIR") model, introduced in Chapter 2, assumes that the catchability coefficient of the survey gear remains constant across years and seasons. However, in practice, survey catchability may be affected seasonally by a variety of factors such as changes in water temperature (Paloheimo 1963), life history stage (Ziegler et al. 2002) or fishing gear. If catchability varies seasonally, both the annual model and 1qIR will provide biased results, with a decrease in catchability over the season causing a negative bias in the population estimate and a positive bias in the exploitation estimate.

In this paper we develop and test a multiple-year IR model, the 2qIR model, which allows for catchability to vary by season. The 2qIR model can be used when: 1) pre- and post-harvest survey indices of abundance have been obtained in at least two years, 2) exploitation rate varies among years, and 3) the seasonal catchability coefficients remain constant across years. We use simulation to evaluate the performance of the 2qIR model. We then apply the model to a rock lobster fishery on the South coast of Tasmania, Australia.

METHODS

Model Development

Annual and 1qIR models.—Both the annual and the 1qIR models have been previously described, and are only briefly reviewed here. The annual model was described by Petrides (1949), and its performance was evaluated by Eberhardt (1982). The 1qIR model was described and evaluated in Chapter 2.

Assume catch I_j in survey j (for j = 1,2) is distributed as a Poisson random variable, $I_j \sim P(\lambda_j)$, where the mean λ_j is modeled as $\lambda_j = qN_jf_j$, where N_j is the population size at the time of survey j, f_j is the sampling effort expended in survey j, and q is the catchability coefficient. That is, survey catch is proportional to abundance and sampling effort. Let $N_2 = N_1 - R$, where R is the removal between surveys. The likelihood function, Λ_{ann}, for the annual model is:

$$\Lambda_{ann} = \prod_{j=1}^{2} \frac{(qN_j f_j)^{I_j} e^{-qN_j f_j}}{I_j!} \quad . \tag{1}$$

For the multi-year model, we generalize the notation by adding a second subscript to account for year. Thus, N_{ij} refers to the abundance at the time of survey j in year i and, similarly for f_{ij} and I_{ij} . The likelihood function, Λ_{1qIR}, for the 1qIR model for n years of data is:

$$\Lambda_{1qIR} = \prod_{i=1}^{n} \prod_{j=1}^{2} \frac{(qN_{ij} f_{ij})^{I_{ij}} e^{-qN_{ij} f_{ij}}}{I_{ij}!} \tag{2}$$

with $N_{i2} = N_{i1} - R_i$, and R_i = removal in year *i*.

Seasonal-q model (2qIR).—We follow the model development of the annual and 1qIR models as described in Chapter 2 and assume survey catches are Poisson random variables. If the pre- and post- harvest catchability coefficients differ but are constant over years, the likelihood function, Λ_{2qIR}, for *n* years of data is:

$$\Lambda_{2qIR} = \prod_{i=1}^{n} \prod_{j=1}^{2} \frac{(q_j N_{ij} f_{ij})^{I_{ij}} e^{-q_j N_{ij} f_{ij}}}{I_{ij}!} \tag{3}$$

with q_j referring to the catchability coefficient in season *j* and the other symbols as before. A more generalized model could incorporate $j = 1, 2, \ldots, k$ surveys. However, corresponding removals must be known for the time period between each pair of successive survey indices. For simplicity, we assume only two surveys are conducted per year. For this case, 2qIR requires a minimum of two years of pre- and post-harvest indices of abundance, and requires different exploitation rates in at least two years. After two years of data collection, we have four survey indices that can be modeled as a system of four equations with four unknown parameters:

$$E(I_{11}) = q_1 f_{11} N_1 \tag{4a}$$
$$E(I_{12}) = q_2 f_{12} (N_1 - R_1) \tag{4b}$$
$$E(I_{21}) = q_1 f_{21} N_2 \tag{4c}$$
$$E(I_{22}) = q_2 f_{22} (N_2 - R_2) \tag{4d}$$

where *E* denotes expectation. The four expected values can be replaced with observed survey indices and the four equations solved simultaneously to obtain moment estimates of the parameters. Without contrast in exploitation rates between years, the four equations (4a-4d) reduce to two sets of replicate observations, which is insufficient to estimate four parameters. Parameter estimates can be calculated analytically when two years of data are available:

$$\hat{N}_1 = \frac{I_{11}(I_{12}R_2 - I_{22}R_1)}{I_{12}I_{21} - I_{11}I_{22}} \tag{5}$$

$$\hat{N}_2 = \frac{I_{21}(I_{12}R_2 - I_{22}R_1)}{I_{12}I_{21} - I_{11}I_{22}} \tag{6}$$

$$\hat{q}_1 = \frac{I_{12}I_{21} - I_{11}I_{22}}{I_{12}R_2 - I_{22}R_1} \tag{7}$$

$$\hat{q}_2 = \frac{I_{12}I_{21} - I_{11}I_{22}}{I_{11}R_2 - I_{21}R_1} \quad , \tag{8}$$

where "^" denotes an estimate, I_{ij} = catch in survey j of year i, and other symbols are as before. When more than two years of data are available, the aid of non-linear maximization software is required to make parameter estimates. Degrees of freedom accumulate as years of data are added (Table 3.1).

Model Evaluation by Simulation

We performed three types of simulations. In the first type, the effect of exploitation rate was studied. In the second type, we compared results across a range of values for the catchability coefficient in the second surveys. For the first two simulation types, two years of data were analyzed. In a third type of simulation, the effect of increasing the number of years of data was studied.

Survey data were generated by Monte Carlo simulation. Data used in all comparisons were Poisson random variables:

$$I_{ij} \sim \text{Poisson}(q_j \cdot N_{ij} \cdot f_{ij}) \;,\; i = 1, 2, \ldots, n, \; j = 1, 2, \text{ and } N_{i2} = N_{i1} - R_i \quad (9)$$

and were created by application of the "rpois" function in S-PLUS statistical software (MathSoft 2000). Survey effort (f_{ij}) was assumed constant over all surveys in all years and, for convenience, was set equal to 1.

When pre- and post-harvest catch rates are similar in magnitude, extremely large abundance estimates can result for all IR models. When post-harvest survey catch is greater than or equal to pre-harvest survey catch, annual estimates are infeasible (i.e., negative or infinite), and multiple-year model estimates may be infeasible. Additionally, multiple year models that make parameter estimates by non-linear maximization may fail to converge on solutions. Infeasible estimates and simulations with convergence failures were counted and excluded. Chen *et al.* (1998b) concluded that the mean and variance were unreliable indicators of the performance of the estimator because extreme values of the estimates sometimes occur. Consequently, we used the median estimate and the central 95% of the feasible estimates to assess the accuracy and precision of the estimator, respectively.

Model performance was evaluated by: 1) the proximity of the median estimate to the known abundance, 2) the width of the central 95% of the estimates, and 3) the percentage of unusable simulations.

Exploitation rate variation.— The performance of the 2qIR model was examined over a range of exploitation rate contrasts between years when only two years of data are available. The exploitation rate in the first year was fixed at 10% for all scenarios, but exploitation rate varied from 10% to 80% in the second year. Each simulation was performed at three different levels of contrast between pre- and post-harvest catchability coefficients. The simulation parameters were:

1) population size prior to removals: $N_{11} = N_{21} = 1{,}000{,}000$ animals

2) catchability, either:

a) $q_1 = 0.0002$ and $q_2 = 0.0001$

b) $q_1 = 0.0001$ and $q_2 = 0.0002$, or

c) $q_1 = q_2 = 0.0001$

3) removals: $R_1 = u_1 \cdot N_{11} = 100{,}000$

$R_2 = u_2 \cdot N_{21}$, for $u_2 = 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8$

4) survey effort: $f = 1$

5) number of years of data: $n = 2$.

Survey data were simulated 10,000 times for each comparison.

Catchability variation.—The performance of the 2qIR model was evaluated over a range of contrasts between pre- and post-survey catchability coefficients, when only two years of data are available. Catchability for the pre-harvest surveys was set at 0.0001. Catchability for the post-harvest survey varied from 1/10 to 10 times the pre-harvest survey catchability (but was constant over years). To ensure that model requirements for contrast in exploitation rates (u) between years was met, in this type of simulation, u was set at 0.2 for year 1 and 0.6 for year 2. The simulation parameters were:

1) population size prior to removals: $N_{11} = N_{21} = 1{,}000{,}000$ animals

2) catchability: $q_1 = 0.0001$

$q_2 = \{1 \cdot 10^{-5}, 3 \cdot 10^{-5}, 5 \cdot 10^{-5}, 7 \cdot 10^{-5}, 9 \cdot 10^{-5}, 0.0001, 0.00011,$

0.00013, 0.00015, 0.00017, 0.0002, 0.0003, 0.0004, 0.0005, 0.0006, 0.0007, 0.0008, 0.001}

3) exploitation rate: $u_1 = 0.2$

$u_2 = 0.6$

4) removals: $R_1 = u_1 \cdot N_{11} = 200{,}000$

$R_2 = u_2 \cdot N_{21} = 600{,}000$

5) survey effort: $f = 1$

6) number of years of data: $n = 2$.

Survey data were simulated 10,000 times for each of the twelve catchability scenarios.

Additional years of data.—In the third type of simulation, 2qIR model performance was evaluated for improvement when more years of data are analyzed together; and 2qIR model performance was compared to that of both the annual and the 1qIR models. Model estimates were made with all three models over a range of contrasts between pre- and post-survey catchability coefficients as described above for the second type of simulation, except that the range of catchability variation in the second survey was restricted to 1/4 to two times that of the first survey. Exploitation rate for years 3 to n, $n > 2$, was assumed to be moderate ($u = 0.3$). Estimates for multiple-year models were made using the "nlminb" function in S-PLUS. The simulation parameters were:

1) population size prior to removals: $N_{11} = N_{21} = \ldots = N_{n1} = 1{,}000{,}000$ animals

2) catchability: $q_1 = 0.0001$

$q_2 = \{2.5 \cdot 10^{-5}, 5 \cdot 10^{-5}, 7.5 \cdot 10^{-5}, 0.0001, 0.000125, 0.00015, 0.0002\}$

3) exploitation rate: $u_1 = 0.2$

$u_2 = 0.6$

$u_3 = \ldots = u_n = 0.3$, $n > 2$

4) removals: $R_1 = u_1 \cdot N_{11} = 200{,}000$

$R_2 = u_2 \cdot N_{21} = 600{,}000$

$R_3 = u_3 \cdot N_{31} = \ldots = R_n = u_n \cdot N_{n1} = 300{,}000$, $n > 2$

5) survey effort: $f = 1$

6) number of years of data: $n = 2$, 3, or 5.

