

# **Catchability of the southern rock lobster**

## ***Jasus edwardsii***

by

Philippe Eric Ziegler, dipl biol

Submitted in fulfilment of the requirements for the Degree of  
Doctor of Philosophy

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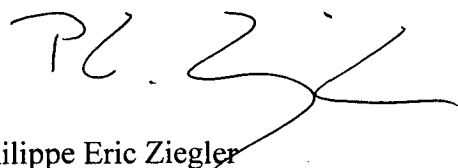
Department of Zoology  
University of Tasmania, Australia

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A handwritten signature in black ink, appearing to read 'P. Ziegler', with a stylized flourish extending from the end.

Philippe Eric Ziegler

July 2002

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## Abstract

Catchability is estimated indirectly as a 'nuisance' variable in the spatially explicit stock assessment model of the southern rock lobsters *Jasus edwardsii* in Tasmania, Australia. This study attempted to identify the key mechanisms influencing catchability to enable direct independent estimates of monthly catchability.

Seasonal variation in catchability of the southern rock lobster *Jasus edwardsii* was estimated in a scientific reserve in southeast Tasmania by comparing estimates of lobster density based on direct visual observations underwater with concomitant estimates from trapping surveys. Underwater density estimates of undersized and legal-sized male and female lobsters greater than 80 mm carapace length did not change significantly over the 14 month study period with the exception of undersized males (smaller than 110 mm carapace length). Sex ratios remained constant at approximately 1:1. In marked contrast, catch rates of males and females and the sex ratio of trapped lobsters varied strongly with season, implying that catchability varies seasonally and with sex. Impact of capture on subsequent catchability appeared to be weak, since the ratios of tagged animals in the population observed underwater generally reflected recapture rates of tagged animals in trap catches.

Size-specific catchability generally increased with size, but also varied with sex and season. During moulting and mating, size-specific catchability and relative selectivity did not increase, and sometimes decreased for larger animals. The size-frequency distributions of lobsters captured in traps therefore rarely reflected the size-frequency distribution of the population on the ground. Negative associations between small and large lobsters in traps were stronger in winter than in summer, indicating strong behavioural interactions. These interactions can account for the lower catchability of smaller lobsters. Relative selectivity estimates using tag-recapture and size-specific catchability data provided similar results.

Seasonal variation in catchability of legal-sized males and females in the scientific reserve was described by modelling the effects of water temperature, moulting and mating. Seasonal changes in water temperature described 63% of the variation of

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catchability for males, but were a poor predictor of catchability for females outside winter. Both moulting and mating were highly synchronised, although males and females moulted at different times of the year. Gaussian probability density functions were used to represent the timing and intensity of moulting, mating and subsequent compensation periods, and were added to the description of seasonal temperature changes. Four Gaussian functions based on independent biological data considerably improved the model fits for the catchability of males ( $R^2 = 0.83$ ). However, adding a single Gaussian function to the temperature model, representing a combined moulting and mating period based on independent biological data, provided a less adequate description of the variation in catchability of females ( $R^2 = 0.49$ ). Only models unconstrained by the observed timing of these events provided a good fit ( $R^2 = 0.74$ ).

The seasonal catchability models developed for the reserve population were applied to catchability over several years in two commercially fished regions of Tasmania. Catchability was estimated using commercial catch and effort data and fishery-independent estimates of exploitation rates. The seasonal catchability models suggest that similar environmental and physiological processes were the main factors determining seasonal catchability in the two fishery regions, but these factors varied considerably in their relative importance between the two regions. Interannual variation in relative catchability was correlated with density-dependent processes. Full models described 72% of the overall variation in catchability over 6 years in the south and 80% of the variation over 4 years in the north.

More work is required before direct estimates of catchability can be included in stock assessment models. In particular, region-specific patterns of seasonal catchability, and the relationship between density-dependent processes and the interannual variation in catchability need to be determined, before catchability can be reliably predicted in future years and in other regions of Tasmania. Nevertheless, this work has greatly improved our understanding of the processes that apparently underpin seasonal catchability.

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## **Chapter 1:**

### **Introduction**

The southern rock lobster *Jasus edwardsii* (Hutton) is distributed from southern Western Australia to southern New South Wales and New Zealand. It supports an important fishery in Southern Australia, Victoria, Tasmania and New Zealand (Kailola et al. 1993). In Tasmania, the annual catch of approximately 1500 tonnes (2000/2001) is valued at \$45-50 million.

#### **Stock assessment of the southern rock lobster *Jasus edwardsii* in Tasmania**

To provide and maintain sustainable lobster stocks in Tasmania, the fishery of *J. edwardsii* in Tasmania has traditionally been managed by a set of input and biological controls, including limited entry, gear restriction, closed seasons, minimum size limits and prohibitions on taking berried females. In response to decreasing catch rates between 1980 and 1995 (Frusher 1997), the government introduced an individual transferable catch quota system in March 1998 in addition to the existing controls. In the lead-up to the introduction of this quota system, a stock assessment model was developed (Punt and Kennedy 1997).

The stock assessment model estimates legal-sized biomass and egg-production levels based on catch rates and the size-frequency distribution in catches. The model is sex- and size-structured with a time step of one month to include closed seasons and seasonal growth. Each of eight regions around Tasmania (Fig. 1.1) are assessed separately to account for spatial heterogeneity among regions in growth rate, size at maturity and fishing mortality. The values for the parameters that define natural mortality, growth, maturation, egg production and selectivity are assumed to be known exactly. Sex- and size-specific selectivity is incorporated and accounts for minimum size limits, size-specific probability of capture, regulations regarding the

taking of berried females, and seasonal closures (Punt et al. 1997). The model is fitted to catch, effort and size-frequency distribution data from commercial and scientific catches, and to estimates of exploitation rates from scientific surveys. Remaining 'free' parameters are estimated, and of these, catchability coefficients play a key role in fitting the model. However, the catchability coefficients are a composite of the actual catchability and any other factors not accounted for elsewhere in the model. The catchability coefficients are assumed to vary among months, but not to vary between years.

Seasonal catchability is therefore an important parameter in the stock assessment process, and is used to scale catch rates relative to the stock size. However, since robust estimates are lacking, catchability is considered as a 'nuisance' variable in the stock assessment model that must be estimated indirectly.

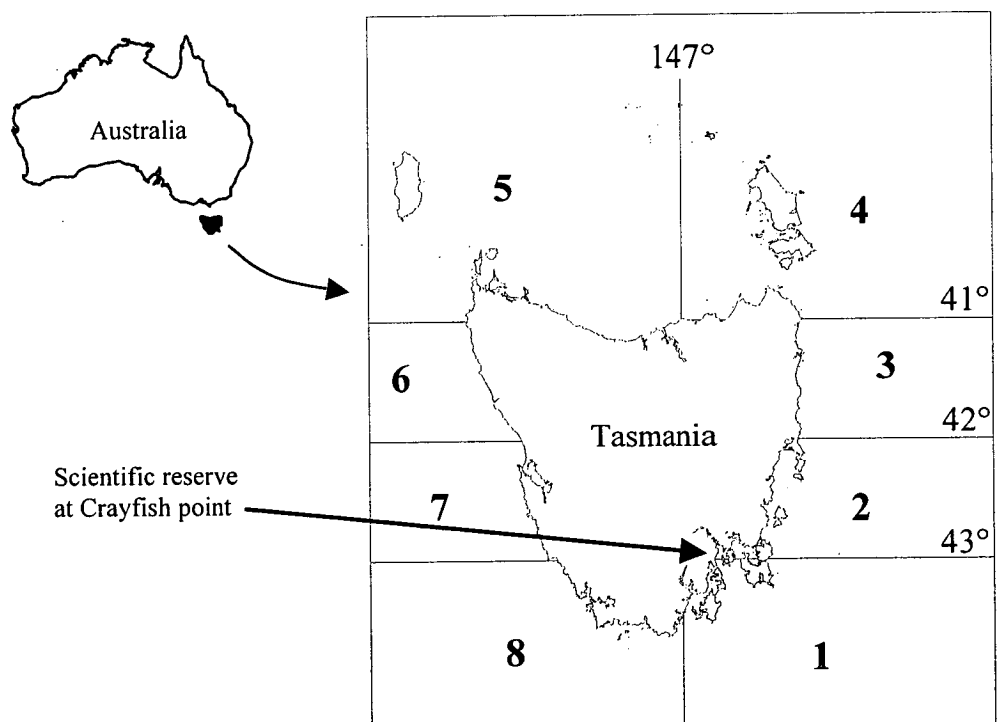


Fig. 1.1: Map of Tasmania and the eight fishing areas of stock assessment for rock lobster.

The aim of this study is to improve our understanding of the mechanisms that influence monthly catchability. This is an important step towards the goal of realising independent estimates of catchability, which would support the stock assessment process in two ways. First, independent estimates would be more accurate than the current model estimates and therefore improve the outcome of the stock assessment. Second, independent estimates can be used to investigate the overall accuracy of the structure and parameter values in the stock assessment model. Since the catchability coefficient in the model includes both catchability and all other factors not accounted for elsewhere in the model, the similarity between independent estimates of catchability and the coefficients derived from fitting the model can be used to evaluate the influence of these other factors. The influence of these other factors is likely to be small if the values of the model parameters and the model structure accurately reflect the biological parameters and processes acting on the fished population.

### **Catchability**

To understand the mechanisms determining catchability and to provide independent catchability estimates that can be used in the stock assessment model, we need a clear understanding of the concept of catchability and what the likely causes of its variation may be.

Catchability refers to the interaction between resource abundance and fishing effort. In the fishery for rock lobster, the catchability coefficient  $q$  describes the probability that a lobster will be captured by a randomly applied unit of effort, e.g. a trap (Paloheimo 1963). If the numbers of lobsters caught by a trap follow a Poisson distribution, the relationship between catch  $C$ , total effort in number of trap hauls  $f$  and population size at the start  $N$  for any given period of time  $t$  can be described as (after Nicholson and Bailey 1935):

$$C_t = N_t (1 - e^{-q_t f_t}) \quad (1.1)$$

If catchability is small and time intervals are short, the relationship may be approximated by (Morgan 1974):

$$C_t = N_t q_t f_t \text{ or } q_t = C_t / (N_t f_t) \quad (1.2)$$

If population size is substituted by density  $D$  (animals per unit area) then:

$$q_t = C_t / (f_t D_t) \quad (1.3)$$

The unit of  $q$  is area ( $\text{m}^2$ ) per trap. Catchability can also be described as effective fishing area (EFA, Miller 1975), which is the theoretical area from which all lobsters would be removed, if all had a probability of capture equal to 1. However, the probability of capture most likely decreases with increasing distance from the trap, and the EFA is usually smaller than the area of attraction, within which at least some animals can detect the bait (Miller 1990; Tremblay 2000).

Estimates of population size are needed to estimate catchability independently. Yet, robust estimates are difficult to obtain. Direct observations of lobster populations by diver observations are rarely possible because of cost, depth and other practical restrictions of diving, and thus only indirect methods based on catch sampling surveys can usually be applied. Depletion methods as described by Leslie and Davis (1939) and DeLury (1947) are often used, but the methods are thought to be inaccurate when assessing lobster stocks due to changes in catchability between surveys (Miller and Mohn 1993). More recently, change-in-ratio and index-removal methods have been applied, which measure the relative change in abundance or composition of the harvestable population over time (Paulik and Robson 1969; Eberhart 1982; Frusher et al. 1997, 1998; Hoenig and Pollock 1998; Pollock and Hoenig 1998). Of the two approaches only the change-in-ratio method is robust against changes in catchability between surveys, if catchability of both the harvested and non-harvested components in the population changes in the same way. Multi-year tagging studies have been suggested, when the population is assumed to be open

due to migration or recruitment (Hearn et al. 1998; Hoenig et al. 1998; Frusher and Hoenig 2001a). Nevertheless, all of these methods require an enormous sampling effort and are often deemed as too expensive for large-scale assessments.

Many attempts have been made to replace the estimation of population size needed to independently estimate catchability (see reviews by Miller 1990 and Arreguín-Sánchez 1996). Relationships between lobster catchability and fishing practices, environmental factors, physiological processes and behaviour at both the individual and population levels have been investigated. However, factors identified to affect the capture of lobsters in traps have generally been shown to interact in complex ways. To help understand the processes involved, different concepts of catchability have been developed describing isolated aspects that influence catchability:

- (i) *Accessibility* refers to the interaction between the distribution of the lobster population and the fishing fleet. Usually it is assumed that a lobster population is evenly distributed and the fishing fleet has complete access to it. If these conditions are not met, estimates of catchability will be made on a fraction of the population and may not be representative.
- (ii) *Availability* is related to the motivation of animals to search for food. The availability of lobsters to fishing may vary with seasonality in the environment (temperature, weather, lunar cycles) and in population processes (migration, reproduction, moulting).
- (iii) *Vulnerability* describes the probability of encounter between fishing gear and lobster. It relies on the fishing strategy (time of fishing, soak time, trap density) and on the range, timing and duration of a foraging trip of the lobster.
- (iv) *Selectivity* describes the efficiency of a specific fishing gear by referring to the probability of retention of lobster of a given size or sex by a trap, and the behavioural interactions between lobsters around a trap. While escapement is important for small lobsters, larger animals have low escapement probability and behavioural interactions are an important factor in determining their selectivity. Unfortunately, vulnerability and selectivity depend on one another and are often difficult to distinguish. What may appear as low selectivity of small animals is often caused simply by the inability of small animals to reach a trap on their foraging trips.

