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Catchability of the southern rock lobster *Jasus edwardsii*. II. Effects of size

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Abstract. For most of the year, the size-frequency distribution of trap-caught southern rock lobster, *Jasus edwardsii*, reflected size-specific catchability rather than the size-frequency distribution of the population in a scientific reserve in Tasmania, Australia. The size-frequency distributions of the population on the ground and of lobsters captured in traps were similar only during a few months, typically during moulting and mating. Small males and females were usually under-represented in traps. Catchability generally increased with size, but varied with sex and season. During moulting and mating, size-specific catchability and relative selectivity of larger animals were similar to or lower than for smaller animals. The relative pattern of catchability throughout the year was similar for most size classes within each sex. Negative associations between small and large lobsters in traps were stronger in winter than in summer, indicating strong behavioural interactions. These interactions could explain the lower catchability of smaller lobsters. Relative selectivity estimates using tag–recapture and size-specific catchability data provided generally similar results.

Introduction

The size-frequency distribution in lobster populations has been applied to estimate the impact of fishing, changes in recruitment and the reproductive potential of a population (Campbell and Pezzack 1986; Campbell 1990; Frusher 1997). Since direct observations of populations *in situ* are rarely available, size-frequency data from trap catches are used. However, it is seldom possible to test whether the size-frequency distribution in traps is a true representation of that in the population.

In many lobster fisheries, animals caught in traps will not reflect the size-frequency in the population. Behavioural interactions and the design of traps often result in an increase in catchability with increasing size of animals in trap catches (e.g. Richards *et al*. 1983; Karnofsky and Price 1989; Miller 1989, 1995; Addison 1995; Pezzack and Duggan 1995; Addison and Bannister 1998; Frusher and Hoenig 2001). In addition, size-specific catchability can vary seasonally, as found in male and female American lobsters, *Homarus americanus* (Tremblay 2000; Tremblay and Smith 2001). Thus, it may be important to account for seasonal variation in size-specific catchability in estimating the size-frequency distribution of a lobster population from the size-frequency distribution of trap catches. Despite this, most studies to date provide only point estimates of size-specific catchability for a specific period of the year.

We have estimated, for the first time, monthly variation in size-specific catchability of an unfished spiny lobster population. By comparing the seasonal variation in the size-frequency distribution of the southern rock lobster, *Jasus edwardsii*, in trap catches and in the population on the ground, we examined whether catchability depends on sex, size and season, and whether the size-frequency distribution of trap-caught lobsters reflects the true size-frequency distribution of the population.

Material and methods

Underwater observations

Underwater visual observations and trapping surveys were conducted on a rocky reef in a scientific reserve at Crayfish Point near Hobart in Tasmania, Australia (42°57.2′S 147°21.2′E). Fishing for rock lobster by commercial and recreational fishermen has been prohibited in the reserve since 1970. Lobster density was estimated *in situ* in most months between February 1999 and April 2000, except for April 1999 and August to November 1999. On each sampling occasion, 10 replicate belt transects (each 4 × 100 m) were used. Transects were set haphazardly from a vessel to avoid diver-bias in the selection of habitat, but in such a way that the sampling intensity was approximately uniform across the entire reef. The bottom, including any cavities under boulders, was searched thoroughly within 2 m of each side of the transect line. All lobsters encountered on each transect were counted, sexed, and their carapace length (CL) estimated by eye to the nearest 5 mm. Lobsters were not handled during these surveys to avoid disturbance to their behaviour. A small number of animals in each series could not be sexed and were omitted from the analysis. All visual counts

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Table 1. Effect of sex, size and time period on size estimation errors in the underwater visual observations

Male and female lobsters were divided in two size classes: small males up to 120 mm carapace length (CL); medium/large males >120 mm CL; small females up to 105 mm CL; medium/large females >105 mm CL). Analysis by three-way ANOVA. Data were homoscedastic and errors were normally distributed (Shapiro–Wilk *W*-test, $P = 0.29$)

Source	df	F	P
Sex	1	0.09	0.76
Size	1	0.43	0.51
Time	9	0.27	0.98
Sex × size	1	0.39	0.53
Sex × time	9	0.89	0.54
Size × time	9	1.23	0.27
Sex × size × time	9	1.23	0.28

were undertaken by the same person to ensure consistency in animal detection and size estimation.

Lobster counts from direct visual observations underwater were similar for males and females and varied between 63 animals in June 1999 and 171 animals in February 2000. The size-frequency distribution of both genders was split into an equal number of size classes. However, different class sizes for males and females were used, since the largest males were approximately 190 mm in size, whereas the largest females attained only 140 mm CL. Males were divided into 20-mm size classes from 81–200 mm CL, and females were divided into 10-mm size classes from 81–140 mm CL. Since only lobsters greater than 80 mm CL were tagged in the trapping surveys, animals smaller than this size limit were excluded from the analysis of the underwater observations.

To improve the accuracy of size estimation of lobsters in visual observations, size estimation was practised before the underwater observations with 298 lobsters, housed in a large outdoor raceway with an artificial rocky reef. During the last of nine training sessions, mean estimation error between the visually estimated and actual measured size of captive animals was –1 ± 4 mm (s.d.; $n = 35$).

Errors associated with visual estimates of size were determined by comparing visual estimates, x_{est}, to known sizes, x_{actual}, of animals with unique antenna tags. These tags were attached when lobsters had been caught, tagged, measured and released in a previous trapping survey. Estimation errors greater than 30 mm were assumed to be incorrect observations of the tag number and these data were omitted. For each visual survey, estimation bias, a, was calculated from a regression of actual error ($= x_{est} - x_{actual}$) versus actual size of individuals as:

$$a = b + c \times x_{actual} \tag{1}$$

and subtracted from each visual estimate x_{est}. Remaining estimation errors were independent of sex, size and time periods (Table 1). The mean estimation error between estimated and measured sizes during all surveys was 0 ± 11 mm (s.d.). Estimation errors for lobsters of 80–190 mm CL were normally distributed around the measured sizes.