Survey data were simulated 1,000 times for each of the 7 catchability scenarios.

Application to Tasmanian Rock Lobster

Study site.— The data used here originated from a rock lobster (*Jasus edwardsii*) population in southwestern Tasmania, Australia. Data were collected from a study site (43.39 ^{o}S 145.88 ^{o}E) near Port Davey from 1996 to 2000. Survey and fishery-removal data were collected by the Tasmanian Aquaculture and Fisheries Institute (TAFI) in Taroona, Tasmania, Australia. Both survey and fishery data were collected at similar locations (the 7E2 block of stock assessment area 8), and from similar depths (40-80m).

Three fishery-independent surveys were performed each year and commercial harvest and effort data were documented for the time periods between the surveys. Surveys were performed during the first week of the fishing season (“spring” survey: early to mid November), in mid-season (late February to mid March), and again during the final weeks of the season (“fall” survey: mid July to mid August). Model estimates were made with each of the IR models (annual, 1qIR, and 2qIR) using two sets of data.

Both datasets incorporated the spring survey, but datasets differed by which survey index was used as the "second" required survey. One dataset incorporated the mid-season survey index as the second survey, while the other dataset incorporated the fall survey as the second survey. The relative performance of each of the models was compared to one another, for each of the datasets used.

Model choice.—Model performance with the rock lobster fishery data was evaluated using two methods, a likelihood ratio test and a diagnostic plot. A likelihood ratio test was applied to decide which of the IR models (annual, 1qIR or 2qIR) was most parsimonious (see, e.g., Miller and Miller (1999)) for the rock lobster data of this population. If the ratio of likelihoods for two possible nested models is θ, then $-2\cdot\log_e \theta$ approximates the X^2_r distribution under the null hypothesis, with the degrees of freedom, r, equal to the difference in the number of parameters estimated in the "unrestricted" likelihood (i.e., the likelihood with more parameters estimated) and that of the more "restricted" likelihood.

To test whether the annual model or 1qIR model was more appropriate, both equations (1) and (2) are fitted to the data. For n years of data (n>1):

$$\theta = \frac{\Lambda_{restricted}}{\Lambda_{unrestricted}} \tag{10}$$

and $-2\cdot\log_e \theta$ approximates X^2_r with $r = n$-1 degrees of freedom. The null hypothesis is no difference in catchability coefficients across years. If the test fails to reject the hypothesis, the restricted model (1qIR) is appropriate. If the hypothesis is rejected, there is evidence the catchability coefficients differ among years and the unrestricted annual model is more appropriate.

When applying a likelihood ratio test to determine if the 2qIR model is more appropriate than the 1qIR model, 1qIR is again the more restricted model. The null hypothesis is that there is no difference between the pre- and post-harvest catchability coefficients. The test statistic follows equation (10), but now r = 1 degree of freedom. If the test fails to reject the hypothesis, 1qIR is again the most appropriate model. If the hypothesis is rejected, 2qIR is more appropriate.

Model choice was also evaluated with diagnostic plots. If a model is effective in estimating biomass, one should expect that 1) biomass estimates will be directly related to pre-harvest survey catch per unit effort (CPUE), and that 2) a regression of model estimates on pre-season survey indices will have an intercept close to the origin. Consequently, model performances will be evaluated by the strength of the relationships between pre-harvest survey CPUE and estimated biomass (using R^2 values) and by the proximity of y-intercepts to the origin.

RESULTS

Simulation results

Exploitation rate variation.—The 2qIR model worked well when there was moderate contrast in exploitation rates between years (i.e., u_2 was 0.4 or more), regardless of the degree of contrast between the catchability coefficients (Fig. 3.1). With moderate exploitation contrast, 2qIR model estimates were always accurate, precise, and seldom unusable. Annual model performance, however, was very sensitive to changes in the survey catchability coefficient, and model performance varied greatly among scenarios.

Median 2qIR model estimates were always accurate when $|u_1 – u_2|$ was at least 20%, regardless of the degree of contrast in catchability coefficients (Fig. 3.1). Annual model estimates, however, were only accurate when catchability coefficients were equal (Fig. 3.1C).

The 2qIR model estimates were most variable when the simulated population was lightly (u = 0.2) or moderately (u = 0.3) exploited. But the bounds of 2qIR model estimates always included the true abundance when u was greater than 0.1. Though 2qIR estimates were somewhat variable, the upper tails of the distribution of estimates were long, and when the upper 10% of estimates were excluded, estimates were always precise (Fig. 3.1). Annual model estimate variability, however, differed greatly for the three different scenarios. Annual model estimates had virtually no variability when pre-harvest catchability was double that of post-harvest catchability, but the estimates never included the known abundance (Fig. 3.1A). When catchability of the second survey was double that of the first survey (Fig. 3.1B), the central 95% bands of annual estimates were roughly an order of magnitude greater than for the other scenarios, and the bands never included the known abundance when exploitation rate was 60%. When catchability was equal for both surveys, annual bands were wide at very low exploitation rate, but bands were narrow when at least 30% of the population was harvested in the second year (Fig. 3.1C).

The estimates of the 2qIR model were feasible more often (92%) than annual model estimates (80% for all simulations of year 2), when all scenarios were combined. Most unusable 2qIR estimates (81%) were observed when exploitation contrast was low (i.e., when the difference between exploitation rates was ≤10%). When exploitation rate contrast was at least 20%, the percentage of the 2qIR estimates that were infeasible never exceeded 12% in any scenario.

Catchability variation.—The 2qIR model worked well over a wide range of contrast in catchability coefficients between pre- and post-harvest surveys, but the annual model was very sensitive to catchability change (Fig. 3.2). The 2qIR model estimates were accurate and precise over the entire range of catchability ratios (q_2/q_1) examined. Further, 2qIR model estimates were almost always feasible. In contrast, annual model estimates, on average, were accurate, precise, and feasible only if catchability ratios were close to unity.

The 2qIR model produced accurate estimates when post-harvest catchability differed from pre-harvest catchability by a factor of 0.3 to 10 (Figs. 3.2 and 3.3). The 2qIR model performed better when post-harvest catchability was greater than pre-harvest catchability, than vice versa. But, even the situations with the most extreme medians were only slightly below the true abundance. In the worst-case scenario, post-harvest catchability was 1/10 that of pre-harvest catchability, but estimates still were within 9% of the true value on average. In all other cases, estimates were within 2% of the true abundance on average.

In contrast, median estimates of the annual model were within 10% of the actual abundance only when there was no change, or nearly no change, in catchability between pre- and post-harvest surveys. When exploitation rate was low (u = 0.2, year 1), annual model estimates always differed at least 30% from the true value on average when pre- and post-harvest catchability coefficients differed. When exploitation rate was high (u = 0.6, year 2), the annual model made accurate estimates (within 10% of known abundance on average) more often, but only if the difference in catchability coefficients was 10% or less.

The width of the central 95% of feasible estimates of both models was characterized by upper bounds that were at least three times the magnitude of the lower bounds (Fig. 3.2). Though the precision of the 2qIR model estimates varied somewhat over the range of catchability ratios examined, the central 95% of the estimates always contained the known abundance (Fig. 3.2). Variability of 2qIR estimates was greatest when pre-harvest catchability was greater than post-harvest catchability. This trend was especially pronounced when the catchability ratio was < 0.5. However, the variability of the 2qIR estimates was relatively constant when catchability ratios were ≥ 2 (Fig 3.2C). Annual model estimates were more precise than 2qIR estimates when the q-

ratios were < 1. But when catchability ratios were < 0.7 or > 1.3 the central 95% bands of annual estimates never included the true abundance.

Estimates of the 2qIR model were almost always feasible; in contrast, just more than half of the annual model estimates were feasible (Fig. 3.2b). Of 120,000 simulations analyzed with the 2qIR model (catchability ratios from 0.1 to 3.0), only 1% of the estimates were infeasible. Most infeasible estimates of the 2qIR model (87%) were from the lowest *q*-ratios examined (0.1, and 0.3). Twice as many simulations were possible for the annual model because each year of data was analyzed separately. Of the 240,000 possible annual model estimates made, 24% were infeasible. The year under high exploitation had more feasible estimates (92%) than did the year under low exploitation (60%). However, no annual model estimates were feasible for catchability ratios ≥ 2 when exploitation rate was low (u = 0.2), or for ratios ≥ 4 when exploitation rate was high (u = 0.6)(Fig. 3.3).

Additional years.—With five years of data, the 2qIR model estimates were accurate, precise and almost always usable (Fig. 3.4). Even with 5 years of data, however, the annual and 1qIR model estimates were accurate, precise, and largely usable on average, only when the catchability ratio was close to one.

The width of the central 95% of 2qIR estimates was wider when only two years of data were available than when three or five years were available (Fig. 3.5). The improvement gained by using five years of data instead of three was marginal. With any number of years, annual model estimate variability, accuracy and usability are as shown in figure 3.4, because the estimate for each year is made independently. With two years of data however, 1qIR model estimates were more accurate and usable a greater proportion of the time than the 1qIR results shown in figure 3.4; but overall patterns of the estimates were similar (Fig. 3.6).

Variation in simulated surveys

There was a wide range of variation in simulated surveys (Table 3.2). Because surveys were Poisson random variables, the low portion of this range was unreasonably low for a potentially clumped fisheries resource like rock lobster. Consequently, it is possible that some surveys were overly precise, and there was concern that overly precise surveys may have affected parameter estimates in a similar fashion. Simulations were performed to test this.