## The project

In this study, I sought to quantify seasonal variation in catchability by modelling the underlying mechanisms that are likely to cause the variation. These models were then investigated for their potential to provide independent estimates of catchability beyond the available estimates.

A lobster population in a scientific reserve near Hobart (Fig. 1.1), where fishing for rock lobster by commercial and recreational fishermen is prohibited, provided a unique opportunity to study how the behaviour of lobsters, i.e. their availability, influences seasonal variation in catchability. Sex-specific seasonal patterns in catchability were investigated by comparing density estimates of the population obtained by direct visual observations underwater with catch rates in trapping surveys conducted at the same time (Chapter 2). Since the population was fished in a similar way during each survey, we could minimise the influence of accessibility and vulnerability due to consistency in access of the traps to the population and in fishing practices. In addition, fishing mortality did not influence the catchability estimates.

Since the reserve had been established over 30 years ago, a wide range of animal sizes and high density of larger animals allowed investigation of changes in size-specific catchability throughout the year (Chapter 3). Size-specific catchability is important in determining how well the size-frequency distribution in the population is represented by that in trap catches.

Using the data collected in Chapter 2, catchability models were developed based on environmental and physiological processes to describe the observed seasonal catchability of the legal-sized populations of male and female lobsters in the scientific reserve (Chapter 4). Models of monthly catchability in crustaceans have been presented earlier (Morgan 1974; Morrissy and Caputi 1981; Williams and Hill 1982), but the models developed here are the first attempt to combine the effects of water temperature and biological processes associated with moulting and mating. They also show that gender is an important contributor to variation in catchability.

I then examined whether these models could be applied to estimate catchability in two fishing regions around Tasmania, viz. areas 5 and 8 (Fig. 1.1; Chapter 5). In contrast to the approach to estimating catchability in the reserve, these estimates were based solely on commercial and scientific catch and effort data, and no diver



surveys were undertaken. Independent estimates of exploitation rates were used to estimate population density over several years in the two regions. These two regions were selected for the study because they represent different extremes in Tasmania of environmental and physiological parameters used in the models, they are at the extremes of growth rate for *J. edwardsii* in Tasmania, and they exhibit dissimilar population densities and size-frequency distributions. For both regions I investigated the catchability models in respect of regional trends and interannual variation, and assessed whether these models would allow the prediction of catchability in further years and in other fishing regions.

Finally, the results of this study are discussed in light of stock assessment models and in particular of that for *J. edwardsii* in Tasmania (Chapter 6).

## Chapter 2:

### Effects of sex, season and catch history on catchability

(Accepted by the Journal of Marine and Freshwater Research)

#### Abstract

Seasonal variation in catchability of the southern rock lobster *Jasus edwardsii* was estimated in a scientific reserve in southeast Tasmania by comparing estimates of lobster density based on direct visual observations underwater with concomitant estimates from trapping surveys. Underwater density estimates of undersized and legal-sized male and female lobsters greater than 80 mm carapace length did not change significantly over the 14 month study period with the exception of undersized males (smaller than 110 mm carapace length). Sex ratios remained constant at approximately 1:1. In marked contrast, catch rates of males and females and the sex ratio of trapped lobsters varied strongly with season, implying that catchability varies seasonally and with sex. Catchability of males and females was highest in early summer and lowest in winter. Impact of capture on subsequent catchability appeared to be weak, since the ratios of tagged animals in the population observed underwater generally reflected recapture rates of tagged animals in trap catches. Recapture rates increased with size and were higher for medium-sized and large males than for similar-sized females. However, for each particular sex-size group, recapture rates remained relatively constant throughout the study period.

## Introduction

Catch rates or catch per unit effort (CPUE) is often taken as an index of population abundance. However, catch or fishing mortality depends on both the resource abundance and the efficiency of the fishing gear (e.g. Arreguín-Sánchez 1996). The relationship between these two factors is catchability, given as:

$$q_t = C_t / (f_t N_t) = C_t / (f_t D_t) \quad (2.1)$$

where  $q$  denotes the catchability coefficient of a particular fishing gear for any given period of time  $t$ ,  $C$  is the catch,  $f$  is the fishing effort, and  $N$  the population size, which can be substituted by density  $D$  (number of animals per area). Catchability is usually an important parameter in stock assessments, being necessary to scale the catch rates relative to the stock size. However, when robust estimates of catchability in stock assessment models are lacking, this parameter is often considered as a 'nuisance' variable that must be estimated indirectly, as in the case of the assessment in the southern rock lobster *Jasus edwardsii* fishery in Tasmania (Punt and Kennedy 1997).

Since fishermen capture lobsters using baited traps, catchability depends in part on the feeding response of the animals. It is well established that feeding in decapod crustaceans is affected by environmental factors such as temperature (McLeese and Wilder 1958; Morgan 1974, 1978; Branford 1979; Smith et al. 1999), and endogenous physiological cycles such as moulting and mating (Chittleborough 1975; Lipcius and Herrnkind 1982; Zoutendyk 1988; Miller 1990; Kelly et al. 1999). Catchability may therefore show a strong seasonal signal, although few attempts have been made to determine catchability on a seasonal or monthly basis. In this study, we assess catchability of rock lobster in a scientific reserve over a 14-month period by comparing estimates of density from monthly trap lifts to estimates from in-situ observations of divers.

## Material and methods

### *Study site*

Underwater observations and trapping surveys were conducted on a reef in a scientific reserve at Crayfish Point near Hobart in Tasmania, Australia (42°57.2'S, 147°21.2'E), where any fishing for rock lobster by commercial and recreational fishermen is prohibited. The continuous area of rocky reef (ca. 0.15 km<sup>2</sup>) and additional isolated reef patches across sandflats surrounding the reef ranges from 0-12 m depth at MLW. The reef consists of a field of boulders 0.5-3 m in diameter supporting dense algal cover dominated by the kelp *Lessonia corrugata*.

### *Underwater observations*

Lobster density was estimated in-situ in most months between February 1999 and April 2000, using 10 replicate belt transects (each 4x100 m) on each sampling occasion. Transects of 400 m<sup>2</sup> were used to overcome the highly aggregated distribution of lobsters on the reef, while being sufficiently small to accommodate the shape and patchiness of the reef. 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. Only on two occasions lobsters were found free-walking. All lobsters encountered on each transect were counted, sexed, and their carapace length (CL) estimated by eye to the nearest 5 mm. A small number of animals in each series could not be sexed and were omitted from the analysis. Lobsters were not handled during the underwater surveys to avoid disturbance to their behaviour. Except for the October 1999 sample, all visual counts were undertaken by the same person to ensure consistency in detecting animals and estimating their size.

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

prior trapping survey. 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:

$$a = b + c * x_{actual} \quad (2.2)$$

and subtracted from each visual estimate  $x_{est}$ . The remaining mean measurement error showed no trend across time periods and was  $0 \text{ mm} \pm 11 \text{ mm}$  (SD) for lobsters of 80-190 mm CL. Because lobsters smaller than 80 mm CL were not tagged in the trapping survey, animals smaller than this size limit were excluded in the analysis of the underwater observations. To stabilise variances, the visual count data were square-root transformed. Monthly changes in density of lobsters per  $100 \text{ m}^2$  were compared by ANOVA. Note that diver surveys were not conducted in April, August, September and November 1999, and the October 1999 sample was obtained by a different dive team who did not record sex or size.

### *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 observation. Since it was unknown whether *J. edwardsii* follows a lunar periodicity in behaviour as found in other lobsters, e.g. *Panulirus cygnus* in Western Australia (Morgan 1974), the trapping surveys were conducted whenever possible at similar lunar stages. Over four consecutive days 24 traps were set daily on reef in a similar way, resulting in 96 trap lifts per monthly survey. After the first day, when traps were set in the early afternoon, they were hauled and set again in the early mornings of each of the following days with a soak-time of about 24 hours. 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 were trapezoidal in shape with a square base of  $0.6 \text{ m}^2$ , a top surface of  $0.5 \text{ m}^2$ , and a height of 0.4 m. Lobsters enter the one-chambered trap through a round top entrance of 280 mm diameter. 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, 27 Jacobsen Crescent, Holden Hill, SA 5088, Australia) and an antenna tag (numbered plastic label tied to the base of the antenna), their carapace length measured to the nearest millimetre, and the animal released immediately at the site of capture. The largest lobsters caught in the trapping surveys were 193 mm CL for males and 143 mm CL for females. Only animals greater than 80 mm CL were tagged and included in the analysis. Legal-size limits for male and female lobsters are 110 mm CL and 105 mm CL, respectively. Monthly catch rates were calculated from the number of lobsters per 24 traps per day. These data were square-root transformed to stabilise variances and compared by ANOVA.

Monthly trapping surveys were undertaken from April 1999 to April 2000 inclusive, except in May 1999, when there were two surveys two 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 standardise the effort for the catch rate analysis, only the data from the first 4 days of the additional surveys were included. For each day 24 traps were randomly selected 1000 times and the mean value of the resulting catch rates calculated as representative of the daily catch rate. In the first two of the additional surveys, lobsters were removed from the reef, held in tanks and returned at the end of the survey. Although catch rates generally decreased over the 20- and 10-day periods of these surveys due to the removal of lobsters, the impact on the first 4 days was minimal (Frusher and Hoenig 2001b).

#### *Estimation of catchability*

The ratio of catch rates obtained in the trapping surveys to the density of lobsters on the reef at the same time provided an estimate of catchability (Equation 1). However, the impact of capture on catchability had to be investigated before estimating catchability, because individual lobsters were returned to the reef after capture and thus could be recaptured several times. If the capture of lobsters alters their subsequent behaviour towards a trap and they become either 'trap-happy' or 'trap-shy', then catchability estimates of lobsters could be biased and not represent those of a fished population. Comparing proportions of tagged animals in the population

with proportions of recaptures in the catches allowed the impact of capture on catchability to be estimated. For that purpose, 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).

## Results

### *Seasonal changes in density determined from underwater visual observations*

Monthly density estimates of lobsters on the reef from visual counts showed little variation, with an average of  $4.8 \pm 0.3$  (SE) lobsters per 100 m<sup>2</sup> over the period from February 1999 to April 2000 (Fig. 2.1). Densities of males and females averaged  $2.4 \pm 0.2$  (SE) and  $2.7 \pm 0.2$  (SE) animals per 100 m<sup>2</sup> respectively, and did not differ significantly between sex and months. Only undersized males showed significantly higher densities in March 2000 than in March, June and December 1999, while monthly densities of legal-sized males and undersized and legal-sized females remained relatively constant over the study period.

### *Seasonal changes in catch rates and estimates of catchability*

In contrast to results of the diver observations, catch rates in traps showed strong seasonal variation and significant differences between sexes depending on months (Figs. 2.2a and 2.2c). Catch rates declined in winter and were elevated in summer, although the magnitude of seasonal differences was greater in males than in females. Males and females were caught in high numbers during the first January survey. Catch rates of males decreased during the austral autumn in April and May and reached their lowest values in August in the middle of winter. They increased sharply to a high peak in early summer and remained at high levels until the end of sampling in April. Female catch rates dropped to low levels in March, before reaching a winter low similar to that of males. Catch rates of females recovered earlier in spring than that of males, but the recovery was modest. Due to the different pattern of catch rates, sex ratios in trap catches were skewed towards males in summer and autumn, but were more equal in winter, and skewed towards females in spring (Fig. 2.3).

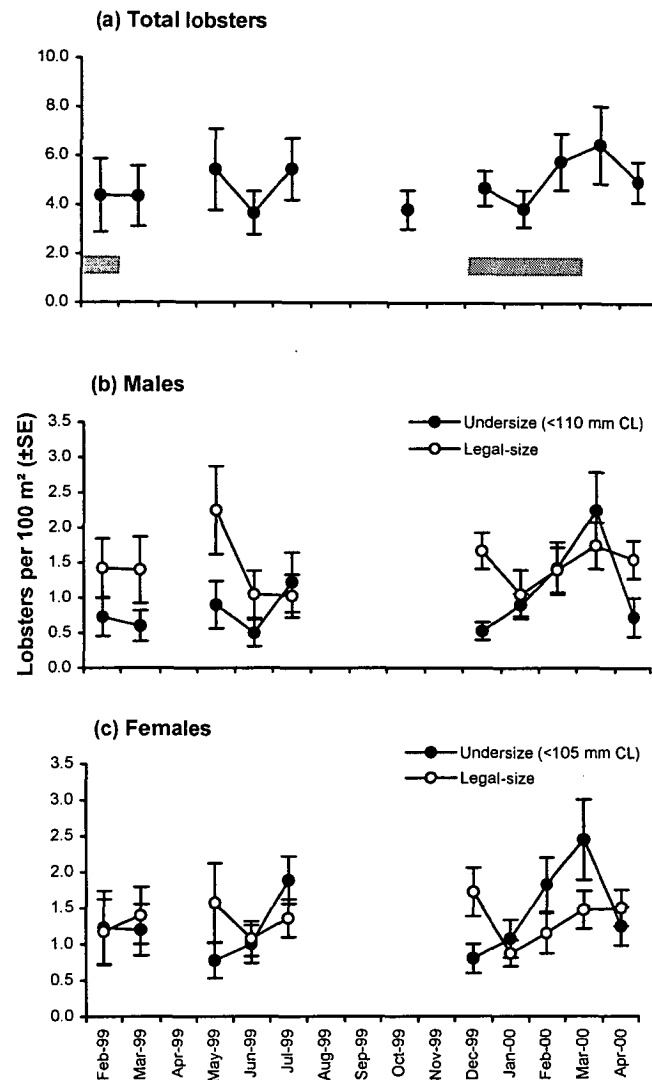


Fig. 2.1: Monthly densities of lobsters estimated using underwater visual observations. Mean counts per 100 m<sup>2</sup> (± SE) from February 1999 to April 2000 of (a) total lobsters, (b) undersized (filled circles) and legal-sized males (open circles), and (c) undersized (filled circles) and legal-sized females (open circles). Grey bars indicate summer months. Average density was not significantly different between months (1-way ANOVA;  $F_{10,110} = 0.461$ ,  $P = 0.91$ ). Densities of males and females were not significantly different between sexes and months (2-way ANOVA; sex:  $F_{1,180} = 0.84$ ,  $P = 0.36$ ; month:  $F_{9,180} = 0.91$ ,  $P = 0.52$ ; sex\*month:  $F_{9,180} = 0.34$ ,  $P = 0.95$ ). Monthly densities of undersized and legal-sized males averaged  $1.0 \pm 0.2$  (SE) and  $1.5 \pm 0.1$  (SE) animals per 100 m<sup>2</sup> respectively, while monthly densities of undersized and legal-sized females averaged  $1.4 \pm 0.2$  (SE) and  $1.3 \pm 0.1$  (SE) animals per 100 m<sup>2</sup> respectively. Only densities of undersized males differed significantly between months (1-way ANOVA;  $F_{9,100} = 2.78$ ,  $P < 0.01$ ), with significantly higher densities in March 2000 than in March, June and December 1999 (Tukey HSD-test). Other sex-size categories did not show significant temporal fluctuations in density (1-way ANOVAs; legal-sized males:  $F_{9,100} = 1.03$ ,  $P = 0.42$ ; undersized females:  $F_{9,100} = 1.86$ ,  $P = 0.06$ ; legal-sized females:  $F_{9,100} = 0.53$ ,  $P = 0.85$ ).