To correct the size-frequency distributions of the population for the observed errors in size estimation, proportions of observed numbers in each size class were assigned to adjacent size classes according to a normal distribution with the observed standard deviation of estimation errors. An average of 24% of all lobster counts, n, in each 10-mm size class, y, of females were assigned to adjacent greater and smaller size classes in equal amounts, and 8% to the next following size classes:

$$n_{y\,corr} = 0.08 \times n_{y-2} + 0.24 \times n_{y-1} + 0.36 \times n_y + 0.24 \times n_{y+1} + 0.08 \times n_{y+2} \tag{2}$$

For the larger size classes, y, of males, 18% of all lobster counts, n, in a size class were assigned to adjacent greater and smaller size classes in equal amounts:

$$n_{y\,corr} = 0.18 \times n_{y-1} + 0.64 \times n_y + 0.18 \times n_{y+1} \tag{3}$$

Only the smallest and largest size classes were treated differently. To account for lobsters that were greater than 80 mm CL but estimated to be smaller than 80 mm CL and hence not counted in the study, we assumed similar numbers of male and female lobsters just smaller and greater than 80 mm CL and added respective proportions of animals to the size classes greater than 80 mm CL. The proportions of observations in the largest size class, which were theoretically assigned to sizes of animals greater than present in the population, were assigned to the largest size class.

Monthly means of the corrected densities in each size class were compared using ANOVA. To stabilize the variances, the data were square-root transformed.

Trapping survey

The reef was also fished by trapping each sampling period. Trapping surveys usually took place within the 2-week period of each underwater survey. Over four consecutive days, 24 traps were set daily, resulting in 96 trap lifts per monthly survey. After the first day, when the traps were set in the early afternoon, they were hauled and set again in the early morning of each of the following days, with a soak time of about 24 h. Care was taken to fish the entire reef with equal effort to avoid bias that may arise from concentrating effort in a particular part of the reef. The traps were set over the reef in similar positions on consecutive days, with at least 10–20 m distance between traps. The traps had a mesh size of 40 mm and were not equipped with escape gaps.

All lobsters captured were sexed, tagged ventrally with a T-bar tag (Hallprint T-bar anchor tag, TBA1; Hallprint Pty Ltd, Holden Hill, Australia) and an antenna tag (numbered plastic label tied to the base of the antenna), their CL measured to the nearest millimetre, and the animal released immediately. The largest lobsters caught in the trapping survey were 193 mm for males and 143 mm CL for females. Only animals greater than 80 mm CL were tagged and included in the analysis. All males and most females were mature. Size at onset of maturity was approximately 65 mm CL for males (C. Gardner, unpublished data) and 81 mm CL for females (P. E. Ziegler, unpublished data).

Monthly trapping surveys were undertaken from April 1999 to April 2000 inclusive, except in May 1999, when there were two surveys 2 weeks apart. Three additional surveys were undertaken, the first two in January and March 1999 using 50 traps each day over 20 and 10 days, respectively, and a third in January 2000 using 78 traps each day over 8 days. To standardize the effort for the catch rate analysis, only the data from the first 4 days of the additional surveys were included, and 24 traps were randomly selected for each day. In the first two of the additional surveys, lobsters were removed from the reef, held in tanks and returned at the end of each survey. Although catch rates generally decreased over the whole period of these surveys as a result of the removal, the impact on the first 4 days was minimal (Frusher and Hoenig 2001).

Catches were more variable for males than for females throughout the study. Only 14 males were captured in August 1999, compared with 209 males in February 1999. To ensure total catches of at least 50 animals, catches were pooled in July and August and in September and October for both sexes, and in March and April for females only.

Size-specific catchability

Catchability, q, or the effective fishing area of a trap (in m^2 per trap) for any given period of time, t, was estimated for size class, l, as the ratio of lobsters per trap haul to lobster density:

$$q_{lt} = C_{lt} / (f_t D_{lt}) \tag{4}$$

where C is catch in number of animals, f is total effort in number of trap hauls, and D is density of animals per m^2.

To investigate the interaction between small and large lobsters, the numbers of small and large males and females in traps were correlated using the Spearman's rank correlation. Lobsters of the smallest size class (males: 81–100 mm CL, females: 81–90 mm CL) were correlated to large lobsters (males: >140 mm CL, females: >120 mm CL) during the austral winter from April to October 1999 and during the summer months in November 1999 to February 2000.

Relative selectivity estimated by size-specific catchability and tag–recapture method

Relative selectivity at time t was estimated by using either size-specific catchability or tag–recapture data. Catch rate data and density estimates of males and females were split into small (undersize), medium and large size classes (males: small 81–110 mm CL, medium 111–140 mm CL, large >140 mm CL; females: small 81–105 mm CL, medium 106–120 mm CL, large >120 mm CL). For estimates using size-specific catchability, relative selectivity ϕ_l of each size class, l, was estimated bimonthly by standardizing size-specific catchability, q_l, to the interval [0,1] as:

$$\phi_l = q_l / q_{l\max} \tag{5}$$

where $q_{l\max}$ refers to the catchability value of the size class with maximum catchability during the period.

For the tag–recapture method, lobsters tagged during the first trapping survey (January 1999) and recaptured in subsequent surveys were used to estimate trap selectivity. Selectivity, ϕ_l, in each size class was estimated bimonthly as the proportion of tags returned, and standardized to the interval [0,1]:

$$\phi_l = (n_{Rl} / n_{Tl}) / \max_l (n_{Rl} / n_{Tl}) \tag{6}$$

where n_{Tl} is the number of lobsters tagged in size class l during the first survey, n_{Rl} is the number of lobsters of size class l tagged in the first survey that were recaptured in each subsequent survey, and $\max_l$ refers to the selectivity value of the size class with maximum selectivity during the period.