Application to southern rock lobster fishery

Parameter estimates.—The 2qIR model predicted lower exploitation rates and catchability coefficients, and considerably higher biomass than those estimates of the other models (Fig. 3.7; Table 3.3). All of the 2qIR model estimates appeared reasonable and were similar, regardless of which dataset was fit to the model. However, patterns for the annual and 1qIR model exploitation estimates differed considerably for each set of data. Moreover, the exploitation rate estimates of both the annual and 1qIR models were unreasonably high for estimates based on the data that included the mid-season surveys. Both the annual and 1qIR models predicted that more than 100% of the population was harvested in two of the five years of data (Fig. 3.7A). Though 2qIR model estimates were also high at beginning of the dataset (they ranged from 80% to 91%, for mid-season, and fall data, respectively), the 2qIR model estimates from both datasets predicted that exploitation rate steadily declined during the next four years (Table 3.3; Fig. 3.7). The 2qIR model almost always estimated lower catchability coefficients than did the other models, and predicted that catchability decreased by more than 70% between the spring and fall surveys. Correspondingly, 2qIR model estimates of abundance were much higher than those predicted by the other models. In 1998, the 2qIR model abundance estimates from both datasets were about 50% higher than those estimates of the annual or 1qIR models (Table 3.3).

Model choice.—A likelihood ratio test found the most parsimonious model was 1qIR, regardless of which dataset was analyzed (Table 3.4). Diagnostic plots, however, suggest that the 2qIR model performed best (Fig. 3.8).

Diagnostic plots of estimates made from the mid-season data (Fig. 3.8A) showed that, although both the 1qIR and 2qIR model estimates of abundance had strong relationships with the pre-harvest survey catch rate (R^2 values were 0.88, and 0.92, respectively), annual model estimates were only weakly related to the pre-harvest survey catch rate ($R^2 = 0.06$). Intercepts for both 1qIR (8,121) and 2qIR (8,093) were similar and very close to the origin for the mid-season data, but the annual model intercept was over 50,000 kg.

When fall survey data was fit to each of the models, all model estimates of abundance had strong relationships with pre-harvest survey catch rate (R^2 values were 0.94, 0.95, and 1.00 for the annual, 1qIR and 2qIR model estimates, respectively), but the 2qIR model demonstrated the strongest relationship. Intercepts were similar for the annual (11,679) and 1qIR (10,415) models, but the 2qIR model intercept (3,698) was the closest to the origin.

Equations for the regression lines were:

mid-year data:

$$\hat{N}_{ann-mid} = 10{,}099 \cdot I_1 + 50{,}403\,\text{kg} \tag{11}$$

$$\hat{N}_{1q\text{IR-}mid} = 25{,}647 \cdot I_1 + 8{,}121\,\text{kg} \tag{12}$$

$$\hat{N}_{2q\text{IR}-mid} = 38{,}584 \cdot I_1 + 8{,}093\,\text{kg}\,. \tag{13}$$

fall data:

$$\hat{N}_{ann-fall} = 22{,}484 \cdot I_1 + 11{,}679\,\text{kg} \tag{14}$$

$$\hat{N}_{1q\text{IR}-fall} = 23{,}410 \cdot I_1 + 10{,}415\,\text{kg} \tag{15}$$

$$\hat{N}_{2q\text{IR-}fall} = 39{,}442 \cdot I_1 + 3{,}698\,\text{kg}\quad. \tag{16}$$

The slope of the regression line estimates the reciprocal of survey gear catchability (1/*q*) for the annual and 1qIR models. The estimates for *q* then, using the mid-season data were $9.9 \cdot 10^{-5}$, and $3.9 \cdot 10^{-5}$ for the annual and 1qIR models, respectively. When the fall data were used instead, annual and 1qIR model estimates of survey gear catchability were $4.4 \cdot 10^{-5}$ and $4.3 \cdot 10^{-5}$, respectively.

DISCUSSION

Model evaluation by simulation

The 2qIR model was accurate, precise and usable with almost all simulated data when exploitation rate differed by at least 30% between at least 2 years, regardless of the contrast in catchability coefficient between pre- and post-harvest surveys. Performance indicators for the 2qIR model improved when a third year of data was added, but model performance with 5 years of data was similar to that with 3 years.

When catchability varied seasonally, model performance for the 1qIR model deteriorated somewhat when additional years were added (Fig. 3.6). The 1qIR model is based on the assumption that catchability is constant. So, as more data that violate the assumptions of the model are added to the dataset, the chances of getting a particularly troublesome catch rate increase. The only instances when the annual or 1qIR models outperformed the 2qIR model were when catchability was constant (or very nearly constant) between surveys, and exploitation rate was very high (60% or more). In such situations, use of the simpler models is appropriate and the 2qIR model suffers a penalty in variability for unnecessarily estimating an extra catchability parameter.

Application to Tasmanian Rock Lobster

Though the likelihood ratio test suggests that the 1qIR model was the most parsimonious in this application, diagnostic plots, and patterns of model estimates suggest the 2qIR model performed best for this population of rock lobster. When using the mid-season data, diagnostic plots showed only a slight improvement of the 2qIR model performance over that of the 1qIR model. However, an examination of the patterns of parameter estimates demonstrated a distinct improvement of the performance of the 2qIR model over that of the other models. The unreasonable exploitation estimates of the annual and 1qIR models suggest that both models performed poorly with the mid-season data. When fall data were incorporated instead, the intercept of the 2qIR model was closer to the origin than those of the other models; and, though all model abundance estimates had strong relationships with survey CPUE, the 2qIR model estimates were directly related (R^2 = 1.0) to CPUE. Additionally, about 5% more of the variation in 2qIR abundance estimates was explained by CPUE than was that of the other models.

Recent work suggests that use of either the annual or 1qIR models may be inappropriate for the dataset that included the fall surveys. Ziegler et al. (2003) predicted that the relative catchability of rock lobster in this region decreases markedly after the mid-season survey is conducted, and that catchability at the time of the fall survey is distinctly lower than that of the spring and mid-season surveys. The 2qIR model results presented here appear to support the conclusions of Ziegler et al. (2003). The 2qIR model estimated that catchability declined by more than 70% between the spring survey in November and the fall survey in August. If this predicted change in catchability is real, it is important to account for. When the IR models were applied to the dataset that included the fall data, the 2qIR model predicted that abundance was 44% higher and exploitation was 28% lower, on average, than corresponding estimates of the annual and 1qIR models, because those models could not accommodate the catchability change. Previous studies of different populations of this species have also documented the importance of accounting for seasonal catchability change (Ziegler et al. 2002; Frusher and Hoenig 2003). Simulations presented here suggest that biases can be severe for annual and 1qIR model estimates when the assumption of constant catchability is not met for these models. Thus, it appears likely that the 2qIR model is the most appropriate model to use in the stock assessment of this population, regardless of which dataset is used.

The choice of assessment model may depend on the management question and the management goal. For instance, if the task is to set a quota, basing the decision on 1qIR estimates would be more conservative in this fishery, because the 1qIR model predicts that the population is experiencing a higher level of exploitation than the 2qIR model does. Alternatively, if the manager needs to decide what level of exploitation the population can withstand, it would be safer to use the 2qIR model estimates, which predict that this population has resisted lower levels of exploitation.

It appears to be important to account for catchability change in this fishery. Many other fishery situations require a model that accommodates changing catchability. When pre- and post-harvest surveys are conducted with different gear, or when the catchability of a species is known to change seasonally (Paloheimo 1963; Ziegler et al. 2002), a 2qIR model will be appropriate, as long as exploitation rate varies between two of the years in the dataset.

If there is any doubt as to which model to apply, our simulation results suggest that the 2qIR model will probably give the most accurate estimate. Though estimates may suffer slightly in precision if a simpler model is truly appropriate, 2qIR model estimates will still be accurate on average, and they do not demonstrate the serious biases that both the annual and 1qIR models demonstrate when their assumption of constant catchability is not met.

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TABLE 3.1

Comparison of degrees of freedom accumulated for each model discussed in the text, given *n* years of data.

Model	Number of Observations	Number of Parameters to Estimate	Degrees of Freedom
Annual	$2n$	$2n$	0
1qIR	$2n$	$n+1$	$n-1$
2qIR	$2n$	$n+2$	$n-2$, for $n\geq 2$

TABLE 3.2

Ranges of the coefficient of variation observed for the pre-harvest survey and the post-harvest survey for each simulation performed, and the number of simulations (*n*) performed for each scenario. Simulation type corresponds to sub-headings in the text where each simulation is described in detail.

Simulation Type	*n*	Pre-harvest survey cv	Post-harvest survey cv
Exploitation rate variation			
$q_1 >> q_2$	10,000	7.1%	10.4% - 22.4%
$q_1 = q_2$	10,000	10.1%	10.4% - 22.4%
$q_1 << q_2$	10,000	10.1%	7.4% - 15.8%
Catchability variation		$q_1 = 0.0001$	q_2 varies
	10,000	10.1%	6.4% - 50.2%
Additional years		$q_1 = 0.0001$	q_2 varies
2 years	1,000	9.8% - 10.2%	8.1% - 32.1%
3 years	1,000	9.8% - 10.2%	8.1% - 32.1%
5 years	1,000	9.7% - 10.3%	8.0% - 31.8%

TABLE 3.3

Comparison of parameter estimates for a rock lobster fishery near Port Davey, Tasmania, Australia. Estimates of (a) abundance (kg), (b) survey catchability coefficients, and (c) exploitation rate were made for each IR model. (A) Parameter estimates were made using spring and mid-season survey data; (B) estimates were made using spring and fall survey data. Year indicates the calendar year at the beginning of the fishing season (November).