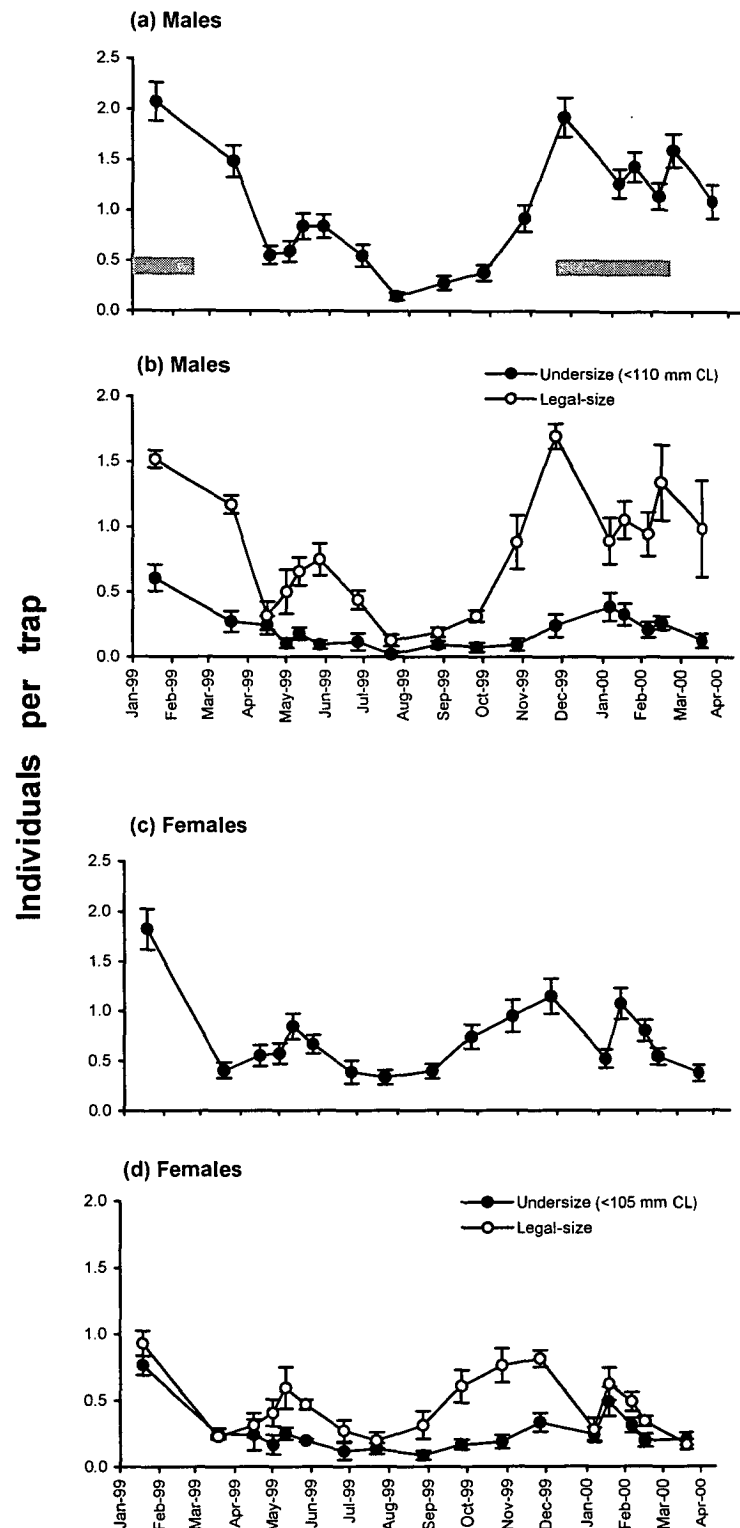


Fig. 2.2: Catch rates of lobsters in traps for (a) total population of males and (b) undersized (filled circles) and legal-sized males (open circles), and (c) total population of females and (d) undersized (filled circles) and legal-sized females (open circles) from January 1999 to April 2000 (means  $\pm$  SE). Grey bars indicate summer months. Catch rates of males and females differed significantly depending on season (2-way ANOVA; sex\*month:  $F_{16,136} = 2.97$ ,  $P < 0.001$ ). Similarly, catch rates of undersized and legal-sized males and females differed significantly between months (1-way ANOVAs; undersized males:  $F_{16,68} = 4.42$ ,  $P < 0.0001$ ; legal-sized males:  $F_{16,68} = 9.70$ ,  $P < 0.0001$ ; undersized females:  $F_{16,68} = 3.94$ ,  $P < 0.0001$ ; legal-sized females:  $F_{16,68} = 6.26$ ,  $P < 0.0001$ ).

Undersized and legal-sized animals showed similar trends (Figs. 2.2b and 2.2d), but despite comparable densities on the ground, both catch rates and seasonal variability in catches were notably larger for legal-sized animals. This pattern held for both sexes. Catch rates of all groups differed significantly between months.

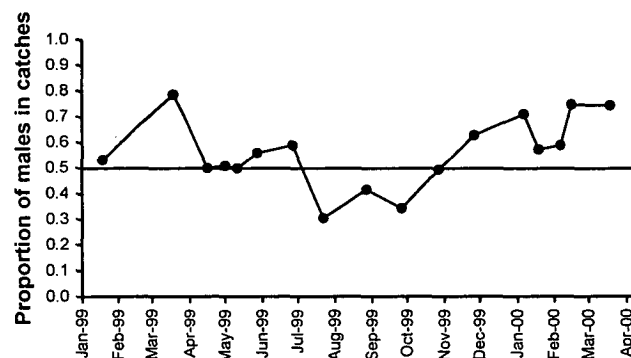


Fig. 2.3: Proportion of male lobsters in catches from January 1999 to April 2000.

#### *Impact of capture on catchability*

Estimating the impact of capture and tagging on catchability of lobsters was necessary, because individual lobsters were returned to the reef after capture and thus could be recaptured several times. Of the 2292 males and 2225 females greater than 80 mm CL which were tagged during the course of this study, 901 males (39.3%) and 530 females (23.8%) were recaptured at least once.

Proportions of male and female lobsters in the population that were tagged reflected proportions of tagged males and females that were recaptured in catches in most size classes (Table 2.1). Proportions of tagged small males and females of all sizes in the population agreed well with the proportions of recaptured animals in catches. Only recaptures of medium-sized and large males were over-represented in catches when compared to tagged animals in the population.

Table 2.1: Proportions of tagged male and female lobsters in the underwater visual observations and trap samples. Samples are restricted to periods before moulting started in August (males) and March (females) due to loss of antenna tag in the moult.  $N$  indicates the total number of animals in the sample. Observed frequencies of medium-sized and large recaptured males in catches were significantly different from frequencies expected on the basis of ratios of tagged animals in different size classes in the population (G-test; all sizes:  $G_{adj} = 32.19$ ,  $P < 0.001$ ; 81-110 mm CL:  $G_{adj} = 1.11$ ,  $P > 0.05$ ; 111-140 mm CL:  $G_{adj} = 22.08$ ,  $P < 0.001$ ; >140 mm CL:  $G_{adj} = 8.99$ ,  $P < 0.005$ ). Observed frequencies of recaptured females in catches did not differ from expected frequencies based on ratios of tagged females in each size class in the population (G-test; all sizes:  $G_{adj} = 2.55$ ,  $P > 0.05$ ).

	Underwater observations		Trap samples	
	February - July 1999		March - July 1999	
Males				
Size (mm CL)	$N$	Proportion tagged	$N$	Proportion recaptured
81-110	163	0.43	93	0.48
111-140	139	0.50	204	0.67
>140	130	0.69	186	0.79
Females				
Size (mm CL)	$N$	Proportion tagged	$N$	Proportion recaptured
81-105	49	0.27	72	0.28
106-120	26	0.50	148	0.45
>120	21	0.62	99	0.57

Nonetheless, the proportions of tagged and recaptured animals in the population and in catches respectively, depended on sex and size (Fig. 2.4). Recapture rates were relatively high from the beginning, since over 60% of all individual males and females captured during the course of this study were tagged already in the extended first trapping survey. The proportions of recaptured animals in catches generally increased with size. Within the smallest size class, male and female recaptures from previous trapping surveys appeared in similar proportions in catches, although the proportions of recaptured small males decreased slightly over time. The proportions of recaptured animals were significantly higher in the medium and large size classes of males than in the equivalent size classes of females, but within sexes were similar for medium-sized and large animals.

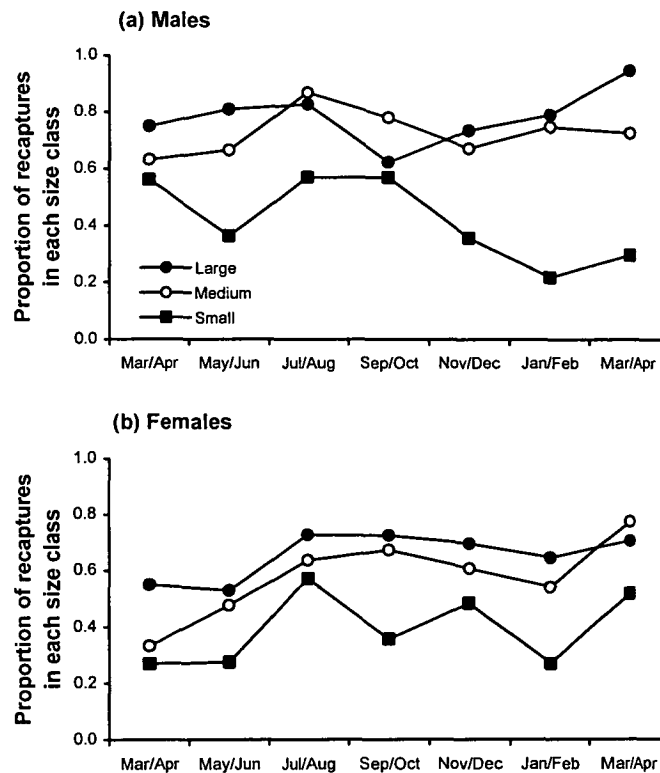


Fig. 2.4: Proportions of recaptured (a) male and (b) female lobsters from previous trapping periods in total catches for small (filled squares), medium (open circles) and large (filled circles) size classes between March/April 99 and March/April 2000. Data are pooled bimonthly due to low numbers of recaptures in some size classes. Proportions of recaptured males and females differed significantly between sexes and size (2-way ANOVA; sex:  $F_{1,42} = 8.16$ ,  $P < 0.01$ ; size:  $F_{2,42} = 27.80$ ,  $P < 0.0001$ ; sex\*size:  $F_{2,42} = 1.12$ ,  $P = 0.34$ ). The smallest size classes of males and females had similar proportions of recaptures, although small males showed a weak negative trend. Proportions of recaptures generally increased with size and were significantly higher for males, but within sexes were similar for medium-sized and large animals (Tukey HSD-test).

## Discussion

### *Seasonal changes in population density and catch rates*

No significant changes in lobster density, except in undersized males, could be detected on the reef using visual observations over the 14 months of this study. Similarly, densities of male and female *J. edwardsii* on a reef in New Zealand remained relatively constant over a 3-year period (MacDiarmid 1991). However,

MacDiarmid reported seasonal movement of lobsters within the reef between shallow and deeper areas. And in other studies in New Zealand, mostly large lobsters were found to move seasonally to sandy areas and mussel patches adjacent to reefs (Kelly et al. 1999; Kelly 2001). These small-scale movements were correlated with the moult cycle and seasonal patterns in feeding activity, and led to marked seasonal fluctuations of densities and sex ratios on the reef. The small reef investigated in this study did not encompass deep areas and the seasonal fluctuations in density, which were only detected for undersized males, can be attributed to the highly over-dispersed distribution of small males (Chapter 3). We conclude that significant small-scale movements to and away from the study area were unlikely.