The number of recaptured lobster and the size class limits used in the tag–recapture method needed adjustment for growth due to moulting. Males 81–110 mm CL and 111–140 mm CL grew on average 8.7 ± 0.9 mm (n = 45) and 7.3 ± 0.3 mm (n = 122) per moult respectively. Females 81–105 mm CL and 106–120 mm CL grew on average 4.1 ± 0.4 mm CL (n = 74) and 2.4 ± 0.3 mm (n = 68) per moult respectively. For selectivity estimates after moulting (September/October to January/February for males; all periods for females), recaptured males and females were excluded from the analysis if they had grown into a higher size class between tagging and subsequent recapture. The numbers of small and medium-sized lobsters in the initial survey also needed adjustment to account for animals that grew out of their initial size class. The size classes including animals during the first survey were reduced by the mean growth increments. For example, the 81–110 mm CL size class of males was reduced to 81–101 mm CL to account for the 8.7 mm growth. No adjustment was needed for the size class of large males and females, since these animals did not change their size class through moulting.

Results

Size-frequency distribution in the population

Visual counts of the density of most size classes of males and females showed little monthly variation (Fig. 1). Only the smallest size class of males (81–100 mm CL) showed significant seasonal changes. Significantly more males were found in February and March 2000 than in February, March, June and December of the previous year, and in April 2000 (Tukey–Kramer HSD test). Although immigration of small lobsters into the reef region during February and March 2000 and subsequent emigration could not be discounted, we considered that the variation in density estimates was more likely to have resulted from the variable chance of encounter of small males. The variance to mean ratio decreased with size for males and females and indicated that small males were highly aggregated compared with large males at the scale of 400 m^2 (linear regressions for males: $R^2 = 0.94$, $F_{1,5} = 64.75$, $P < 0.005$; females: $R^2 = 0.91$, $F_{1,5} = 38.43$, $P < 0.005$; Fig. 2).

Thus, we considered that densities of all size classes were constant throughout the study period. Accordingly, each observation was treated as a sample of the population on the ground and all samples were pooled to provide the most robust estimate of the population. Densities of males were highest for small animals (0.64 males per 100 m^2) and decreased with size, whereas densities were similar for females between 81 and 120 mm CL, and decreased only for females larger than 120 mm CL (Fig. 3).

Size-frequency distribution in trap catches

The size-frequency distribution of animals in catches varied considerably between months and was significantly different from the size-frequency distribution in the population estimated from the visual observations for most times of the year (Figs 4, 5). The smallest size classes of males and females were usually under-represented. Large males between 121–180 mm CL were over-represented in most catches from June to August and from November to March; their proportions in the population and in catches were similar in April and May and in September and October. Large females between 111–130 mm CL tended to be over-represented in catch samples in February and from May to December. Similar proportions as in the population were found in January, March and April.

Size-specific catchability over the year

Size-specific catchability coefficients or effective fishing areas per size class ranged from 6 to 201 m^2 per trap for males and from 2 to 143 m^2 per trap for females. Catchability of the largest size class in both sexes was not calculated because of the small sample sizes in the catches.