A. *Spring & mid-season data*

Year	Annual	1qIR	2qIR
(a) Abundance (kg)			
1996	52,877.9	46,408.5	57,184.8
1997	40,681.5	55,160.0	83,514.7
1998	103,460.7	104,499.8	150,564.7
1999	32,493.1	37,406.6	54,544.7
2000	120,563.1	46,162.9	69,312.4
(b) Catchability Coefficient (q)	$\bar{q} = 3.354 \cdot 10^{-5}$ Range: $1.045 \cdot 10^{-5}$ to $5.727 \cdot 10^{-5}$	$3.326 \cdot 10^{-5}$	Pre-harvest: $2.339 \cdot 10^{-5}$ Post-harvest: $1.591 \cdot 10^{-5}$
(c) Exploitation rate (u)			
1996	0.86	0.98	0.80
1997	1.42	1.05	0.69
1998	0.78	0.78	0.54
1999	1.16	1.01	0.69
2000	0.23	0.60	0.40

B. *Spring & fall data*

Year	Annual	1qIR	2qIR
(a) Abundance (kg)			
1996	46,622.5	46,177.9	50,236.9
1997	63,930.3	64,548.0	94,688.3
1998	90,525.2	92,680.6	141,941.1
1999	43,930.0	43,106.3	62,300.7
2000	31,710.0	32,872.7	52,307.0
(b) Catchability Coefficient (q)	$\bar{q} = 3.458 \cdot 10^{-5}$ Range: $2.617 \cdot 10^{-5}$ to $3.974 \cdot 10^{-5}$	$3.478 \cdot 10^{-5}$	Pre-harvest: $2.419 \cdot 10^{-5}$ Post-harvest: $6.400 \cdot 10^{-6}$
(c) Exploitation rate (u)			
1996	0.98	0.98	0.91
1997	0.91	0.90	0.61
1998	0.90	0.87	0.57
1999	0.86	0.87	0.60
2000	0.87	0.84	0.53

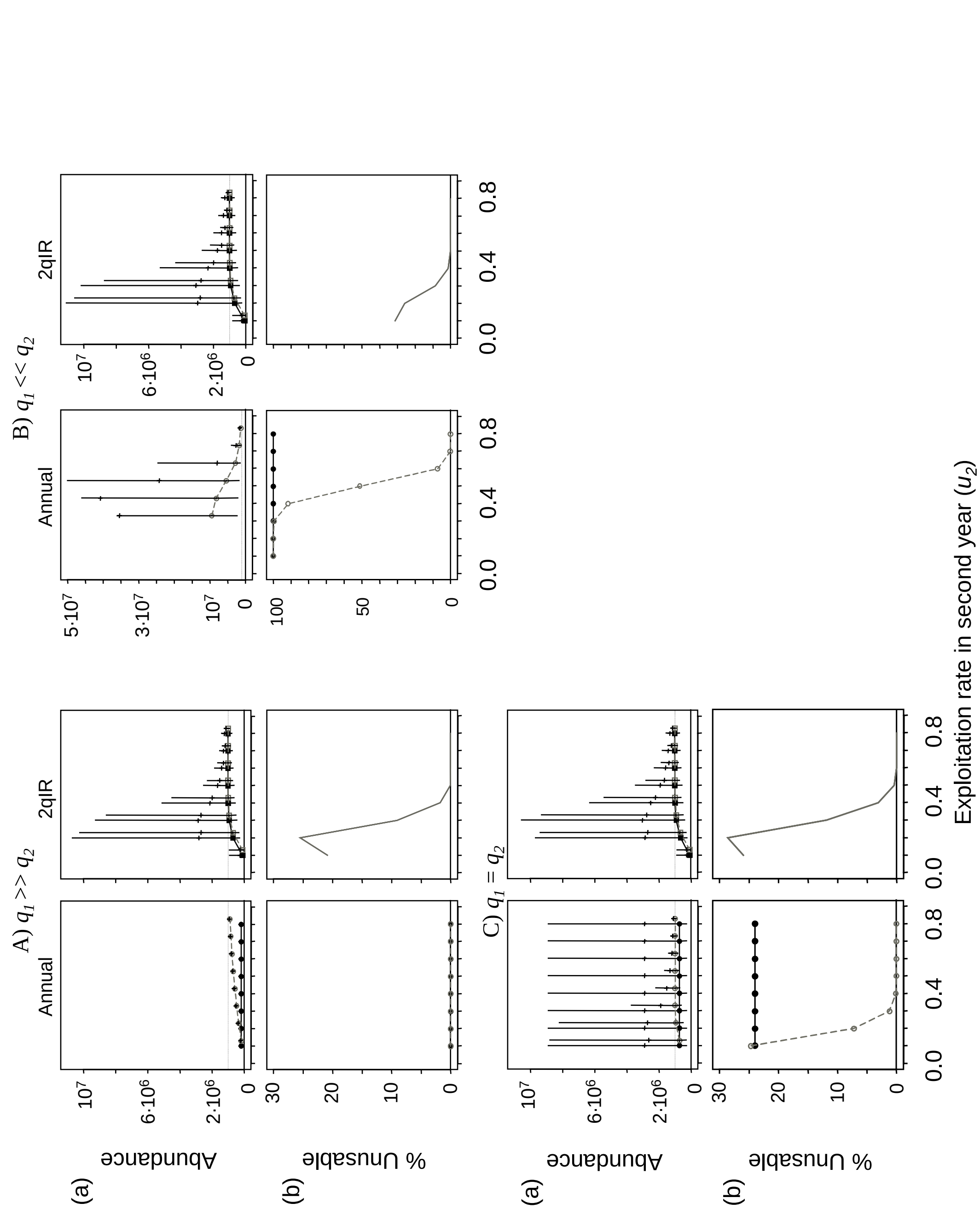
TABLE 3.4

Models compared by the likelihood ratio test. Displayed are: $\log_e$ likelihood objective values, likelihood ratio test statistics ($-2{\cdot}\log_e \theta$), degrees of freedom (r), and critical values ($\alpha_r = 0.05$) of the X^2 distribution. Results are displayed for data that included (A) the spring and mid-season survey indices, and (B) the spring and fall survey indices.

Models Compared	Objective value	$-2{\cdot}\log_e \theta$	Degrees of freedom (r)	Critial values X^2 ($\alpha_r = 0.05$)
A. *Spring & mid-season data:*				
1qIR	-6.8843			
Annual	-6.6929	0.3828 ns	4	9.488
1qIR	-6.8843			
2qIR	-6.8668	0.0350 ns	1	3.841
B. *Spring & fall data:*				
1qIR	-4.8178			
Annual	-4.7408	0.1540 ns	4	9.488
1qIR	-4.8178			
2qIR	-4.7525	0.1306 ns	1	3.841

FIGURE 3.1

Comparison of annual and 2qIR model performance for three contrasts in exploitation rate. Each vertical bar represents the central 95% of feasible estimates from 10,000 simulations of 2 years of survey data. Ten percent of the estimates were greater than the location of the horizontal hash marks on a bar. Circles (annual model) and squares (2qIR) show the medians of the central 95% of the estimates. Exploitation rate was fixed at 0.1 in year 1 (solid line, filled symbols) for all simulations. Exploitation rate varied among simulations in year 2 (dashed line, open symbols), and ranged from 0.1 to 0.8. A, B, and C differed in catchability contrast between pre- and post-harvest surveys: (A), catchability in the pre-harvest survey was double that of the post-harvest survey (q_1 = 0.0002; q_2 = 0.0001); (B), catchability in the pre-harvest survey was half that of the post-harvest survey (q_1 = 0.0001; q_2 = 0.0002); (C), catchability coefficients were equal (q_1 = q_2 = 0.0001). Row (a) depicts abundance estimates. True abundance is indicated by the light grey line. Year 1 and year 2 plots in (a) were slightly offset horizontally so both estimates were visible. All abundance plots are the same scale except for the annual model plot of scenario (B). Row (b) depicts the percentage of unusable (infeasible) estimates for each model. Only one line is drawn for the 2qIR model because years are estimated simultaneously and a failure for either or both years is counted as a failure.



A) $q_1 >> q_2$
B) $q_1 << q_2$
C) $q_1 = q_2$
Annual
2qIR
(a)
Abundance
(b)
% Unusable
Exploitation rate in second year (u_2)

FIGURE 3.2

Comparison of annual model performance with that of the 2qIR model, using 10,000 simulations of 2 years of data. Performance is compared over a range of seasonal change in the survey gear catchability coefficient. In both years, catchability of the first survey was equal to 0.0001. The catchability coefficient of the second survey was the same for both years in any one simulation, but varied from 0.00001 to 0.0003 among scenarios. Columns (A) and (B) are plotted at the same scale. Column (C) presents the same results as (Ba) but at one-tenth the scale to show details. Performance indicators were (row a): 1) the median estimate (symbols), 2) the width of the interval containing 95% of the feasible estimates (vertical lines), and (row b): 3) the percentage of unusable simulations. Simulations were considered unusable if estimates were infeasible (negative or infinite). Ten percent of the estimates were greater than the location of the horizontal hash marks on the vertical lines. Exploitation rates were 20% in year 1 (solid lines, filled symbols) and 60% in year 2 (dashed lines, open symbols). Year 1 and year 2 plots in (a) were offset slightly so both estimates were visible. A light grey line was added for reference in (a) to indicate known abundance.