Further evidence of stability in the lobster density is drawn from recaptures by fishermen from areas outside the reserve. Although over 4500 lobsters have been tagged in this reserve since 1998, only two lobsters have been recaptured outside the reserve (S. D. Frusher unpublished data). We therefore assume that no large net emigration or immigration occurred. However, the relatively small increase in abundance of undersized males during the second summer of the study may indicate a weak immigration of small males. Small proportions of *J. edwardsii* populations, mainly immature females and males of similar size, have been found to migrate distances greater than 5 km around Tasmania and New Zealand (Booth 1997; C. Gardner, Tasmanian Aquaculture and Fisheries Institute, personal communications). The weak decrease in the proportion of recaptured undersized males over the study period also suggests immigration of small males. In contrast, the proportions of legal-sized males and both size classes of females were consistent throughout the year indicating constant population sizes.

In sharp contrast to the stable population density, catch rates of males and females in traps showed marked differences depending on season. Both declined in winter and were elevated in early summer, but the magnitude of seasonal fluctuations was smaller for females with generally lower catch rates than that of males in summer.

*Impact of capture on catchability*

No significant impact of capture on catchability could be detected in small males and females of all sizes, since similar proportions of tagged and recaptured males and females in these size classes were found in the population and in catch samples. Only recaptures of medium-sized and large males were over-represented in catches. This may arise because catchability increases with a history of previous capture, and/or individuals have different motivational levels (Morgan 1974). Similar to Morgan (1974), we were not able to distinguish between the two effects. However, it seems to be more likely that any behavioural changes due to a history of previous capture were weak also in medium-sized and large males.

In addition, no evidence for subsequent avoidance or attraction to traps after capture of lobsters was found in tank studies (Karnofsky and Price 1989; Miller and Addison 1995). Rather, there appears to be a large variation in individual lobsters in the rates of approach and capture in traps (Karnofsky and Price 1989). This variation in motivation levels of lobsters may have caused the observed differences between population and trap catches. Although variation in motivation is likely to occur throughout the population, the effect of the variability will become most evident in those animals that are captured frequently in traps. The observed differences in the proportion of tagged and recaptured animals were strongest for medium-sized and large males, which have the highest selectivity for most periods of the year and were thus most abundant in traps (Chapter 3). Increasing selectivity with size can also explain the sex- and size-specific pattern in the proportions of tagged animals in the population, since a higher proportion of the population of large animals and males were captured and tagged than small animals and females respectively.

*Estimation of catchability*

Since the impact of capture on catchability appeared to be small, combined catches of tagged and untagged animals were used to estimate seasonal catchability (Fig. 2.5). Catchability of males and females showed a strong seasonal signal, but also followed distinct gender-specific patterns. This indicates that catchability may be influenced not only by environmental factors such as temperature (McLeese and

Wilder 1958; Morgan 1974; Branford 1979; Smith et al. 1999), but also by endogenous gender-specific cycles of moulting and mating (Lipcius and Herrnkind 1982; Zoutendyk 1988; Miller 1990; Kelly et al. 1999). Where male and female lobsters moult at different times of the year as in *J. edwardsii* (Frusher 1997), gender may be an important contributor to variation in catchability. The results of this study suggest that a gender-specific description of catchability incorporating environmental and physiological parameters is needed in stock assessment models.

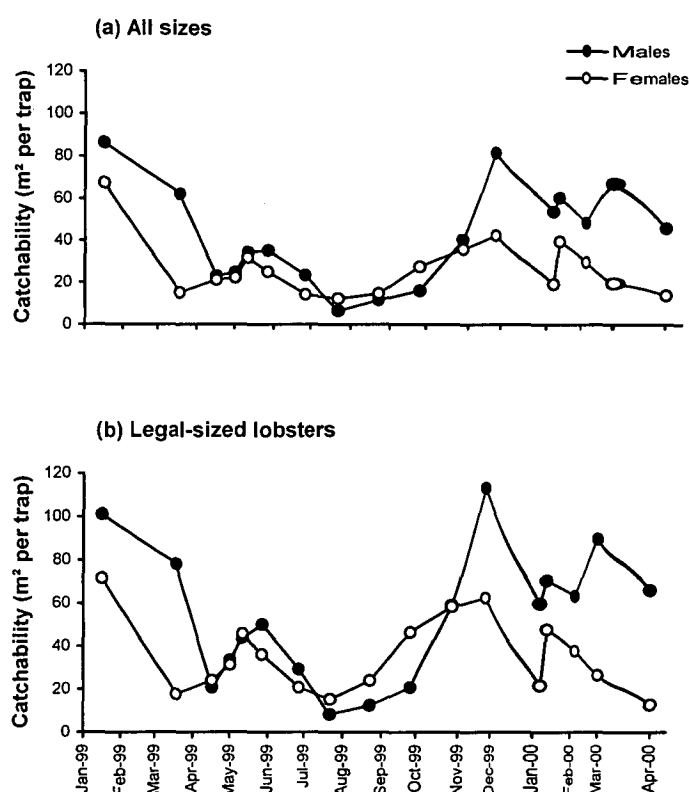


Fig. 2.5: Catchability in m² per trap of male (filled circles) and female lobsters (open circles) from January 1999 to April 2000 for (a) undersized and legal-sized animals combined and (b) legal-sized animals.

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Catchability of legal-sized animals was often higher than that of the population as a whole ignoring size-structure. Since catchability has been found to increase with animal size and since the presence of large animals influence the outcome of trapping surveys as implied by the selectivity curves found in *J. edwardsii* and other lobsters (Miller 1989, 1995; Pezzack and Duggan 1995; Tremblay 2000; Frusher and Hoenig 2001b; Chapter 2), catchability depends on the size-frequency distribution of the population. Further investigation of size-specific catchability and behavioural interactions between lobsters is needed for incorporating estimates of catchability into stock assessments. This is particularly important in areas where sub-populations of large lobsters are depressed due to fishing pressure.



### **Chapter 3:**

## **Effects of size on catchability**

(Accepted by the Journal of Marine and Freshwater Research)

#### **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 catchability to increase with the size of animals in trap catches (e.g. Richards *et al.* 1983; Karnofsky and Price 1989; Miller 1990, 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 so far provide only point estimates of size-specific catchability for a specific period of the year.

Here we estimate, 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 examine 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 4x100 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. Only on two occasions lobsters were found free-walking. 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 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, while 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 in the analysis of the underwater observations.

To improve the accuracy of size estimation of lobsters in visual observations, size estimation was practised prior to the underwater observations with 298 lobsters, housed in a large outdoor raceway with an artificial rocky reef. During the last of 9

training sessions, mean estimation error between the visually estimated and actual measured size of captive animals was  $-1 \text{ mm} \pm 4 \text{ mm SD}$  ( $N = 35$ ).

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 prior 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:

$$a = b + c * x_{actual} \quad (3.1)$$

and subtracted from each visual estimate  $x_{est}$ . Remaining estimation errors were independent of sex, size and time periods (Table 3.1). The mean estimation error between estimated and measured sizes during all surveys was  $0 \text{ mm} \pm 11 \text{ mm (SD)}$ . Estimation errors for lobsters of 80-190 mm CL were normally distributed around the measured sizes.

Table 3.1: 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 CL, medium/large males greater than 120 mm CL; small females up to 105 mm CL, medium/large females greater than 105 mm CL). Analysis by 3-way ANOVA. Data were homoscedastic and errors normally distributed (Shapiro-Wilk W-test,  $P = 0.29$ ).

Source	DF	<i>F</i>	<i>P</i>
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

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:

$$\text{Females: } N_{y \text{ corr}} = 0.08 * N_{y-2} + 0.24 * N_{y-1} + 0.36 * N_y + 0.24 * N_{y+1} + 0.08 * N_{y+2} \quad (3.2)$$

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:

$$\text{Males: } N_{y \text{ corr}} = 0.18 * N_{y-1} + 0.64 * N_y + 0.18 * N_{y+1} \quad (3.3)$$

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 theoretically were 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 by ANOVA. To stabilise 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 observation. 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 mornings of each of the following days with a soak-time of about 24 hours. 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, 27 Jacobsen Crescent, Holden Hill, SA 5088, Australia) and an antenna tag (numbered plastic label tied to the base of the antenna), their carapace length 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, Tasmanian Aquaculture and Fisheries Institute, personal communications) 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 two 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 standardise 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 due to the removal, the impact on the first 4 days was minimal (Frusher and Hoenig 2001b).

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 (EFA in m<sup>2</sup> 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:

$$q_{lt} = C_{lt} / (f_t D_{lt}) \quad (3.4)$$

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<sup>2</sup>.

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 of relative selectivity using size-specific catchability, relative selectivity  $\phi_l$  of each size class  $l$

was estimated bimonthly by standardising size-specific catchability to the interval [0,1] as:

$$\phi_l = q_l / q_{lmax} \quad (3.5)$$

where  $q_{lmax}$  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  $\phi_l$  in each size class was estimated bimonthly as the proportion of tags returned, and standardised to the interval [0,1]:

$$\phi_l = (N_{Rl} / N_{Tl}) / \max_l (N_{Rl} / N_{Tl}) \quad (3.6)$$

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 which 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  $8.7 \pm 0.9$  mm ( $N = 45$ ) and  $7.3 \pm 0.3$  mm ( $N = 122$ ) per moult respectively. Females 81-105 mm CL and 106-120 mm CL grew on average  $4.1 \pm 0.4$  mm CL ( $N = 74$ ) and  $2.4 \pm 0.3$  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 which 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. 3.1). 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. 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 indicated that small males were highly aggregated compared with large males at the scale of 400 m<sup>2</sup> (Fig. 3.2).

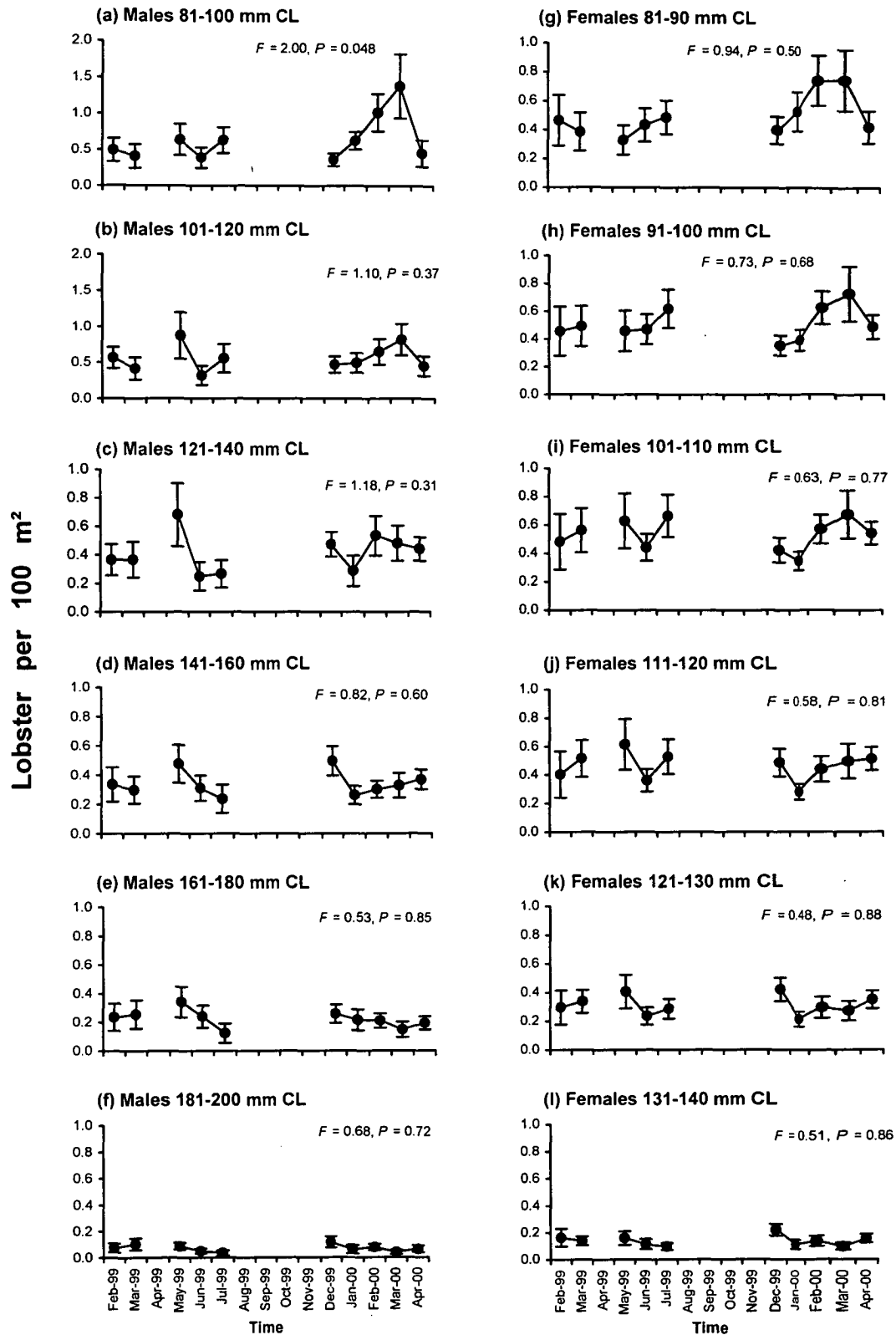


Fig. 3.1: Densities of lobsters per size class estimated using underwater visual observations. Data are mean counts per 100 m² ( $\pm$  SE) from February 1999 to April 2000. Note that y-axis scale differs for the two smallest size classes of males. Seasonal changes in density were tested with 1-way ANOVA. Only the smallest size class of males between 81-100 mm CL showed significant seasonal fluctuations in density. For this size class, significantly more males were found during the periods in February and March 2000 than in February, March, June and December in the year before, and in April 2000 (Tukey-Kramer HSD test).