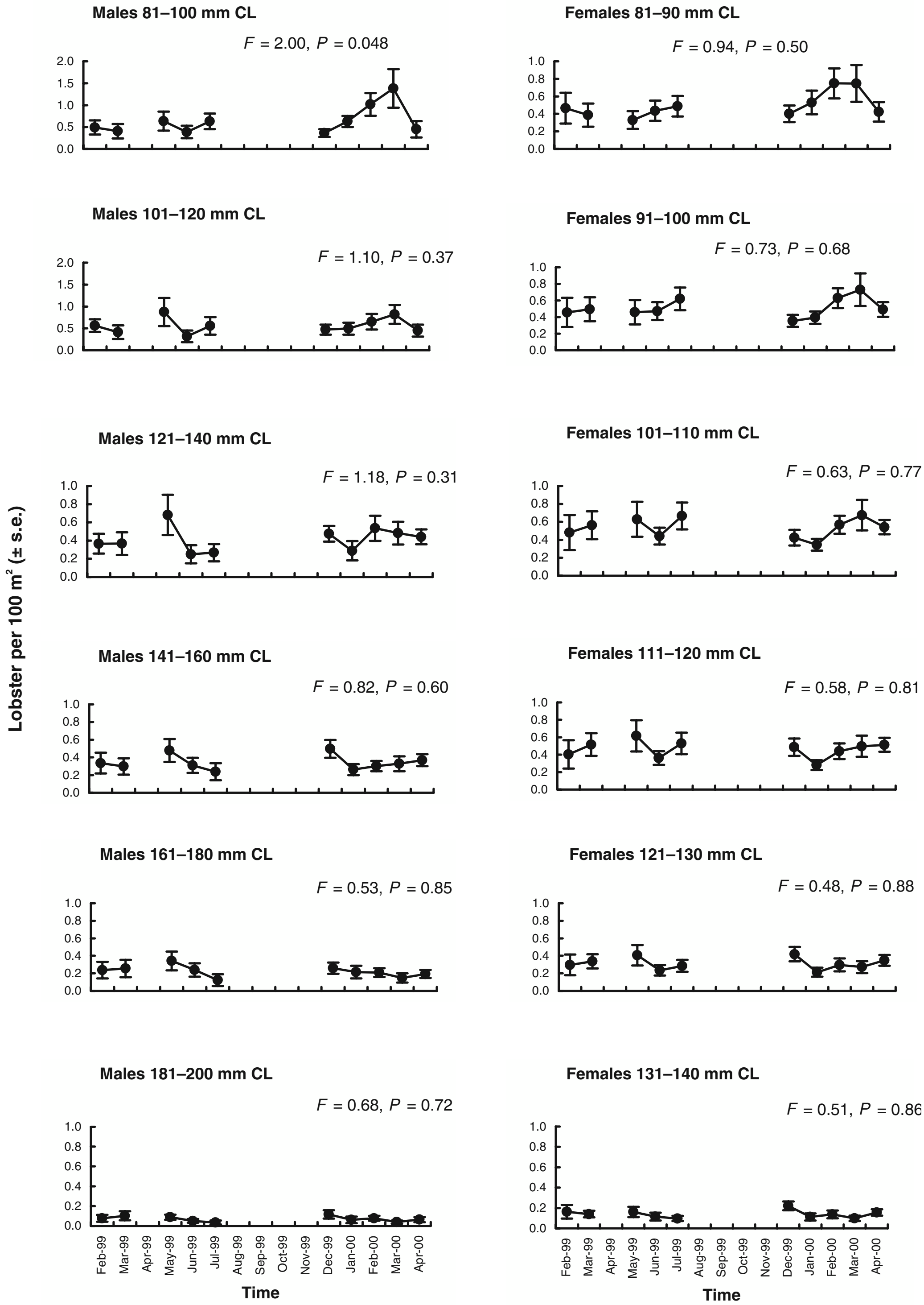

Fig. 1. Densities of lobsters per size class estimated using underwater visual observations. Data are mean counts per 100 m^2 (± s.e.) from February 1999 to April 2000. Note that the y-axis scale differs for the two smallest size classes of males. Seasonal changes in density were tested with 1-way ANOVA.

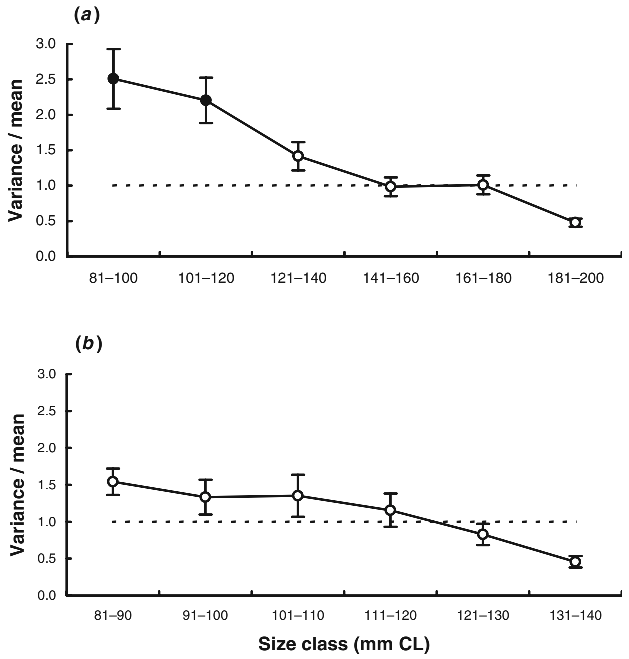

Fig. 2. Variance to mean relationship (± s.e.) of density estimates from transects using underwater visual observations for all size classes of (*a*) male and (*b*) female lobsters. Filled circles indicate size classes for which variance to mean ratios differ significantly from random (index of dispersion test, Krebs 1989). The dotted line indicates random distribution where variance to mean = 1.

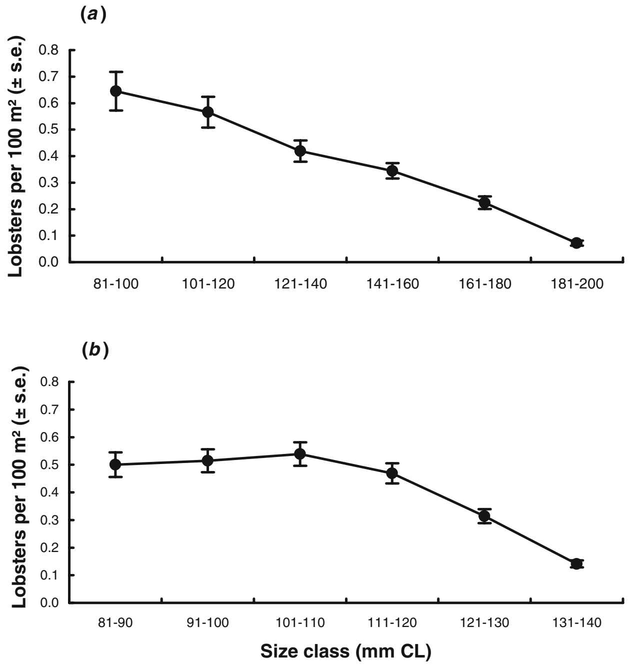

Fig. 3. Mean population density (± s.e.) for each size class of (*a*) male ($n = 899$) and (*b*) female lobsters ($n = 981$). Data pooled from all underwater visual observations.

Catchability generally increased with size, but the magnitude of the increase varied with season (Fig. 6). Catchability of the smallest size class of both sexes was low during the whole year. Catchability of the larger size classes was generally highest from November to May for males and from October to January for females. A smaller peak occurred in May for both sexes, although it was slightly earlier for females.

Despite these differences in catchability between sizes, catchability within each sex and size class mostly followed a similar pattern throughout the year (Fig. 6). Catchability of each size class was standardized to the interval [0,1] throughout the study period, excluding February 1999. The catchability of the two smallest size classes of females was exceptionally high in February 1999 and could not be explained. Males of all except the 101–120 mm CL size class, reached maximum catchability in December and lowest catchability in April and between July and September. The magnitude of seasonal changes was greater for large males than small males. Relative catchability of males between 81–100 mm CL and between 121–180 mm CL described a high proportion of the variation in catchability of the total population of males (Table 2). Relative catchability of females between 91 and 130 mm CL followed similar seasonal trends, but only the catchability of the animals between 111 and 120 mm CL described a high proportion of the variability in the overall catchability of females.

Significant negative correlations between trap catches of large and small lobsters were found during the winter and summer periods, although the effect was weaker in summer (Table 3). Large females had a higher negative correlation with small lobsters of either sex than did large males with small lobsters of either sex.