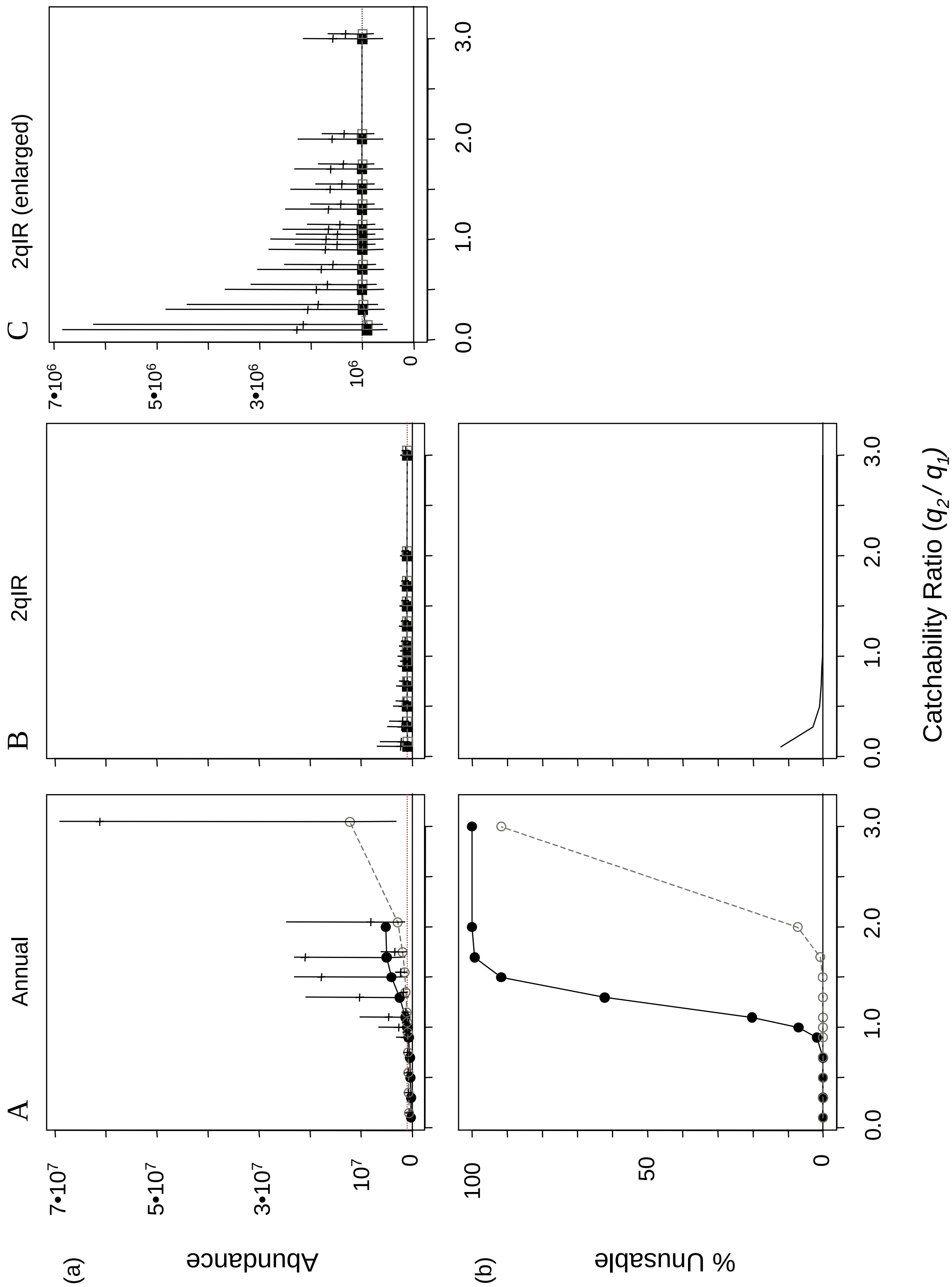

A
Annual
B
2qIR
C
2qIR (enlarged)
(a)
Abundance
(b)
% Unusable
Catchability Ratio (q_2 / q_1)

FIGURE 3.3

Comparison of annual model performance with that of the 2qIR model, using 10,000 simulations of 2 years of data. Performance is compared over a range of seasonal change in the survey gear catchability coefficient. In both years, catchability of the first survey was equal to 0.0001. The catchability coefficient of the second survey was the same for both years in any one simulation, but varied from 0.00001 to 0.001 among scenarios. Columns (A) and (B) are plotted at the same scale. Column (C) presents the same results as (Ba) but at one-tenth the scale to show details. Performance indicators were (row a): 1) the median estimate (symbols), 2) the width of the interval containing 95% of the feasible estimates (vertical lines), and (row b): 3) the percentage of unusable simulations. Simulations were considered unusable if estimates were infeasible (negative or infinite). Ten percent of the estimates were greater than the location of the horizontal hash marks on the vertical lines. Exploitation rates were 20% in year 1 (solid lines, filled symbols) and 60% in year 2 (dashed lines, open symbols). Year 1 and year 2 plots in (a) were offset slightly so both estimates were visible. A dotted line was added for reference in (a) to indicate known abundance.

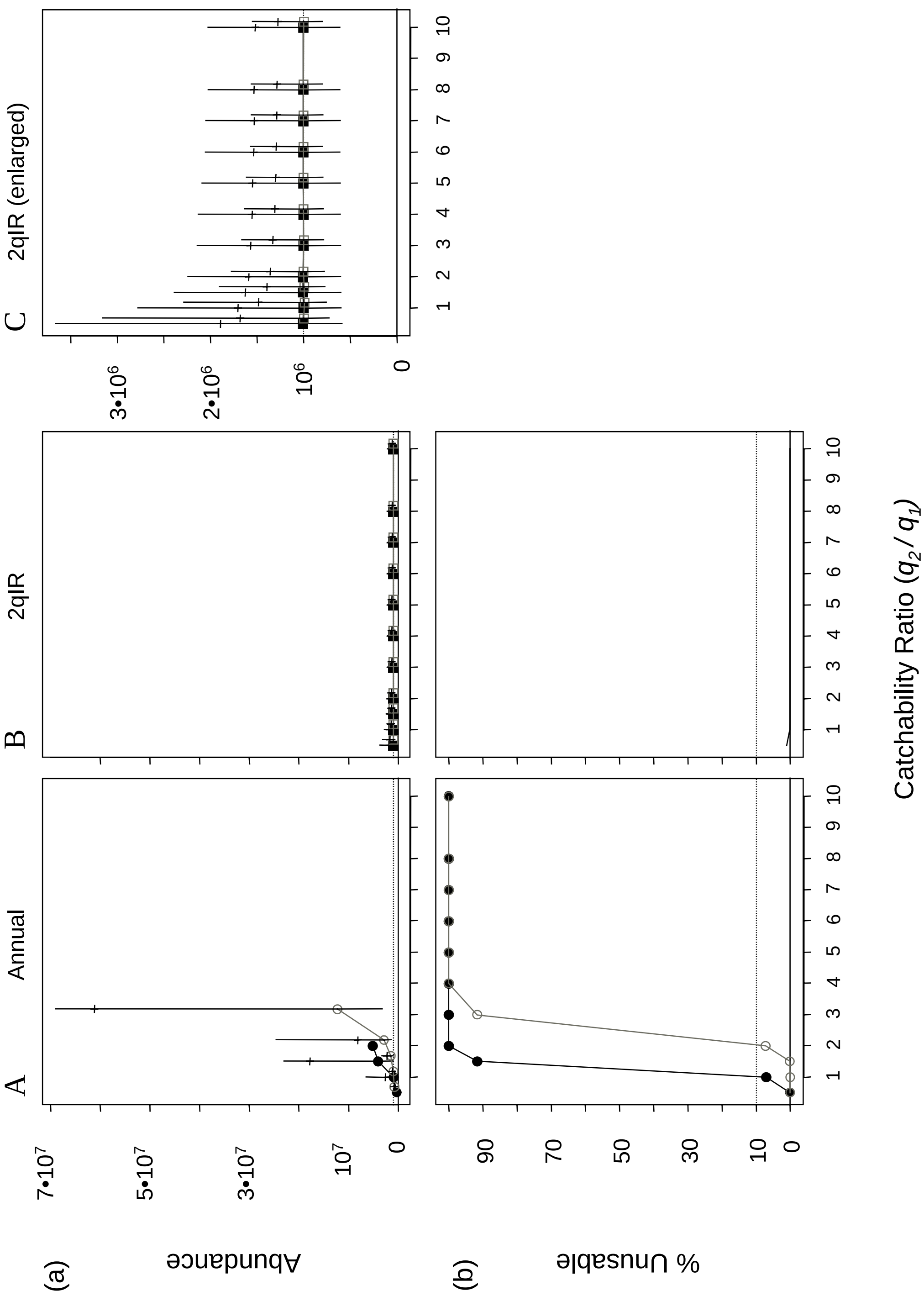

(a)
Abundance
(b)
% Unusable
A
Annual
B
2qIR
C
2qIR (enlarged)
7•10^7
5•10^7
3•10^7
10^7
0
3•10^6
2•10^6
10^6
90
70
50
30
10
1 2 3 4 5 6 7 8 9 10
Catchability Ratio (q2 / q1)

FIGURE 3.4

Comparison of annual, 1qIR, and 2qIR model performance with 5 years of simulated data. Shown are seven scenarios, which varied in the catchability coefficient of the second survey. Each scenario was simulated 1000 times. Plots of each year were offset slightly, so all years were visible. Row (a) depicts abundance estimates for each model (columns). Median estimates for individual years are represented by open circles (low exploitation year, u = 0.2, dashed line), and filled triangles (high exploitation year, u = 0.6, solid line). Filled diamonds represent a mean of the three years with moderate exploitation rate (u = 0.3). Vertical lines extending from the medians represent the central 95% of model estimates. Ten percent of the estimates were greater than the location of the horizontal hash marks on the vertical lines. Row (b) depicts the percentage of unusable simulations for each model.