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<sup>2</sup>) and decreased with size, while densities were similar for females between 81-120 mm CL, and decreased only for females larger than 120 mm CL (Fig. 3.3).

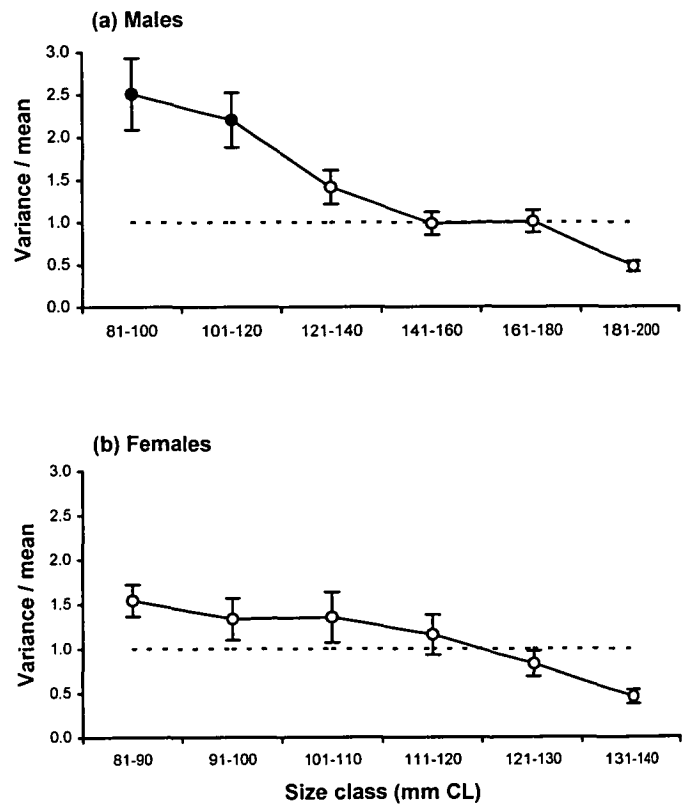


Fig. 3.2: Variance to mean relationship ( $\pm$  SE) of density estimates from transects using underwater visual observations for all size classes of (a) male and (b) female lobsters. Filled circles indicate size classes for which variance to mean ratios differ significantly from random (index of dispersion test, Krebs 1989). The dotted line indicates random distribution where variance to mean equals 1. The variance to mean ratio decreased with size for males and females (linear regressions for males:  $R^2 = 0.94$ ,  $F_{1,5} = 64.75$ ,  $P < 0.005$ ; females:  $R^2 = 0.91$ ,  $F_{1,5} = 38.43$ ,  $P < 0.005$ ).

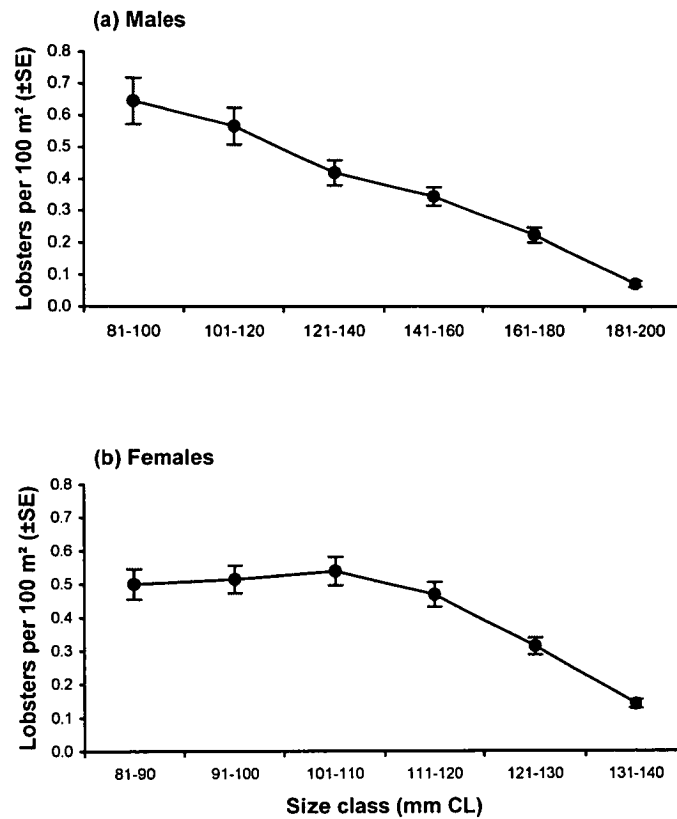


Fig. 3.3: Mean population density ( $\pm$  SE) for each size class of (a) male ( $N = 899$ ) and (b) female lobsters ( $N = 981$ ). Data pooled from all underwater visual observations.

#### *Size-frequency distribution in trap catches*

The size-frequency distribution 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 of the year (Figs. 3.4 and 3.5). 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, while 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.

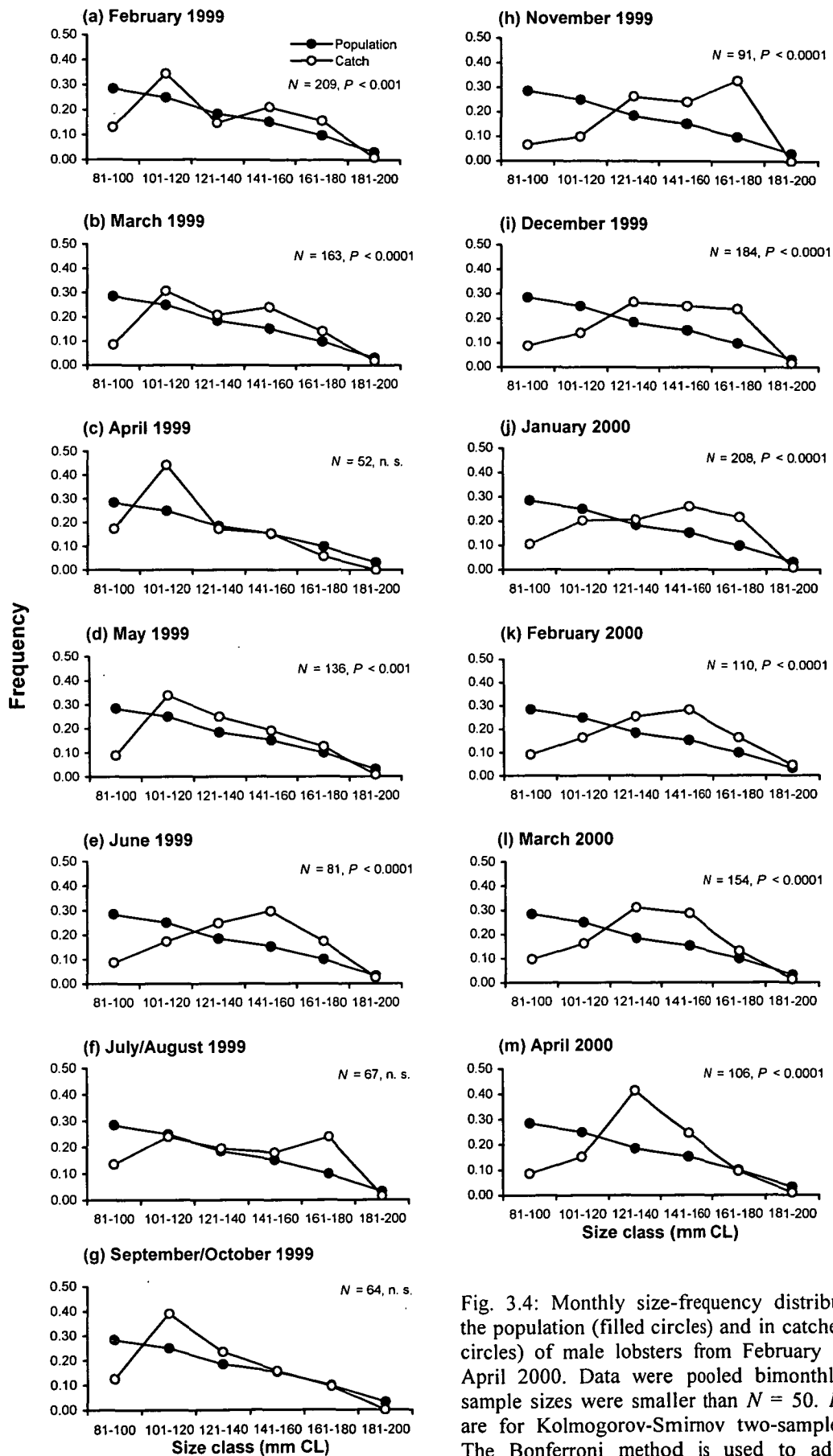


Fig. 3.4: Monthly size-frequency distribution in the population (filled circles) and in catches (open circles) of male lobsters from February 1999 to April 2000. Data were pooled bimonthly when sample sizes were smaller than  $N = 50$ .  $P$ -values are for Kolmogorov-Smirnov two-samples tests. The Bonferroni method is used to adjust the significance level.

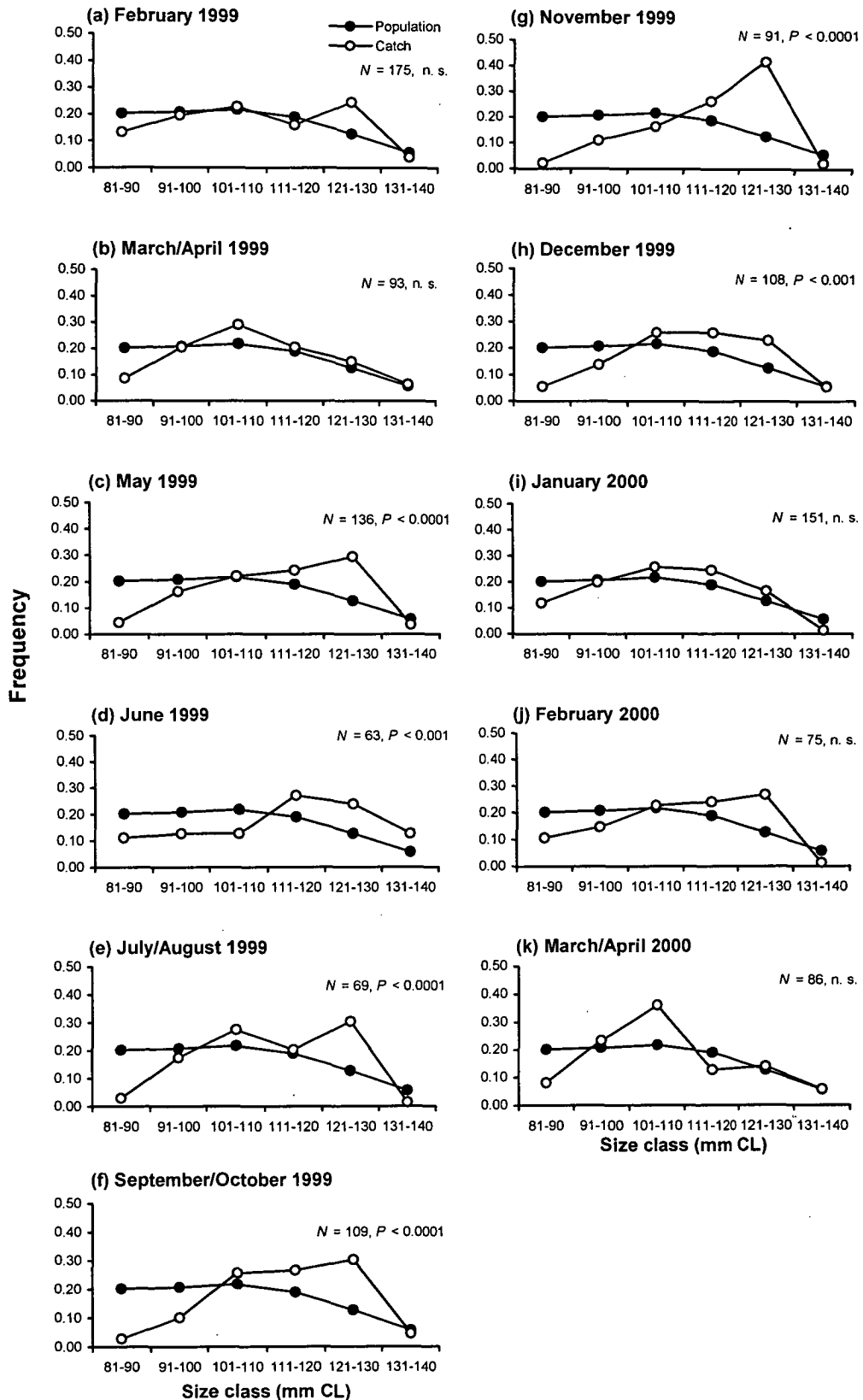


Fig. 3.5: Monthly size-frequency distribution in the population (filled circles) and in catches (open circles) of female lobsters from February 1999 to April 2000. Data were pooled bimonthly when sample sizes were smaller than  $N = 50$ .  $P$ -values are for Kolmogorov-Smirnov two-samples tests. The Bonferroni method is used to adjust the significance level.