Relative selectivity estimated by size-specific catchability and tag–recapture method

During most periods of the year, relative selectivity of male and female lobsters increased with size (Fig. 7). Selectivity of small males and females was similarly low, whereas selectivity of medium-sized and large lobsters was often higher for males than for females. Major exceptions were the periods in July/August and September/October, when the selectivity of the largest size classes was reduced for females and males respectively.

Relative selectivity estimated by size-specific catchability and tag–recapture method provided similar results for all size classes of males and females from March to June, and in November/December. However, in January/February and September/October, relative selectivity for small and medium-sized males and medium-sized females was higher when estimated by the tag–recapture method than by size-specific catchability. In July/August, the tag–recapture method also provided higher estimates for medium-sized

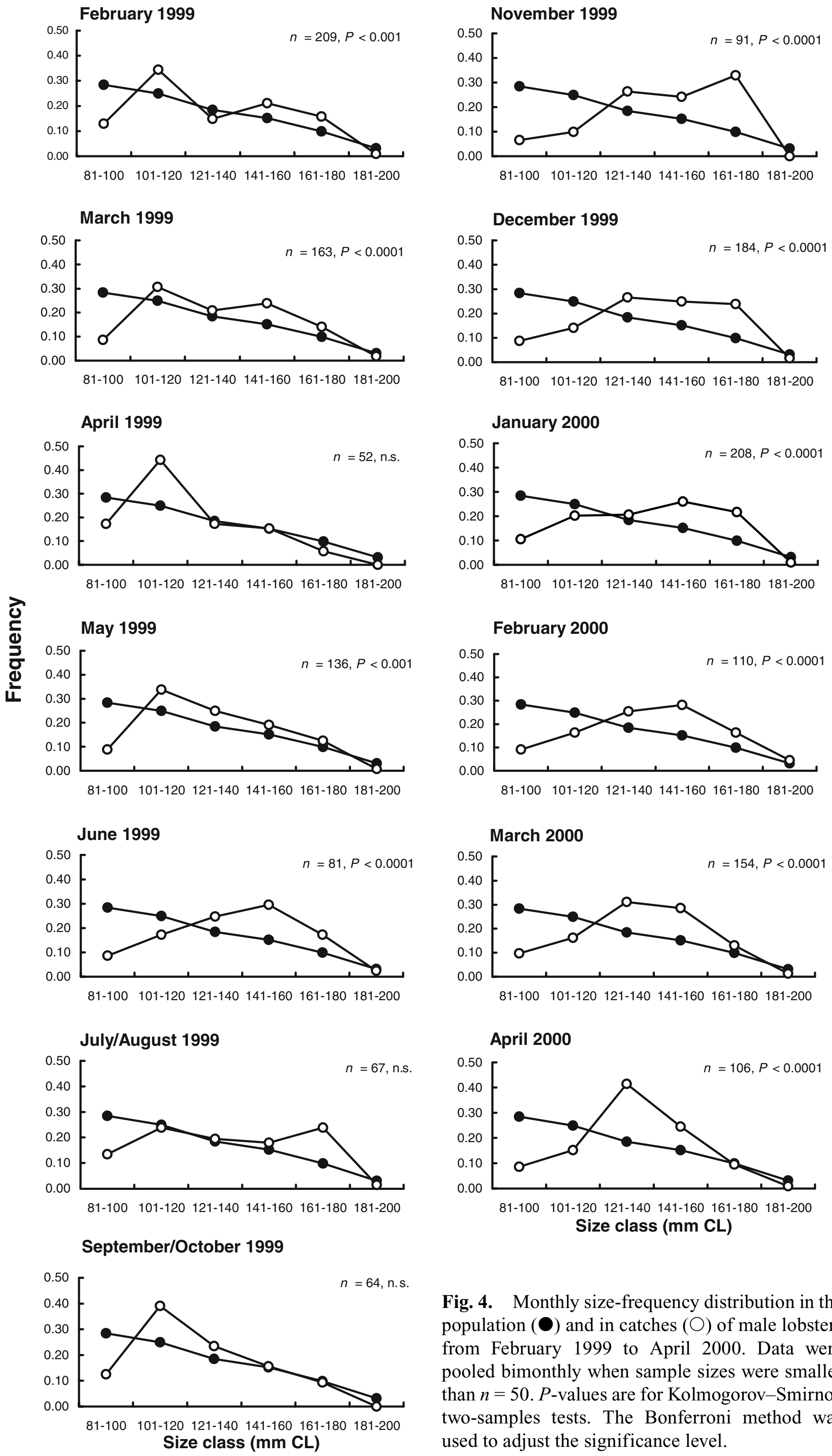

Fig. 4. Monthly size-frequency distribution in the population (●) and in catches (○) of male lobsters from February 1999 to April 2000. Data were pooled bimonthly when sample sizes were smaller than $n = 50$. P-values are for Kolmogorov–Smirnov two-samples tests. The Bonferroni method was used to adjust the significance level.