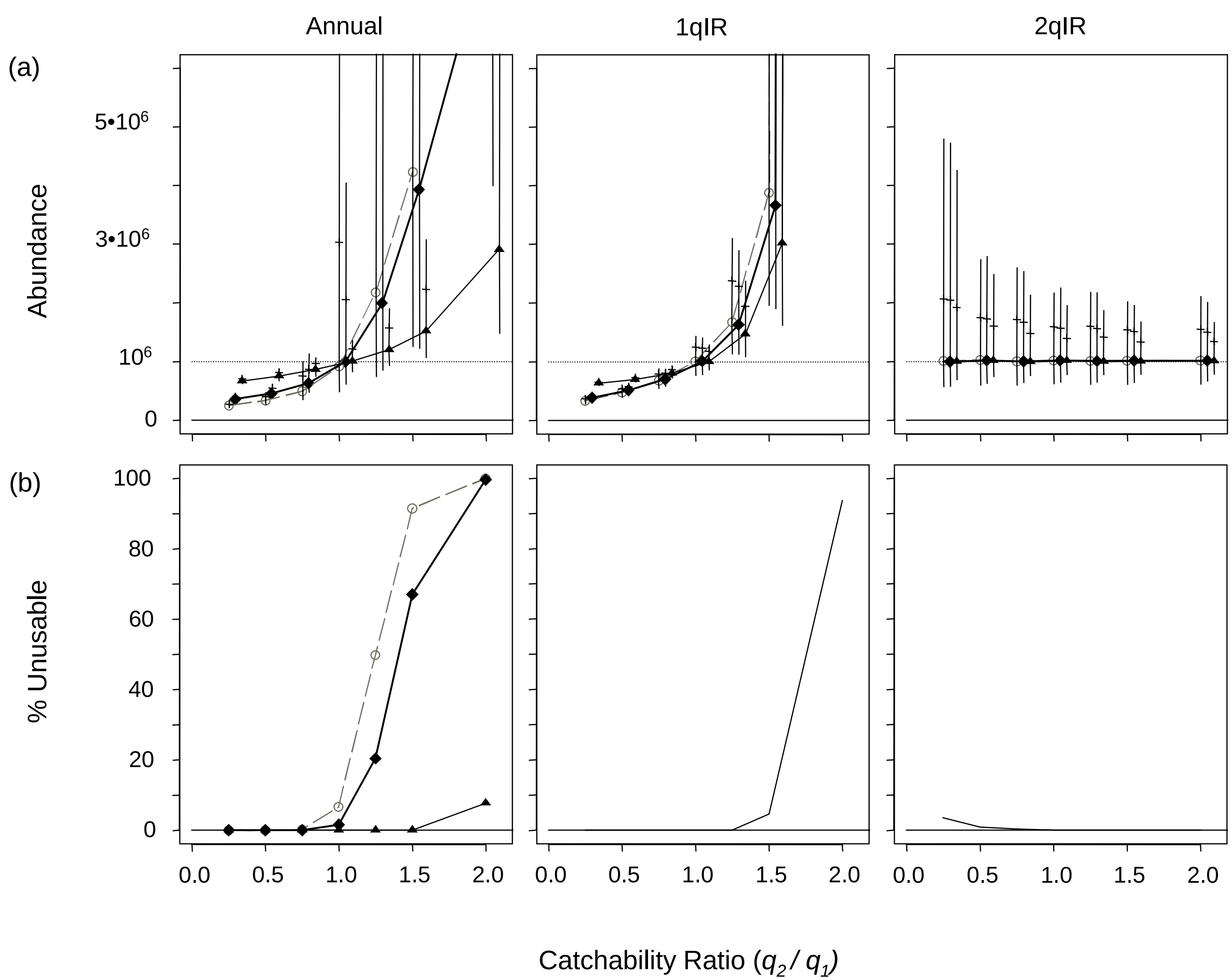

Annual
1qIR
2qIR
(a)
Abundance
5•10^6
3•10^6
10^6
0
(b)
% Unusable
100
80
60
40
20
0
0.0
0.5
1.0
1.5
2.0
Catchability Ratio (q2 / q1)

FIGURE 3.5

Comparison of 2qIR model performance with 2 years, 3 years, and 5 years of data. Model performance improves with a third year of data, but performance is similar with 3 or 5 years. Shown are seven scenarios, which varied in the catchability coefficient of the second survey. Each scenario was simulated 1000 times. Plots of each year were offset slightly, so all years were visible. Row (a) depicts abundance estimates for each model (columns). Median estimates for individual years are represented by open circles (low exploitation year, $u = 0.2$, dashed line), and filled triangles (high exploitation year, $u = 0.6$, solid line). Filled diamonds represent a mean of the three years with moderate exploitation rate ($u = 0.3$). Vertical lines extending from the medians represent the central 95% of model estimates. Ten percent of the estimates were greater than the location of the horizontal hash marks on the vertical lines. Row (b) depicts the percentage of unusable simulations for each scenario.

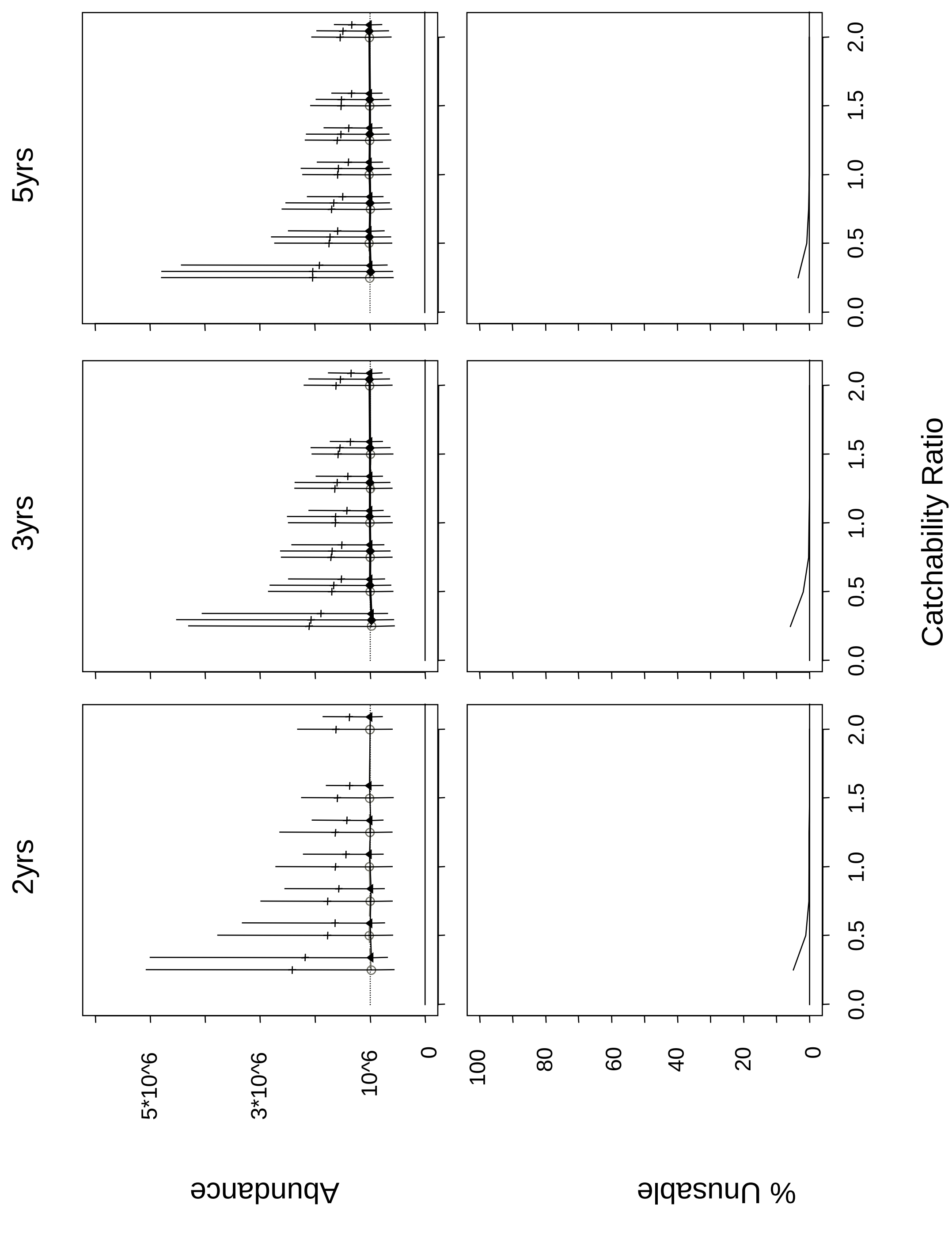

2yrs
3yrs
5yrs
Abundance
% Unusable
Catchability Ratio
5*10^6
3*10^6
10^6
0
100
80
60
40
20
0
0.0
0.5
1.0
1.5
2.0

FIGURE 3.6

Comparison of 1qIR model performance with 2 years and 5 years of data. 1qIR model performance deteriorates somewhat as more years of data are added. Shown are seven scenarios, which varied in the catchability coefficient of the second survey. Each scenario was simulated 1000 times. Plots of each year were offset slightly, so all years were visible. Row (a) depicts abundance estimates for each model (columns). Median estimates for individual years are represented by open circles (low exploitation year, u = 0.2, dashed line), and filled triangles (high exploitation year, u = 0.6, solid line). Filled diamonds represent a mean of the three years with moderate exploitation rate (u = 0.3). Vertical lines extending from the medians represent the central 95% of model estimates. Ten percent of the estimates were greater than the location of the horizontal hash marks on the vertical lines. Row (b) depicts the percentage of unusable simulations for each scenario.

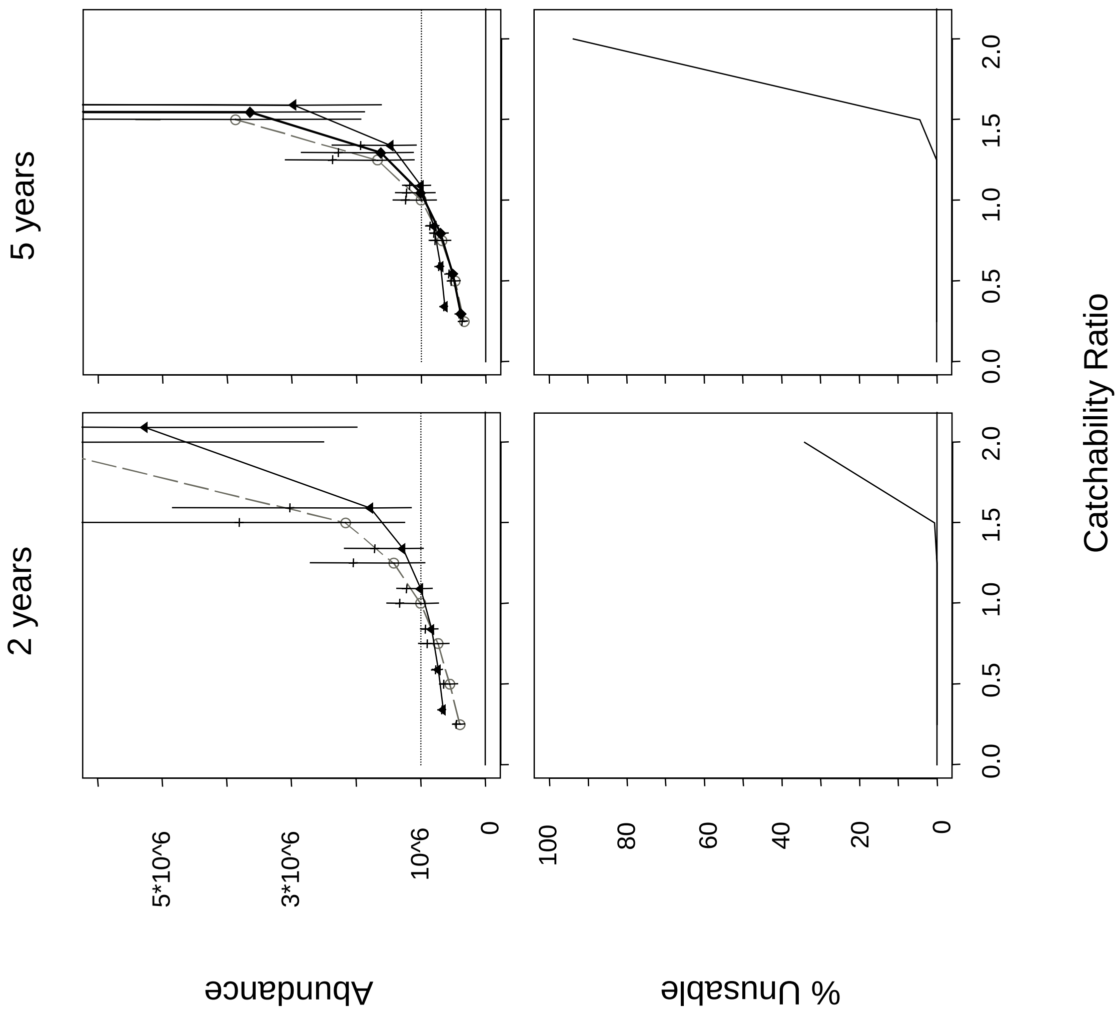

2 years
5 years
Abundance
% Unusable
Catchability Ratio
5*10^6
3*10^6
10^6
0
100
80
60
40
20
0
0.0
0.5
1.0
1.5
2.0