Table 3.2: Variation of catchability in the total population of male and female lobsters described by catchability of each size class for males and females, respectively.

Males		Females	
Size class (mm CL)	$R^2$	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-specific catchability over the year*

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

Catchability generally increased with size, but the magnitude of the increase varied with season (Fig. 3.6). 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 followed mostly a similar pattern throughout the year (Fig. 3.6). Catchability of each size class was standardised 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 3.2). Relative catchability of females between 91-

130 mm CL followed similar seasonal trends, but only the catchability of the animals between 111-120 mm CL described a high proportion of the variability in the overall catchability of females.

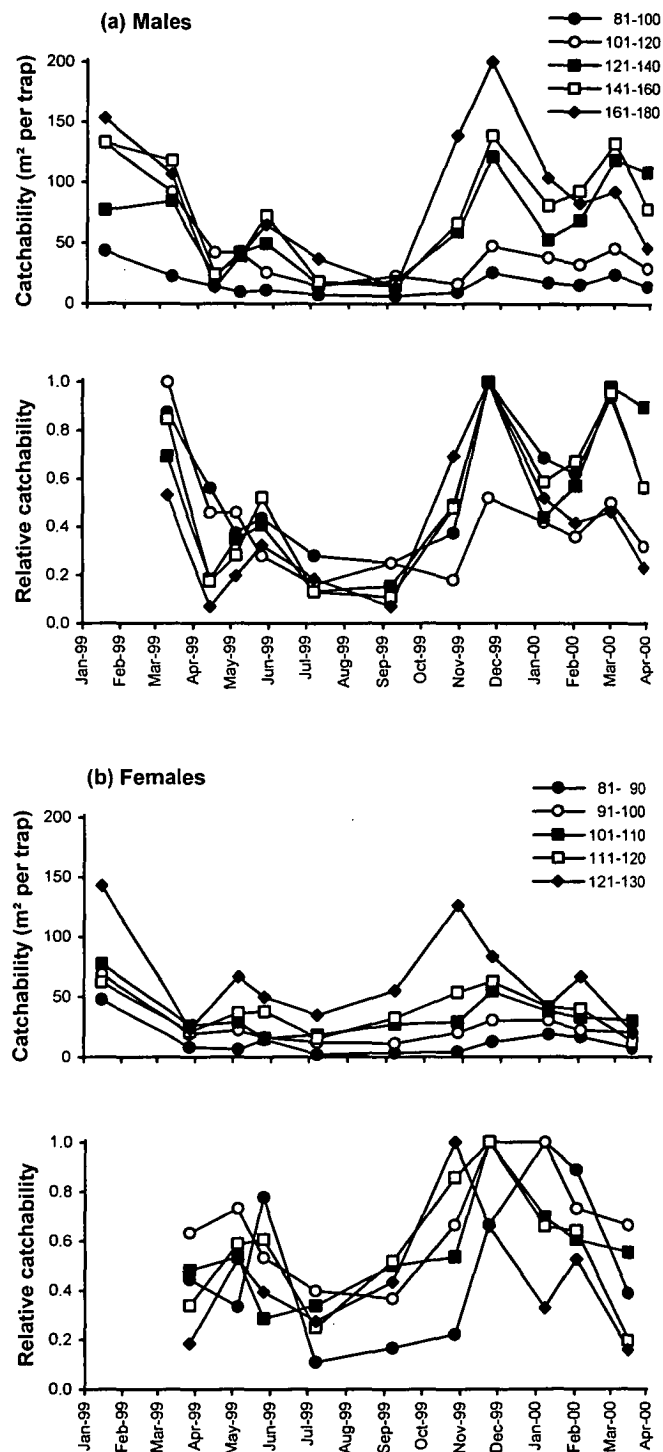


Fig. 3.6: Seasonal changes in absolute and relative catchability for each size class of (a) male and (b) female lobsters. Data for February 1999 are excluded for estimates of relative catchability (see text).



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 3.3). Large females had a higher negative correlation with small lobsters of either sex than did large males with small lobsters of either sex.

Table 3.3: Spearman's 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 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

*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. 3.7). Selectivity of small males and females was similarly low, while 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 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 due to the small sample sizes of recaptured animals.

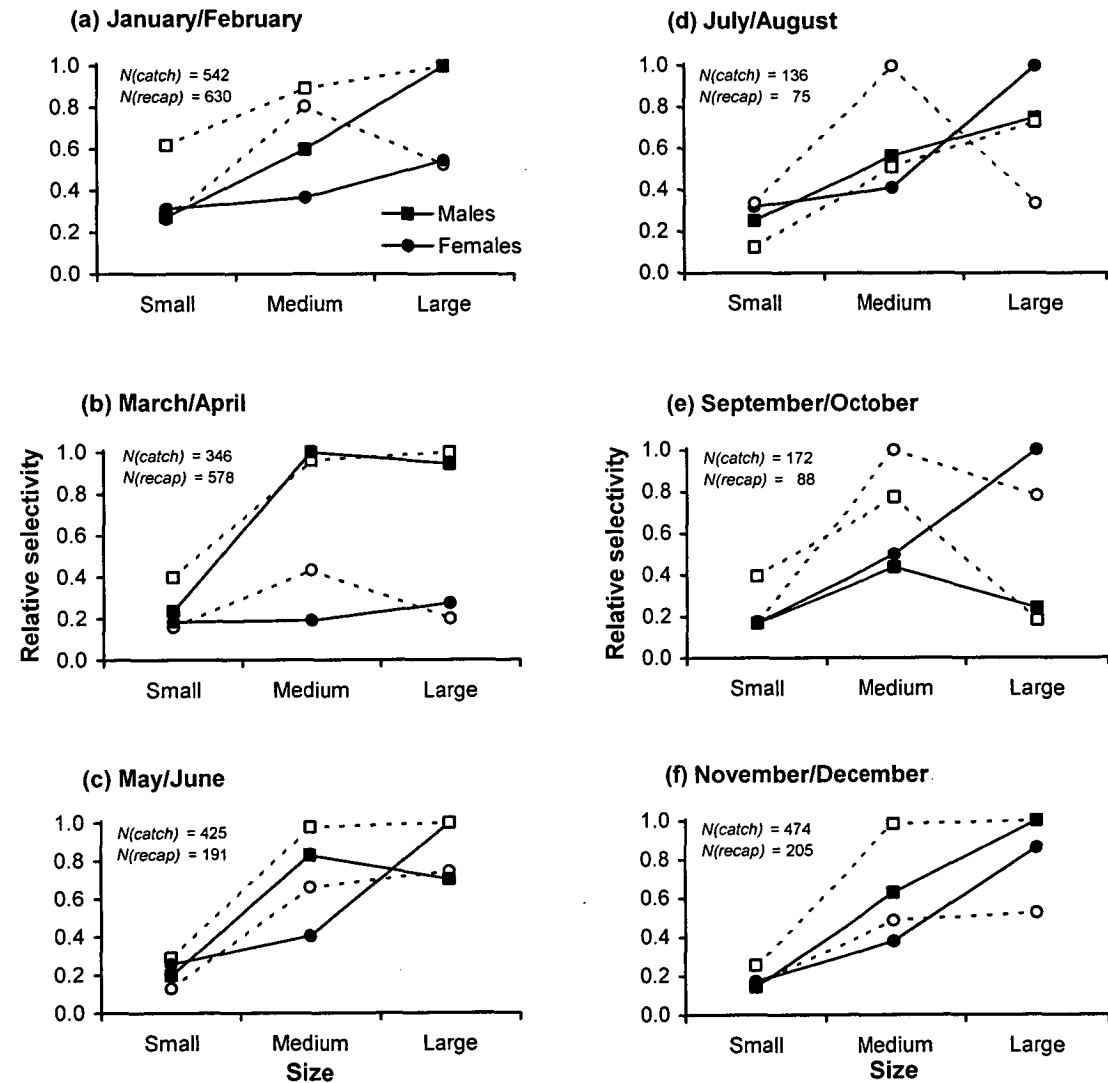


Fig. 3.7: Relative selectivity estimated from standardised size-specific catchability (solid lines and filled markers) and by the tag-recapture method (dotted line and open marker) for small, medium and large male (squares) and female lobsters (circles) during different periods of the year. Data are pooled bimonthly due to low sample sizes. Total sample size  $N(\text{catch})$  refers to combined male and female catches in standardised size-specific catchability, total sample size  $N(\text{recap})$  refers to combined male and female recaptures using tag-recapture method.

## 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, while a sampling bias due to 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, Tasmanian Aquaculture and Fisheries Institute, personal communications). Also, decreasing rates of recaptures in our catches of small males indicated a weak immigration (Chapter 2). 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 year around. By neglecting to account for an apparent increase in their population density during the austral summer, we would only slightly overestimate their low catchability.

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

While the densities of all size classes, and therefore the size-frequency distribution in the population, showed no or little changes over the year, the size-frequency

distribution in trap-catches varied, reflecting size-specific catchability which varied with sex and season.

Size-specific catchability was lowest for smallest lobsters and lead 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 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, i.e. 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 the *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 to September, while large females show the reverse trend.

Intraspecific interactions may have influenced size-specific catchability. The presence of lobster 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 due to the spatial separation of feeding grounds. Seasonal variation in feeding excursions, although 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. It remains therefore 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 *H. 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.

However, while 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 is reduced during winter and during moulting. It seems more likely that the seasonal pattern of catchability, which is largely independent of lobster size, is mainly influenced by factors like water temperature, moulting and mating (McLeese and Wilder 1958; Paloheimo 1963; Morgan 1974; Chapter 4).

*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 inter-annually.

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 e.g. 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 2001b), interactions between size and seasons are 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).

## Chapter 4:

### Seasonal catchability linked to water temperature, moulting, and mating

(Submitted to the Canadian Journal of Fisheries and Aquatic Sciences)

#### Abstract

Seasonal variation in catchability of legal-sized male and female southern rock lobster *Jasus edwardsii* in a scientific reserve in south-east Tasmania, Australia, was described by modelling the effects of water temperature, moulting and mating. Seasonal changes in water temperature described 63% of the variation of catchability for males, but were a poor predictor of catchability for females outside winter. Both moulting and mating were highly synchronised, although males and females moulted at different times of the year. Gaussian probability density functions were used to represent the timing and intensity of moulting, mating and subsequent compensation periods, and were added to the description of seasonal temperature changes. Four Gaussian functions in agreement with independent biological data considerably improved the model fits for the catchability of males ( $R^2 = 0.85$ ). Adding a single Gaussian function to the temperature model, representing a combined moulting and mating period, provided a good fit to the variation in catchability of females ( $R^2 = 0.84$ ). However, a model constrained by the observed timing of these events provided a less adequate description ( $R^2 = 0.47$ ), suggesting that interannual variation in moulting and mating events may play an important role in determining catchability.

## Introduction

Where catch rates or catch per unit effort (CPUE) is taken as an index of population abundance, catchability is an important parameter in stock assessments being necessary to scale catch rates relative to the stock size. Catchability  $q$  for a particular fishing gear over a given time interval  $t$  is given as:

$$q_t = C_t / (f_t N_t) = C_t / (f_t D_t) \quad (4.1)$$

where  $C$  is the catch,  $f$  is the fishing effort, and  $N$  the population size, which can be substituted by density  $D$  (animals per area). However, robust estimates of catchability in stock assessment models are often lacking, and catchability is therefore considered as a ‘nuisance’ variable that must be estimated indirectly. This is the case in the assessment in the southern rock lobster *Jasus edwardsii* fishery in Tasmania (Punt and Kennedy 1997).

Catchability of rock lobsters depends on the probability of animals encountering, entering and being retained in traps (Caddy 1977; Miller 1990; Arreguín-Sánchez 1996). Traps must be set in areas of lobster abundance, and act as a source of food and/or shelter. For baited traps, the soak time must cover periods of lobster activity and allow the odour plume of the bait to spread and the lobster to respond. The response of the lobster is affected by environmental factors such as temperature, swell, weather, and lunar cycle (McLeese and Wilder 1958; Morgan 1974; Branford 1979; Smith et al. 1999), and physiological factors such as moulting and mating (Lipcius and Herrnkind 1982; Zoutendyk 1988; Kelly et al. 1999; Tremblay 2000).

If the fishing method, fishing gear and bait are kept constant, then variation in the behaviour of animals, including how animals react to environmental conditions and their physiological state, are likely to form the main source of variation in the probability of encountering a trap, and therefore in catchability. Strong seasonal signals of catchability have been correlated with water temperature for the American lobster *Homarus americanus* (McLeese and Wilder 1958; Paloheimo 1963). By incorporating the effects of water temperature and moulting, catchability models have been developed for the Western rock lobster *Panulirus cygnus* (Morgan 1974),



and the portunid crab *Scylla serrata* (Williams and Hill 1982). However, existing models of lobster catchability based on environmental and physiological cycles are not gender-specific, although sex was found to be important to *H. americanus* and *J. edwardsii* catchability (Miller 1995; Tremblay and Eagles 1998; Tremblay 2000; Chapter 2). In addition, none of these models incorporate the entire moulting and reproductive cycle.

Here we investigate whether the seasonal variability in catchability of male and female *J. edwardsii*, as described in Chapter 2, can be modelled by the combined effects of water temperature and cycles of moulting and mating.