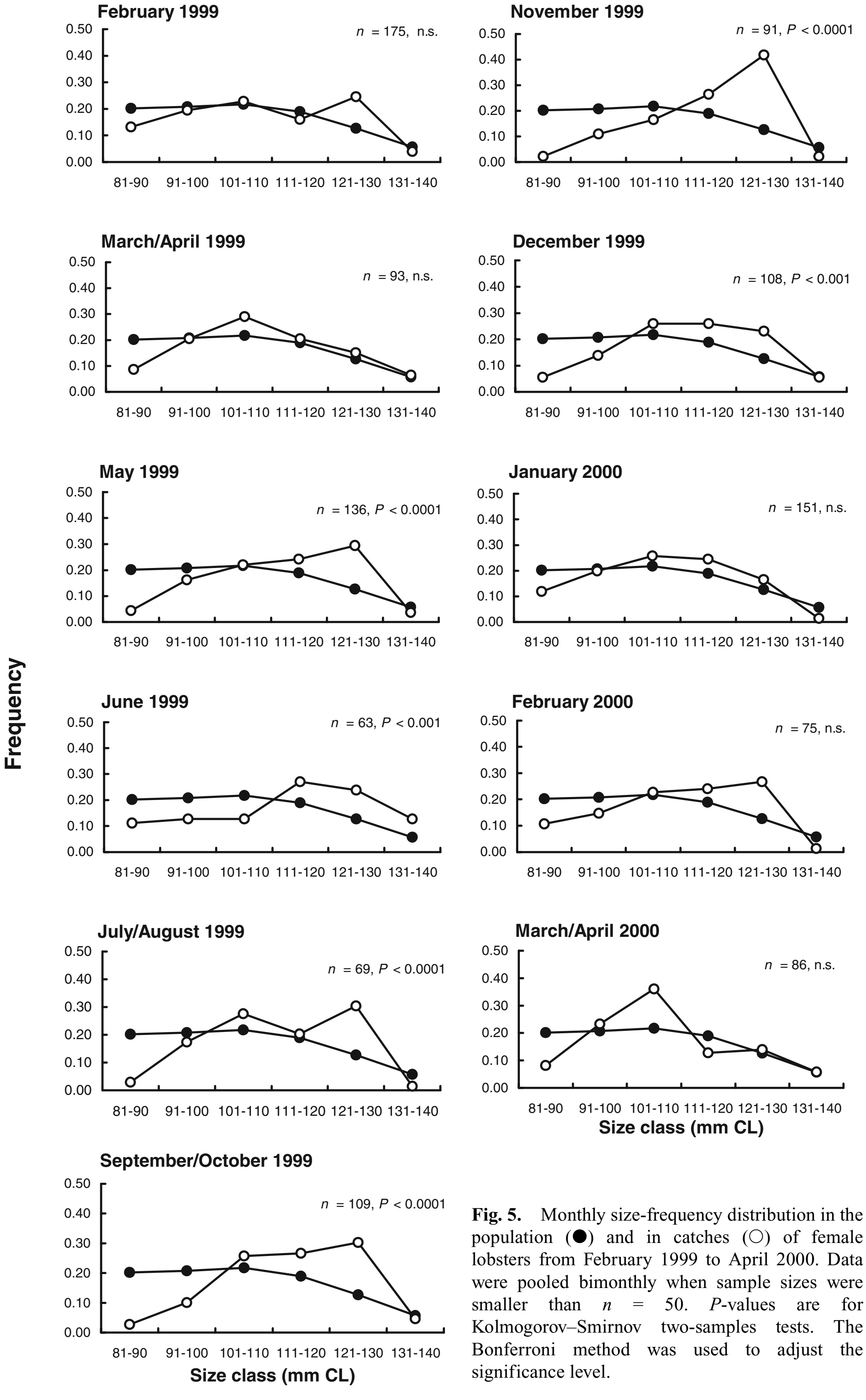

Fig. 5. Monthly size-frequency distribution in the population (●) and in catches (○) of female lobsters from February 1999 to April 2000. Data were pooled bimonthly when sample sizes were smaller than $n = 50$. P-values are for Kolmogorov–Smirnov two-samples tests. The Bonferroni method was used to adjust the significance level.

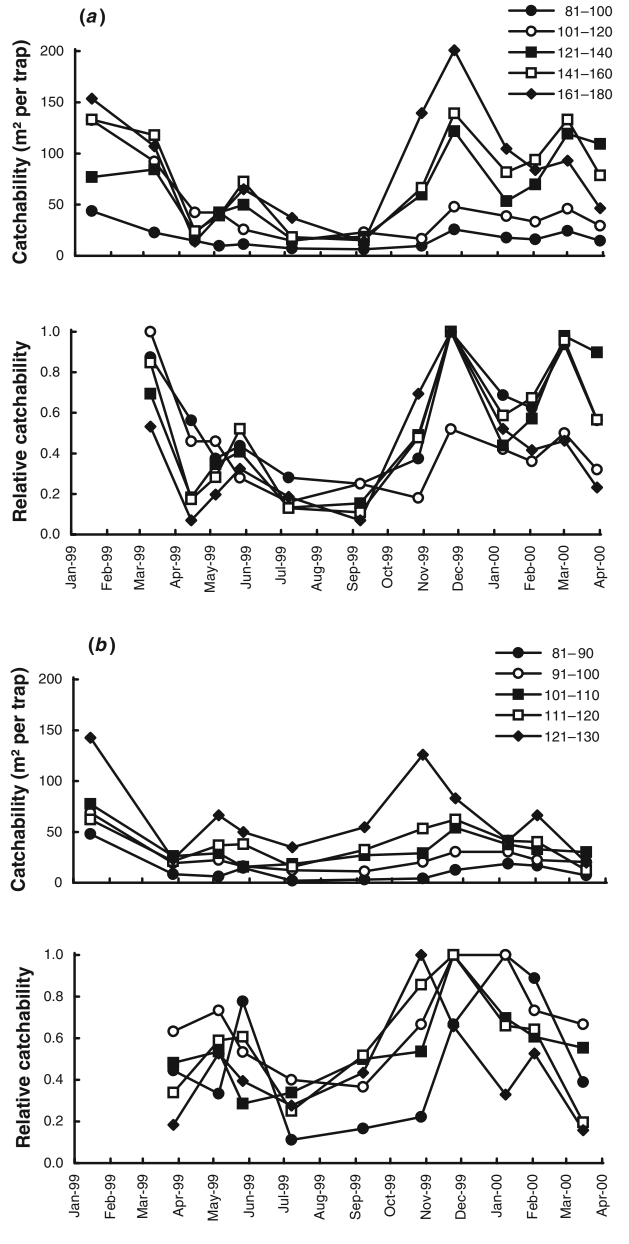

Fig. 6. Seasonal changes in absolute and relative catchability for each size class of (*a*) male and (*b*) female lobsters. Data for February 1999 are excluded for estimates of relative catchability (see text).

females, but lower estimates for large females. Estimates of relative selectivity by the tag–recapture method are considered to be the poorer estimates from July to October owing to the small sample sizes of recaptured animals.