FIGURE 3.7

Parameter estimates of abundance (kg), catchability coefficients, and exploitation rates for two sets of rock lobster fishery data. Estimates in column (A) were based on data collected in spring and mid-season surveys; estimates in column (B) were based on data collected in spring and fall surveys. All data were collected from stock assessment area 8, near Port Davey, Tasmania, Australia, for the fishing seasons that spanned years 1996/1997 to 2000/2001. Open squares denote 2qIR model catchability coefficient estimates for spring surveys.

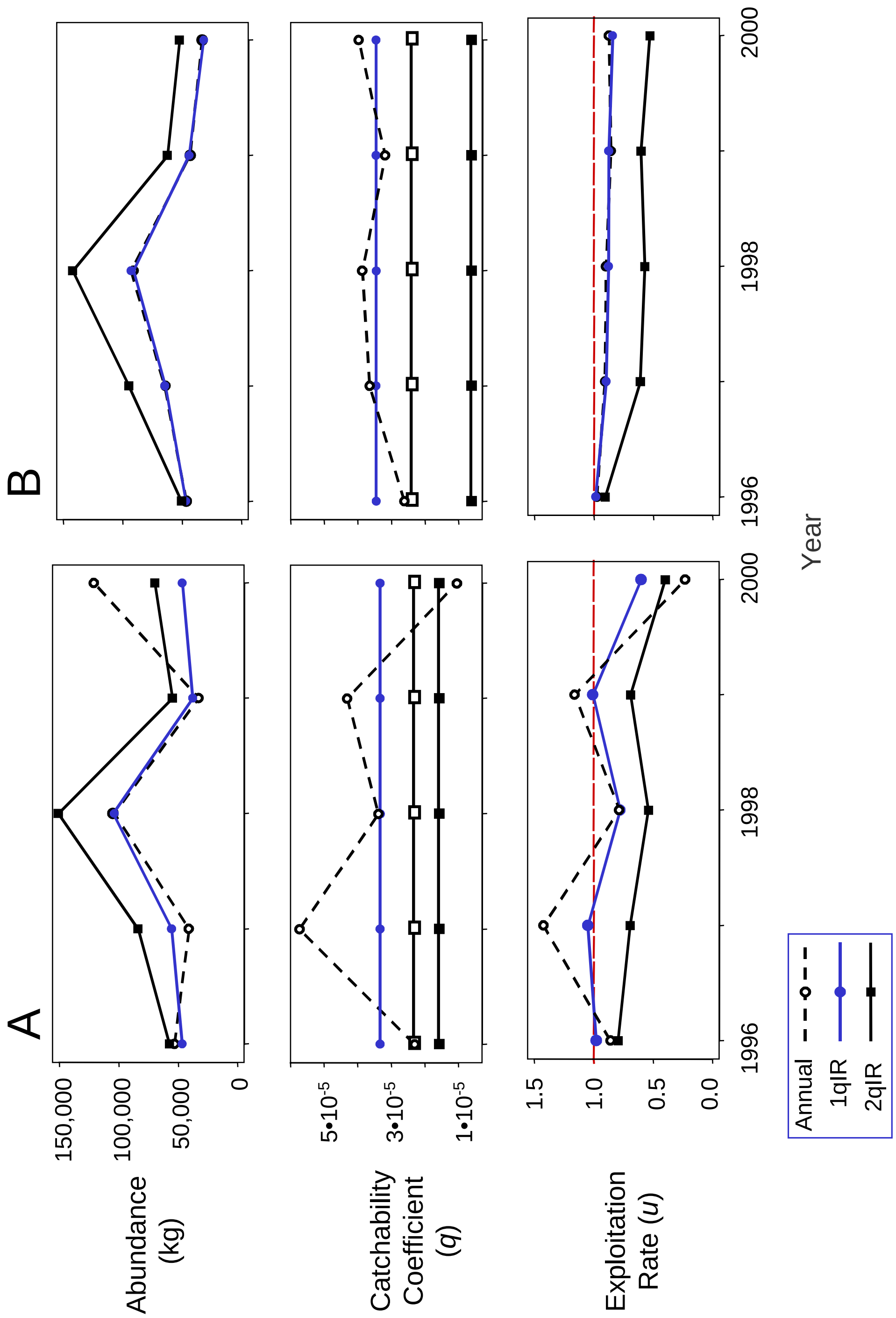
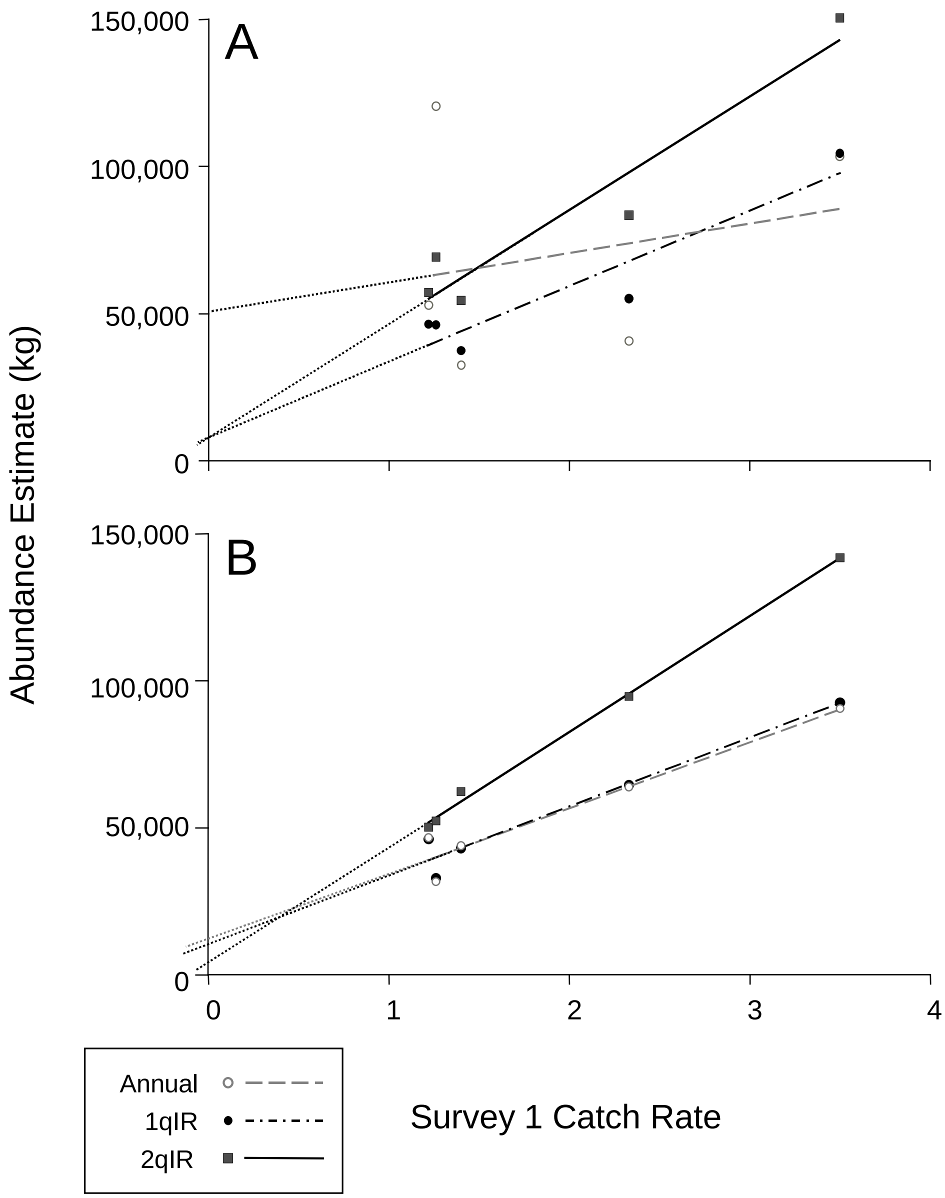

A
B
Abundance (kg)
150,000
100,000
50,000
0
Catchability Coefficient (q)
5•10-5
3•10-5
1•10-5
Exploitation Rate (u)
1.5
1.0
0.5
0.0
1996
1998
2000
Year
Annual
1qIR
2qIR

FIGURE 3.8

Comparison of diagnostic plots for each model. Plots represent regressions model abundance estimates against pre-harvest survey catch rates of corresponding years. Dotted lines indicate the y-intercept for each model. Regressions in (A) were based on data collected in spring and mid-season surveys; regressions in (B) were based on data collected in spring and fall surveys. All data were collected from stock assessment area 8, near Port Davey, Tasmania, Australia, for the fishing seasons that spanned years 1996/1997 to 2000/2001.