## Material and methods

### *Estimates of catchability*

Estimates of catchability for male and female lobsters were determined by comparing estimates of relative abundance from monthly trap lifts to estimates from *in situ* observations by divers (for a detailed description see Chapter 2). The work was conducted in a scientific reserve at Crayfish Point near Hobart in Tasmania, Australia (42°57.2'S, 147°21.2'E), where fishing for lobster by commercial and recreational fishermen is prohibited.

Densities of male and female lobsters were estimated *in situ* by underwater visual censuses in most months between February 1999 and April 2000. In concomitant monthly surveys, the reef and its adjacent areas were also sampled with a total of 96 trap lifts over four days. All lobsters captured in traps during the surveys were sexed, tagged, their carapace length measured to the nearest millimetre, and a pleopod clipped to augment tagging information for analysis of moulting. Animals were released immediately on processing. Only animals greater than the Tasmanian legal-size limits of 110 mm carapace length (CL) for males and 105 mm CL for females were included in the analysis. All captured legal-sized animals were mature. Size at onset of maturity in the reserve is approximately 81 mm CL for females (P. E. Ziegler unpublished data) and between 60-65 mm CL for males (C. Gardner, Tasmanian Aquaculture and Fisheries Institute, Tasmania, personal communication).

*Water temperature model*

Water temperature was recorded daily in water pumped from the middle of the scientific reserve at 6 m depth (Fig. 4.1). Maximum and minimum temperatures of 19.5°C and 10.1°C were recorded in February 1999 and July 1999, respectively. Temperature from 1 January 1999 to 14 April 2000 followed a sine function imposed on a linear trend:

$$\text{temperature (}^{\circ}\text{C)} = (15.03 - 0.00112 * x) - 3.47 * \sin((271.38 + x) * \pi / 194.1) \quad (4.2)$$

where  $x$  denotes the number of days since the starting date at 1 January 1999. The temperature function showed a weak linear trend (-0.00112) and a half-cycle length slightly larger than half a year (194.1 days). This model accounts for 96% of the variation in annual water temperature. The trend and amplitude parameters of the function were subsequently scaled separately to seasonal catchability of males and females, obtaining the best fit by a least-squares procedure.

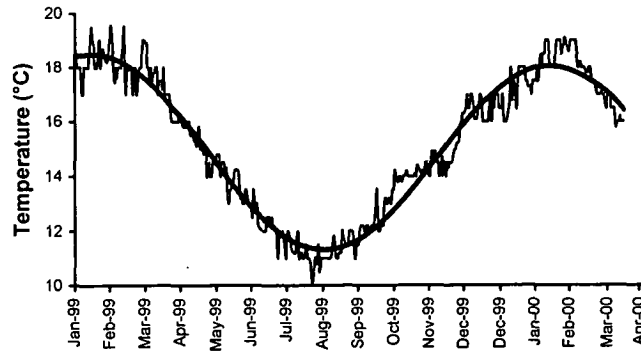


Fig. 4.1: Daily water temperature from the middle of the scientific reserve at 6 m depth. The smooth curve represents a sine function with a half-cycle length slightly larger than half a year (194.1 days) imposed on a linear trend. This curve accounts for 96% of the variation in the daily temperature data.

*Moulting and mating*

To determine timing and frequency of moulting, partial or complete regeneration of clipped pleopods between tagging and recapture events of lobsters was analysed. Of the 908 males and 531 females which were recaptured at least once, 447 males and 274 females covered a time period of at least 12 months between tagging and recapture. Only these animals were considered in the analysis. Multiple recaptures within the 12-month period were used to indicate the timing of moulting.

Since *J. edwardsii* females extrude their eggs within hours following copulation (McKoy 1979; MacDiarmid 1988), the first appearance of females carrying eggs indicates the starting date of the mating period. The monthly proportion of berried versus non-berried mature females with fully developed setae in trap catches was used to indicate the proportion of females involved in mating.

*Combined models of water temperature, moulting and mating*

By comparing two types of models with differing numbers of fixed parameters, we tested how well the physiological effects of moulting and mating were able to explain the residuals of the catchability model based on water temperature. The two types of models were developed separately for each sex. First, a set of 'free models' was used in the fitting process, in which all model parameters were fitted to the residuals. The secondary type were 'biologically-based models', in which estimates of timing and duration for moulting and mating were based on observations from field data. If there were close similarities between the free and biologically-based models in both parameter values and relative fit to the residuals remaining after accounting for the effects of water temperature, we assumed that moulting and mating were the main sources of variation in seasonal catchability in addition to water temperature

Both model types used Gaussian probability density functions to simulate the impact of the timing and intensity in moulting and mating on catchability. Gaussian curves were chosen primarily for their simple form and small number of parameters. Although they may not reflect exactly the underlying mechanisms of the moulting and mating activity, they were assumed to reflect the overall effects of the population

appropriately for the temporal resolution of the monthly catch sampling surveys. Each Gaussian curve:

$$f(x) = k * N(\mu, \sigma) \quad (4.3)$$

was defined by the amplitude  $k$  of the effect used as a scaling term in fitting the Gaussian curve to the catchability data, the mean date  $\mu$  of the effect providing the seasonal timing, and the standard deviation  $\sigma$  of the effect in days related to the duration.

#### (a) Males

Model 1 of the free models for males included a moulting and mating period with a total of 6 fitted parameters for amplitudes, mean dates, and the standard deviations of both periods (Table 4.1). Moulting and mating were expected to have a negative impact on catchability (Lipcius and Herrnkind 1982; Zoutendyk 1988; Miller 1990; Kelly et al. 1999), thus the amplitudes of their respective Gaussian curves were negative.

In model 2, compensation periods were added to allow for a period of high food consumption after moulting and mating when feeding resumes (Lipcius and Herrnkind 1982; Zoutendyk 1988; Miller 1990; Kelly et al. 1999). These subsequent compensation periods were also represented by Gaussian probability density functions, increasing the number of fitted parameters to 12. Compensation periods were expected to have a positive impact on catchability and thus the amplitudes of their Gaussian curves were positive.

Table 4.1: Catchability models for male lobsters, consisting of a water temperature sine function modified by Gaussian curves representing moulting, mating and associated compensation periods. In all cases the water temperature model is structurally identical (Table 4.3; Fig. 4.3). Each moulting, mating and compensation period is represented by a Gaussian function defined by the amplitude  $k$ , mean date  $\mu$  and standard deviation  $\sigma$ . Parameters for moulting, mating and their respective compensation periods are related to one another in models 3 to 6. The numbers of parameters refer to the moulting and mating components of the models. Models are compared with the least-square estimate of Akaike's Information Criterion (AIC). Mean dates and standard deviations for moulting and mating used in the biologically-based models are obtained from empirical observations. See Table 4.5 for parameter values of the optimal moulting and mating models (indicated as <sup>(a)</sup>).

					Free models			Biologically-based models		
Water temperature	Moulting	Moulting compensation	Mating	Mating compensation	Number of parameters	AIC	Adj $R^2$	Number of parameters	AIC	Adj $R^2$
Model 1: Moulting and mating										
$q = f(\text{temperature}) + k_O * N(\mu_O, \sigma_O)$			$+ k_S * N(\mu_S, \sigma_S)$		6	106.0	0.58	2	99.9	0.66
Model 2: Adding compensation periods										
$q = f(\text{temperature}) + k_O * N(\mu_O, \sigma_O) + k_P * N(\mu_P, \sigma_P)$			$+ k_S * N(\mu_S, \sigma_S) + k_T * N(\mu_T, \sigma_T)$		12	99.8	0.63	8	94.1	0.79
Model 3: Prescribed transition of compensation periods										
$q = f(\text{temperature}) + k_O * N(\mu_O, \sigma_O) + k_P * N(\mu_O + 1.96(\sigma_O + \sigma_P), \sigma_P)$			$+ k_S * N(\mu_S, \sigma_S) + k_T * N(\mu_S + 1.96(\sigma_S + \sigma_T), \sigma_T)$		10	94.8	0.77	6	93.9	0.79
Model 4: Identical standard deviations										
$q = f(\text{temperature}) + k_O * N(\mu_O, \sigma_O) + k_P * N(\mu_O + 3.92\sigma_O, \sigma_O)$			$+ k_S * N(\mu_S, \sigma_S) + k_T * N(\mu_S + 3.92\sigma_S, \sigma_S)$		8	92.8	0.80	4	92.0	0.80
Model 5: Identical amplitude										
$q = f(\text{temperature}) + k_O * N(\mu_O, \sigma_O) + k_P * N(\mu_O + 3.92\sigma_O, \sigma_O)$			$+ k_S * N(\mu_S, \sigma_S) - k_S * N(\mu_S + 3.92\sigma_S, \sigma_S)$		7	91.4	0.82	3	90.4	0.81
Model 6: Relating moulting and mating										
$q = f(\text{temperature}) + k_O * N(\mu_O, \sigma_O) + k_P * N(\mu_O + 3.92\sigma_O, \sigma_O)$			$+ 0.5 k_O * N(\mu_S, 0.5\sigma_O) - 0.5 k_O * N(\mu_S + 1.96\sigma_O, 0.5\sigma_O)$		5	88.3 <sup>(a)</sup>	0.85	2	88.6 <sup>(a)</sup>	0.83

Since compensation periods seem to immediately follow moulting and mating (Lipcius and Herrnkind 1982; Zoutendyk 1988; Miller 1990; Kelly et al. 1999), they followed moulting and mating in a prescribed transition in model 3. The mean dates of the compensation periods were delayed compared to the mean dates of moulting or mating by the sum of 1.96 standard deviations of each. Thus both curves, representing the mating or moulting period and the compensation period, overlapped at their 95 percentiles.

Using identical values for parameters of some Gaussian curves describing moulting, mating and their compensation periods further reduced the number of independent parameters. In model 4, the compensation periods after moulting and mating were assumed to have the same duration as moulting and mating, respectively. In model 5 it was assumed that both the duration and amplitude for the compensation period of mating, and the mating period itself, were identical. The duration of moulting and its associated compensation period were also identical. However, the amplitude of the moulting compensation period seemed to follow a different (positive) trend than that of moulting, and was fitted separately in all models.

In model 6, moulting was related to mating. In males, moulting was found to last twice as long as mating (see below). This may arise because individual males take longer to moult than to mate, and/or there is higher synchronicity in mating than in moulting in the population. In the models, we assumed that the duration of moulting and mating reflects the duration of reduced feeding in individuals and that similar proportions of the population are involved in both events. Feeding after ecdysis in male *J. edwardsii* does not resume for up to 4 weeks, and is also likely to cease for a similar period before ecdysis (Lipcius and Herrnkind 1982; Zoutendyk 1988; Kelly et al. 1999). In contrast, the mating period is considerably shorter than the moulting process. Males court females for 1-11 days, although the period of reduced feeding is probably longer, since males defend shelters during the mating period to attract copulation partners (MacDiarmid 1989; MacDiarmid 1994). Based on these observations, the standard deviation and amplitude of the male moult were assumed to be double those of mating, so that the magnitude of the separate impacts of moulting and mating on catchability is identical.

These free models were compared to a similar set of biologically-based models, in which timing of moulting and mating were set by empirical observations, and therefore only the fit of the amplitudes to the catchability data was optimised using least-squares. This reduced considerably the number of fitted parameters. In all biologically-based models, May 7 was used as the mean date of the mating period between mid April and the end of May, and September 15 as the mean date of the moulting period of males between the beginning of August and the end of October, as derived from the moulting and mating analysis (see below). The 1½ and 3 months periods of mating and moulting respectively, were assumed to represent 95% of all events in a Gaussian function and standard deviations were set accordingly.

These alternative models of varying complexity and differing numbers of parameters were compared with empirical observations of catchability. The optimum free and biologically-based models were determined as a balance between the number of independent parameters and the closeness of the fit to the data. The least-square estimate of Akaike's Information Criterion (AIC) was used to differentiate between models (Burnham and Anderson 1998). The model with the smallest AIC value is considered to be the best approximation for the information in the data, relative to the other models tested. Our final choice of models for catchability consisted of the best fit of the temperature model plus the optimal model for moulting and mating as determined by the AIC.

#### (b) Females

A similar comparison between free and biologically-based models as for males was performed for females, but with two major differences (Table 4.2). Firstly, a single Gaussian curve represented the combined moulting and mating period, since mating occurs within an average of 9 to 38 days after the female moult (MacDiarmid 1989). Secondly, the study period covered two combined moulting and mating seasons (see below). We accounted for the possibility of interannual variation in the timing and duration of moulting and mating in a set of five models similar to the models 1 to 5 described for males. In a second set of models we assumed no interannual variation and parameters were assumed to be similar for the two combined moulting and mating periods.

Table 4.2: Catchability models for female lobsters, consisting of a water temperature sine function modified by Gaussian curves representing combined moulting and mating periods and an associated compensation period. In all cases the water temperature model is structurally identical (Table 4.3; Fig. 4.3). Each combined moulting and mating period and the associated compensation period is represented by a Gaussian function defined by the amplitude  $k$ , mean date  $\mu$  and standard deviation  $\sigma$ . Models 1 to 5 allow for interannual variation, while in models 6 to 10 identical parameters are assumed for the two combined moulting and mating periods. Parameters for the combined moulting and mating period and its respective compensation period are related to one another in models 3 to 5 and models 8 to 10. The numbers of parameters refer to the moulting and mating components of the models. Models are compared with the least-square estimate of Akaike's Information Criterion (AIC). Adjusted  $R^2$  for females exclude the outlier in January 2000. Mean dates and standard deviations for moulting and mating used in the biologically-based models are obtained from empirical observations. See Table 4.5 for parameter values of the optimal moulting and mating models (indicated as <sup>(a)</sup>). Indicated models <sup>(†)</sup> are not biologically meaningful.