Discussion

Size-frequency distribution in the population

Population densities of most size classes in each sex remained relatively constant over time. Although there were temporal differences in density of the smallest size class of males, this may well arise as an artefact of this highly aggregated sub-population. Highly over-dispersed distributions, indicated by the high variance to mean ratios for smaller lobsters, are known similarly for other *J. edwardsii* populations (MacDiarmid 1991, 1994; Treble 1996). However, although a sampling bias resulting from the aggregated distribution of small lobsters is the most simple and parsimonious explanation, we cannot exclude migration as another potential cause of the seasonal changes in density. Large-scale migrations, mainly of immature females and small males, have been reported for *J. edwardsii* from New Zealand and Tasmania (Booth 1997; C. Gardner, personal communication). Also, decreasing rates of recapture in our catches of small males indicated a weak immigration (Ziegler *et al.* 2002). Seasonal movements offshore to adjacent feeding areas on sand, as described in New Zealand (Kelly *et al.* 1999; Kelly 2001), seemed less likely. Mainly large animals were found to move offshore, while densities of large animals on the reef in this study remained constant and only the densities of small animals changed.

Even if we wrongly assume a constant population density of small males over the year, the effect of this assumption on catchability is minimal, because small males were greatly under-represented in catches and their size-specific catchability was small all year round. By neglecting to account for an apparent increase in their population density during the austral summer, we would only slightly overestimate their low catchability.

Table 2. Variation of catchability in the total population of male and female lobsters described by catchability of each size class for males and females respectively

CL, carapace length

Males Size class (mm CL)	R^2	Females Size class (mm CL)	R^2
81–100	0.86	81–90	0.18
101–120	0.42	91–100	0.50
121–140	0.82	101–110	0.55
141–160	0.96	111–120	0.95
161–180	0.65	121–130	0.62

Size-frequency distribution in trap catches and size-specific catchability

Whereas the densities of all size classes, and therefore the size-frequency distribution in the population, showed little or no changes over the year, the size-frequency distribution in trap-catches varied greatly, reflecting size-specific catchability, which varied with sex and season.

Size-specific catchability was lowest for the smallest lobsters and led to an under-representation of small males and females in catches for most of the year. Catchability generally increased with size, but the increase varied strongly with sex and season. Mainly during moulting and

Table 3. Spearman rank correlations between pairs of small and large male and female lobsters captured during winter between April and October 1999 when differences in size-specific catchability were low, and during summer in November, December 1999 and February 2000, when differences in size-specific catchability were high

Small males: 81–100 mm carapace length (CL) (SM); large males: >140 mm CL (LM); small females 81–90 mm CL (SF); large females: >120 mm CL (LF). Sample size, *n*, refers to the number of pairs used in each correlation

Period		LM:LF	LM:SM	LM:SF	LF:SM	LF:SF
Winter	*n*	194	134	116	154	128
	Correlation	–0.53	–0.61	–0.45	–0.81	–0.50
	P	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Summer	*n*	156	143	139	89	81
	Correlation	–0.20	–0.25	–0.27	–0.52	–0.43
	P	0.014	0.003	0.002	<0.0001	<0.0001

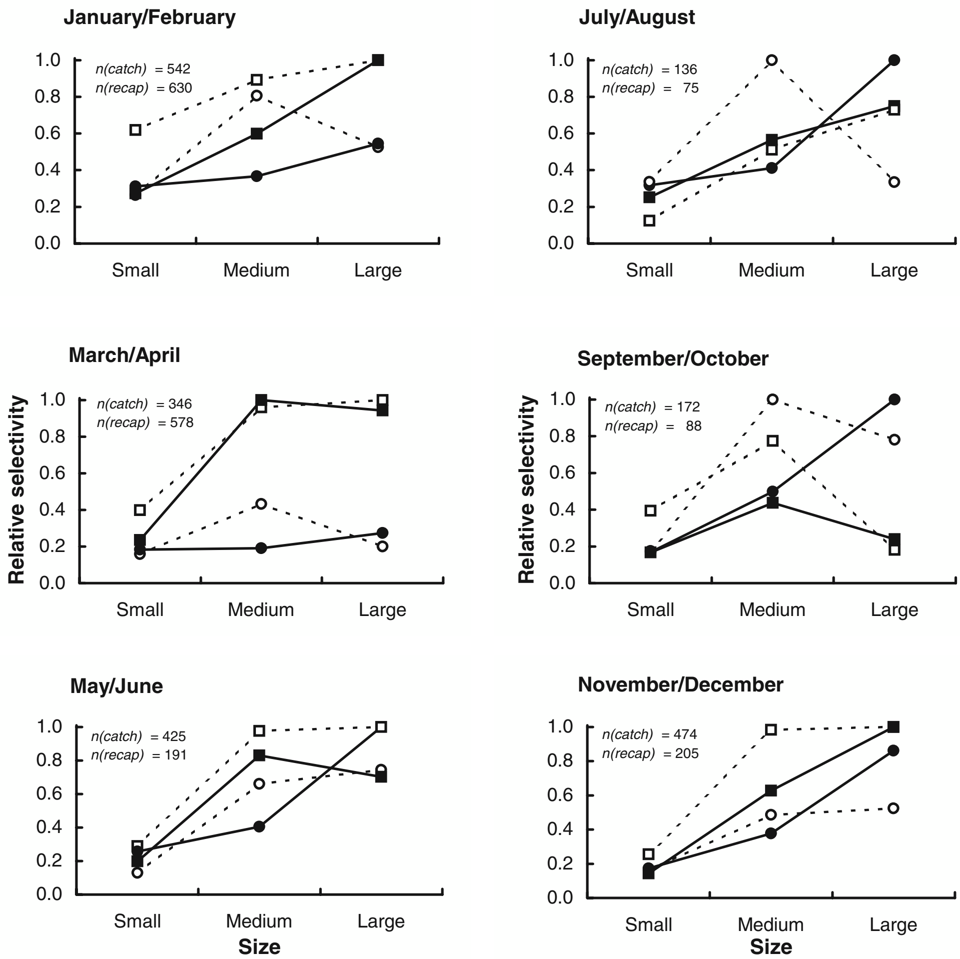

Fig. 7. Relative selectivity estimated from standardized size-specific catchability (solid lines and filled symbols) and by the tag–recapture method (dotted line and open symbols) for small, medium and large male (squares) and female lobsters (circles) during different periods of the year. Data were pooled bimonthly because of low sample sizes. Total sample size *n*(catch) refers to combined male and female catches in standardized size-specific catchability, total sample size *n*(recap) refers to combined male and female recaptures using tag–recapture method.