A
B
150,000
100,000
50,000
0
Abundance Estimate (kg)
0
1
2
3
4
Survey 1 Catch Rate
Annual
1qIR
2qIR

Chapter 4

Conclusions

CONCLUSIONS

<u>*Documenting seasonal trap inhibition of small lobsters*</u>

The experiment described here documented that the catchability of small lobsters in traps containing one large female lobster (seed) was lower in the Austral summer (February) when compared to control traps without seeds. The strongest inhibitory effect was observed in small females. No evidence of heterogeneity in survey catchability was found in the spring (November). If there are no inhibitory interactions in November then the catch rate of small lobsters, at that time, should be uninfluenced by the relative abundance of large lobsters. Thus, the catch rate of small animals in November might track trends in abundance over time. More testing is needed during more months of the year to clearly resolve the annual periodicity of the sex- and size-specific catchability patterns for rock lobster in Tasmania. Additional tests should also be performed with traps seeded with more than one large lobster to determine if an inhibitory (or attractant) effect on small lobsters is proportional to the number of large lobsters already in a trap.

Nonetheless, this study has given fishery managers some indication that a survey of sub-legal sized lobsters performed in November might reliably estimate the relative abundance of these animals. Perhaps just as important, fishery managers are now aware that a sublegal-catch index should not be performed in late summer, when the strong trapping inhibition observed for small animals can lead to serious biases in relative abundance estimates. With this information, managers may now be able to develop a successful index of future recruitment one or two years before animals recruit to the fishery.

Abundance estimation by the index-removal (IR) method

The two new IR models introduced here generalized the IR method to be useful under a much wider variety of conditions than was previously allowed by the annual model. Moreover, both the 1qIR and 2qIR models demonstrated substantial improvements in the precision of their estimates when compared to the annual model. The performance of the new models, both in simulation and in application, show that the IR method can be a valuable assessment tool for crustacean fisheries.

Since its introduction (Petrides 1949), the IR method has received little development. Though many have suggested that the method holds promise (Eberhardt 1982; Dawe et al. 1993; Chen et al. 1998; Hoenig and Pollock 1998), the precision of annual model estimates has been a problem (Eberhardt 1982; Routledge 1989; Roseberry and Woolfe 1991). Until this work, only Chen et al. (1995) have contributed to improving the precision of annual model estimates, by suggesting that the same sampling locations be used for both surveys.

The 1qIR model substantially improves the precision of estimates over that of the annual model estimates, and precision continues to improve as more years are added to the dataset. The proportion of simulated datasets providing feasible estimates also increases with more years of data. The 1qIR model also makes reasonable estimates possible in years where the catch rate increases between the first and second surveys – a situation that would have previously resulted in no feasible estimates for such years with the annual model.

Though the assumption of constant catchability is violated in many fisheries (Paloheimo and Dickie 1964; Hilborn and Walters 1992; Ziegler et al. 2002), evidence was presented by Ziegler (2003), and here in Chapter 2, that the assumption of constant catchability was tenable for some rock lobster datasets. For such fisheries, the 1qIR model offers the greatest precision for parameter estimates of the IR models.

The 2qIR model median estimates were accurate and precise when simulated over wide ranges of both exploitation rate contrast between two years of data, and catchability contrast between surveys. The estimates of the 2qIR model were feasible most of the time. The only 1qIR model and annual model estimates that outperformed those of the 2qIR model occurred when catchability was constant. Though the 2qIR model requires some contrast in exploitation rates between at least two years of a dataset, the model performed reliably (i.e., estimates were accurate and precise), with only two years of simulated data, whenever the difference between exploitation rates in the two years was 0.3 or more. Some gains in model performance were made when an additional year was added to the dataset, but results were essentially the same when three or five years of data were analyzed.

When the 2qIR model was applied to real data from a rock lobster fishery, all parameter estimates appeared reasonable. Three survey indices of the southern rock lobster population are conducted annually in Tasmania (spring, mid-season, and fall). Previous work (Ziegler et al. 2003) suggests that, although catchability is relatively constant between the spring and mid-season surveys, catchability is likely to be lower for the fall survey. The 2qIR model predictions were similar (Fig. 4.1) whether model estimates were made using the spring and mid-season surveys with similar catchabilities, or, the spring and fall surveys whose catchabilities are thought to differ (Ziegler et al. 2003). Moreover, the decrease in fall survey catchability predicted by the 2qIR model (Fig. 4.1) also supported the relative catchability estimates of Ziegler et al. (2003).

Both simulation results and the application of all three IR models to rock lobster data from Tasmania suggest that the 2qIR model can be reliably applied in more situations than can the 1qIR or annual models. Thus, the 2qIR model seems likely to be the most reliable choice for the IR estimators discussed here, unless one is reasonably sure that either the catchability coefficient or the exploitation rate is nearly constant among all years in a dataset.

The extreme biases seen in estimates of the annual and 1qIR models when catchability assumptions were violated in the simulations of Chapter 3, and the seasonal, sex- and size-specific catchability changes presented in Chapter 1, all demonstrate how important it is to have knowledge of the variability of catchability within a season. Such knowledge is important both for designing an unbiased survey, and for translating parameter estimates into advice for management. In Chapter 3, even though a likelihood ratio test could not find evidence that estimation of an extra parameter was required, prior knowledge of evidence of catchability change (Ziegler et al. 2003), along with the diagnostics of model performance, suggested that the 2qIR model parameter estimates were the most appropriate of the IR estimates.

Model choice

The 2qIR model predicted substantially higher abundance than did the 1qIR and annual models for the rock lobster data from Tasmania presented in Chapter 3. If one wishes to take a precautionary approach to management decisions, one is faced with a dilemma because which results are conservative depends on the circumstance. For instance, if the goal of management were to set a new quota, the 1qIR and annual model estimates would be more conservative because they predict the current population is already experiencing a very high level of exploitation. However, if the goal were to decide how much exploitation a population could withstand, then the 2qIR estimates that predict the population has survived a lower level of exploitation would provide more conservative advice on target exploitation levels.

Future work

The IR models described here assume a closed population. They will work best in crustacean fisheries with a well-defined molting season because the discontinuous growth pattern of such crustaceans ensures there is no recruitment between surveys due to growth. The IR models could also be used with vertebrate populations, if the fishery is a pulse (relatively short) fishery. How short the fishery needs to be depends on the life history of the species. If growth and reproduction are highly seasonal, and natural mortality is low, then a fishery lasting several months may approximate a pulse fishery. Alternatively, IR models could also be applied to vertebrate populations if the modeler accounts for growth of the animals within the model.

The closed-population IR models are particularly well suited for a heavily-exploited, recruitment-driven fishery like that of the rock lobster in southern Tasmania. This is because the IR models assume no linkage of the population from one year to the next. Frusher (1997) reported that 88% of the population is composed of new recruits. Thus, there is little carry-over of the stock from one year to the next and a link between years is relatively unimportant for modeling the fishery. However, when information is available that links years, an IR model that relaxes the assumption of a closed population can be developed. When a successful survey of sub-legal sized lobsters is implemented in Tasmania, a linked-year model will be able to be applied. The linked-year model will be useful to model those animals that were not harvested in previous years, and which remain unaccounted for in the current IR models. Such an open-population model would be especially useful for fisheries where the abundance of previous cohorts is as important, or more important than is the abundance of new recruits. An open-population IR model would be analogous to the catch-survey analysis model with one survey per year (as expressed by Mesnil 2003; originally described by Collie and Sissenwine 1983), but would be more efficient, because the open-population IR model would incorporate a second survey each year.

The generalized IR method is now useful for a variety of fisheries, and there is potential to generalize and develop the model further for use in even more applications. It remains a relatively simple model that estimates few parameters. Consequently, it may provide a useful alternative to more complex models that require the estimation of many more parameters. It also remains useful to double-check the estimates of other methods (Dawe et al. 1993) but, with the generalizations made here, the IR method may now be precise enough to be relied upon for its own estimates, whether or not catchability changes between the pre- and post-harvest surveys.

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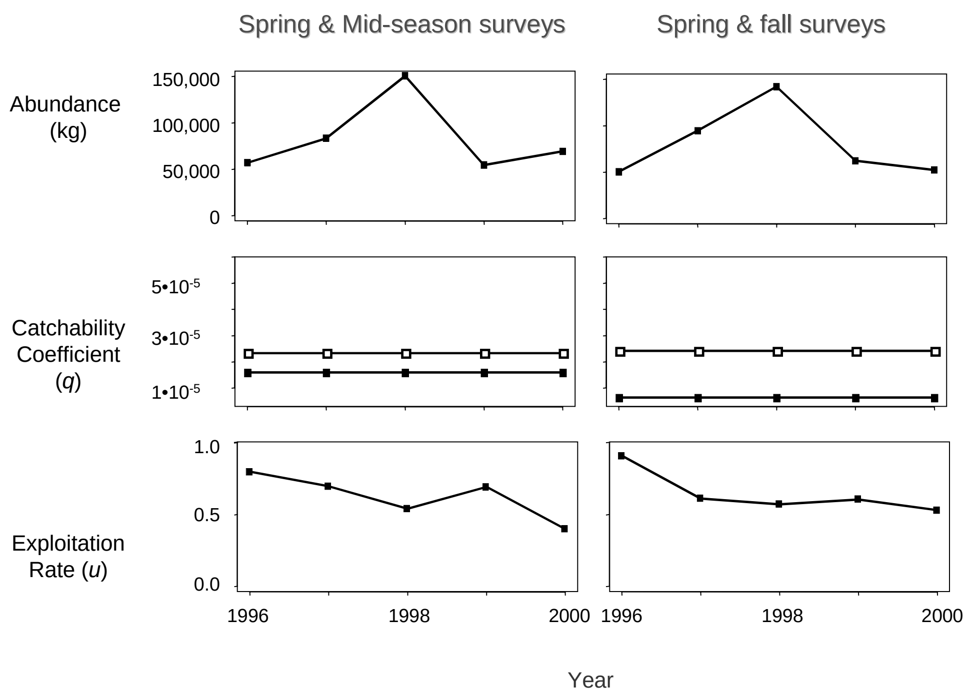
FIGURE 4.1



Abundance and exploitation rate estimates of the 2qIR model. Estimates were similar whether the data analyzed included the spring and mid-season surveys, which are thought to have similar catchabilities (Ziegler et al. 2003), or the spring and fall surveys, which are thought to differ in their relative catchabilities (Ziegler et al. 2003).

VITA

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