mating, catchability did not increase with size and sometimes decreased for larger animals. Only during these months were the size-frequency distributions in the population and in traps similar. Larger males appeared in similar proportions in the population and in trap catches during moulting in September and October and during mating in April and May. Large females appeared in similar proportions in March and April, that is during most of the period of moulting and mating between March and May, and also in January of the second summer. Large males and females were generally over-represented in catches after moulting and mating and during the warmer summer months, when their feeding activity is higher (McLeese and Wilder 1958; Branford 1979; Lipcius and Herrnkind 1982; Zoutendyk 1988; Miller 1990; Kelly *et al*. 1999). This result highlights that there are strong seasonal effects on catchability of lobsters in trapping. This has also been reported for *H. americanus* in Canada, where male and female lobsters differ in the magnitude of the increase in catchability with size between June and September (Tremblay 2000; Tremblay and Smith 2001). The earlier moult of males seems to reduce catchability of large males in June compared with September, whereas large females show the reverse trend.

Intraspecific interactions may have influenced size-specific catchability. The presence of lobsters in traps can inhibit the entry of other lobsters by intraspecific behavioural interactions (Richards *et al*. 1983; Karnofsky and Price 1989; Miller 1990; Addison 1995; Addison and Bannister 1998). We found significant negative correlations between large and small lobsters in trap catches. In a study on the same reef, Frusher and Hoenig (2001) concluded that large lobsters reduce the likelihood that smaller lobsters enter traps, since small lobsters showed a gradual increase in catches when large lobsters declined. Thus, the presence of large animals throughout our study may explain the generally lower catchability of smaller animals.

Nevertheless, the negative correlations in the traps varied with season and were stronger in winter. This is surprising, since a decrease in intraspecific interactions is expected when feeding rates decrease. A tendency of large animals to feed on nocturnal excursions at the reef edge or on adjacent sand flats during winter could have resulted in stronger negative correlations between large and small animals owing to the spatial separation of feeding grounds. Seasonal variation in feeding excursions, with lobsters staying away from the reef over an extended period, has been described in New Zealand. Kelly *et al*. (1999) found large females on the reef edge and adjacent sand flats only during winter, while large males were foraging in these areas in winter and summer. Therefore, it remains unclear whether the actual intraspecific interactions between animals around traps vary, or whether the seasonal variation in negative correlation is the result of a massive reduction in feeding activity in winter for small animals, while larger lobsters continue to feed.

Size-specific differences in the foraging activity of lobsters and the trap design could also have influenced catchability. Large lobsters are expected to have a greater foraging range, increased food requirement and faster walking rates than small lobsters and are therefore more likely to encounter a trap (Zoutendyk 1988). Large American lobsters *H. americanus* spend more time during the day foraging than do small lobsters (Lawton 1987), although there is no evidence that this is the case for the European lobster *Homarus gammarus* (Smith *et al*. 1999). In addition, the design of traps can be selective for large animals, as they often allow small animals to escape (see review by Miller 1990). This mechanism would not operate in the present study, since the traps were not fitted with escape gaps. The design of the traps may have restricted the entry of very large animals (Pezzack and Duggan 1995), but the number of these animals in the population and in catches was too low to estimate catchability.

Although the behavioural interactions, foraging activity and trap design affect catchability, taken together they do not explain the seasonal pattern in catchability that we observed in all size classes. Based on seasonal changes in behavioural interactions, increased catchability of small lobsters would be expected during winter when large animals are rare in traps and the encounter probability low, and low catchability would be expected in summer when large animals were relatively frequent in traps. Instead, catchability of all animals was reduced during winter and during moulting. It seems more likely that the seasonal pattern of catchability, which was largely independent of lobster size, is mainly influenced by factors such as water temperature, moulting and mating (McLeese and Wilder 1958; Paloheimo 1963; Morgan 1974; P. E. Ziegler, unpublished data).

Relative selectivity estimated by size-specific catchability and tag–recapture method

Estimates of relative selectivity using either size-specific catchability or tag–recapture data provided similar results during times of the year when large numbers of animals were recaptured. The similarity in the results of these independent estimates suggests good accuracy of the estimates for size-specific catchability and relative selectivity during these periods. It also confirms that the tag–recapture method, which is easier and more practical to perform, can yield robust estimates of relative selectivity where recapture rates are sufficiently high.

Conclusions

We conclude that catchability and relative selectivity in our study population of *J. edwardsii* depends on sex, size and season. If this effect applies generally, then the timing of trapping surveys is critical if catch rates and size-frequency distributions are to be compared intra- and interannually.

Most importantly, the interaction between size and season in the effect on catchability has considerable consequences for the interpretation of catch data. Thus, surveys using amalgamated catch data are likely to have biases, and if size-frequency data are compared at the beginning and at the end of a fishing season to estimate the impact of fishing pressure, using, for example, the change-in-ratio method, results are also likely to be biased. Given the effects of large lobsters on the catchability of smaller animals (Miller 1995; Frusher and Hoenig 2001), interactions between size and seasons would be further complicated by the removal of large animals in the population within a fishing season. Careful planning of surveys is therefore required to take seasonal variation in catchability into consideration. With the general trend towards length-based models, this becomes increasingly important in the stock assessment (Hilborn 1997).

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