Water temperature	Combined moulting and mating period in 1999	Compensation period	Combined moulting and mating period in 2000	Free models			Biologically-based models		
				Number of parameters	AIC	Adj $R^2$	Number of parameters	AIC	Adj $R^2$
With interannual variation									
Model 1: Combined moulting and mating periods									
$q = f(\text{temperature})$	$+ k_O * N(\mu_O, \sigma_O)$		$+ k_S * N(\mu_S, \sigma_S)$	6	81.2 <sup>(a)</sup>	0.84	2	105.0	0.46
Model 2: Adding compensation period									
$q = f(\text{temperature})$	$+ k_O * N(\mu_O, \sigma_O)$	$+ k_P * N(\mu_P, \sigma_P)$	$+ k_S * N(\mu_S, \sigma_S)$	9	84.1	0.85	5	109.1	0.46
Model 3: Prescribed transition of compensation period									
$q = f(\text{temperature})$	$+ k_O * N(\mu_O, \sigma_O)$	$+ k_P * N(\mu_O + 1.96(\sigma_O + \sigma_P), \sigma_P)$	$+ k_S * N(\mu_S, \sigma_S)$	8	82.2	0.87	4	108.5	0.43
Model 4: Identical standard deviation									
$q = f(\text{temperature})$	$+ k_O * N(\mu_O, \sigma_O)$	$+ k_P * N(\mu_O + 3.92\sigma_O, \sigma_O)$	$+ k_S * N(\mu_S, \sigma_S)$	7	83.2	0.62	3	107.0	0.42
Model 5: Identical amplitude									
$q = f(\text{temperature})$	$+ k_O * N(\mu_O, \sigma_O)$	$- k_O * N(\mu_O + 3.92\sigma_O, \sigma_O)$	$+ k_S * N(\mu_S, \sigma_S)$	6		(†)	2		(†)



(Table 4.2 cont.)

Water temperature	Combined moulting and mating period in 1999	Compensation period	Combined moulting and mating period in 2000	Free models			Biologically-based models		
				Number of parameters	AIC	Adj $R^2$	Number of parameters	AIC	Adj $R^2$
No interannual variation									
Model 6: Combined moulting and mating periods									
$q = f(\text{temperature})$	$+ k_O * N(\mu_O, \sigma_O)$		$+ k_O * N(\mu_O+365, \sigma_O)$	3	85.1	0.74	1	103.4 <sup>(a)</sup>	0.47
Model 7: Adding compensation period									
$q = f(\text{temperature})$	$+ k_O * N(\mu_O, \sigma_O)$	$+ k_P * N(\mu_P, \sigma_P)$	$+ k_O * N(\mu_O+365, \sigma_O)$	6	86.0	0.84	4	107.5	0.50
Model 8: Prescribed transition of compensation period									
$q = f(\text{temperature})$	$+ k_O * N(\mu_O, \sigma_O)$	$+ k_P * N(\mu_O+1.96(\sigma_O+\sigma_P), \sigma_P)$	$+ k_O * N(\mu_O+365, \sigma_O)$	5	88.6	0.68	3	107.4	0.41
Model 9: Identical standard deviations									
$q = f(\text{temperature})$	$+ k_O * N(\mu_O, \sigma_O)$	$+ k_P * N(\mu_O+3.92\sigma_O, \sigma_O)$	$+ k_O * N(\mu_O+365, \sigma_O)$	4	86.9	0.71	2	105.4	0.44
Model 10: Identical amplitudes									
$q = f(\text{temperature})$	$+ k_O * N(\mu_O, \sigma_O)$	$- k_O * N(\mu_O+3.92\sigma_O, \sigma_O)$	$+ k_O * N(\mu_O+365, \sigma_O)$	3		(†)	1		(†)

Model 1 of each set of models included two combined moulting and mating periods. In model 2, a compensation period after the first combined moulting and mating period was added (the end of the study period restricted the addition of a compensation period after the second moulting and mating season). In model 3, the timing of the compensation period after moulting and mating was prescribed as in model 3 for male lobsters. In model 4 we assumed similar duration of moulting and mating and the subsequent compensation period, and in model 5 the absolute amplitudes of the moulting and mating period and corresponding compensation period were identical, but of opposite sign.

In the biologically-based models, April 15 was taken as the mean date of the combined moulting and mating period between the beginning of March and the end of May (see below), and the respective standard deviation calculated for this 3 month period. Unfortunately, no estimates for timing and duration of moulting and mating were available for the second year, so that estimates for the first year were used instead. As for males, our final choice of models for catchability consisted of the best fit of the temperature model plus the optimal model for moulting and mating as determined by the AIC.

## Results

### *Estimates of catchability*

Differences in catchability of legal-sized male and female lobsters were marked depending on season, although catchability of both sexes generally declined in winter and was elevated in summer (Fig. 4.2). Catchability of females dropped to low levels earlier in autumn and recovered earlier in spring than that of males, but the recovery was modest. These patterns are described with more detail in Chapters 2 and 3.

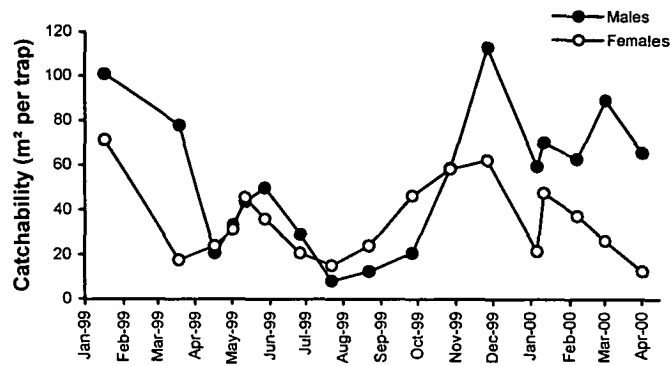


Fig. 4.2: Catchability of legal-sized male (filled circles) and female lobsters (open circles).

Water temperature model

The water temperature model described 63% of the variation in the catchability trend of males (Fig. 4.3; Table 4.3). The residuals showed distinct patterns such that between April and May and between August and October catchability of males was lower than predicted by the temperature model. Both periods were followed by higher than predicted values between May and July and between November and December, while during the second summer and autumn between January and April, catchability appeared to fluctuate without trend.

Table 4.3: Optimum models for catchability of male and female lobsters based solely on water temperature. Parameters of trend and amplitude of the sine function are adjusted to catchability for the complete period (January 1999 to April 2000) for males, and for winter and spring only (May 1999 to December 1999) for females.

Water temperature model:  $f(\text{temperature}) = (a * x + b) + c * \sin((x + d) * \pi / e)$

	Males	Females
<hr/>		
<i>x</i> = Days since start at 1 January 1999		
Gradient of trend <i>a</i>	-0.011	-0.011
Intercept of trend <i>b</i>	53.2	54.3
Amplitude of sine function <i>c</i>	-34.3	-33.0
Phase shift <i>d</i>	271.4	271.4
Oscillation frequency <i>e</i>	194.1	194.1
<i>R</i> <sup>2</sup>	0.63 (complete period)	0.06 (complete period) 0.92 (winter and spring only)

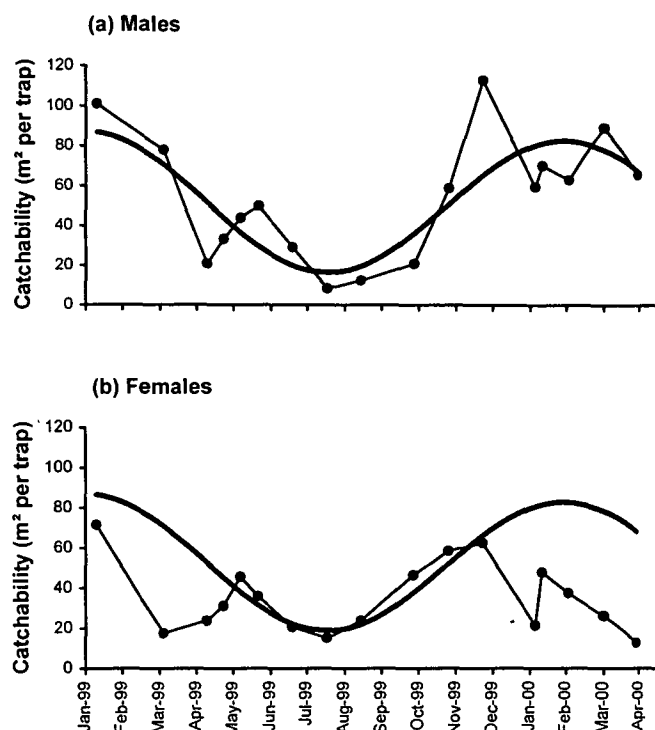


Fig. 4.3: Sine functions based on water temperature fitted to catchability data for (a) male lobsters from January 1999 to April 2000 and (b) female lobsters from May to December 1999.

Catchability of females did not follow the trend of water temperature, since the summer modal peaks of catchability and water temperature did not coincide (Fig. 4.3; Table 4.3). While changes in temperature were closely related to changes in catchability during the winter months, catchability dropped to low levels by February 2000, during the period of highest water temperature. A good localised fit was achieved by fitting the temperature model to the period from May to December, when 92% of the catchability variation could be explained. However, the overall fit remained poor with only 6% of the total variation explained.

*Moulting and mating*

In both males and females, distinct moulting periods lasting approximately three months in the year were identified. Males moulted later than females. Moulting of males occurred mainly from August to the end of October, while females moulted mainly from March to May (Table 4.4). Only 1.1% of males, all greater than 155 mm CL, did not moult at all during the 12-month period, while the remaining 98.9% exhibited regenerated pleopods at some stage during the year indicating that a moult had occurred. The majority of males (94.4%) appeared to moult between August and October (Fig. 4.4). Only a small fraction of recaptured male lobsters, tagged in January or March 1999, had moulted by June 1999. The proportion of moulted males increased from July to October, and after October 1999 almost all recaptured males had moulted. Males captured after September 1999 and subsequently recaptured showed little evidence of moulting. A small number of animals (4.0%) moulted a second time outside the main moulting period, largely during the summer months. Only 2 males (0.5%) showed a single moult outside the main moulting period.

Table 4.2: Observed timing and frequency of moulting in male and female lobsters in the scientific reserve.

	Males	Females
Main moulting period	August to October	March to May
Total animals ( <i>N</i> )	447	274
Not moulted	5 (1.1%)	11 (4.0%)
Total moulted	442 (98.9%)	263 (96.0%)
Single moult during main period	422 (94.4%)	233 (85.0%)
Single moult but outside main period	2 (0.5%)	3 (1.1%)
Two moults (at least one in main period)	18 (4.0%)	27 (9.9%)

Pleopod regeneration in the relatively few females recaptured between May and November indicated that a majority of females (85.0%) moulted between March and May (Table 4.4). After a steep increase in the proportion of recaptured females that had moulted, almost all females tagged in January or March had moulted by June (Fig. 4.4). The majority of females caught after July and recaptured in subsequent months had not moulted again by the end of the survey in April of the following year. Only 4.0% of females across all sizes did not moult at all during the full year of the study. More females than males moulted a second time outside the main moulting period (9.9%), while only 1.1% moulted singly and outside the main period.

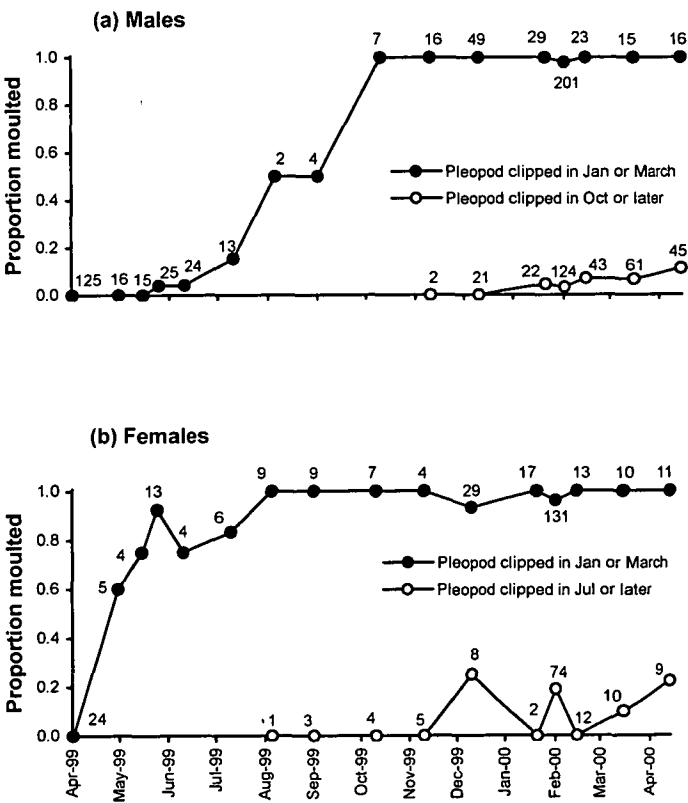


Fig. 4.4: Proportion of lobsters that moulted between capture and recapture in subsequent months derived from regeneration of clipped pleopods. Numbers denote sample size for each month. (a) Males captured and clipped in January or March 1999 (filled circles,  $N = 580$ ) and in October or later (open circles,  $N = 318$ ). (b) Females captured and clipped in January or March 1999 (filled circles,  $N = 296$ ) or in July or later (open circles,  $N = 93$ ).

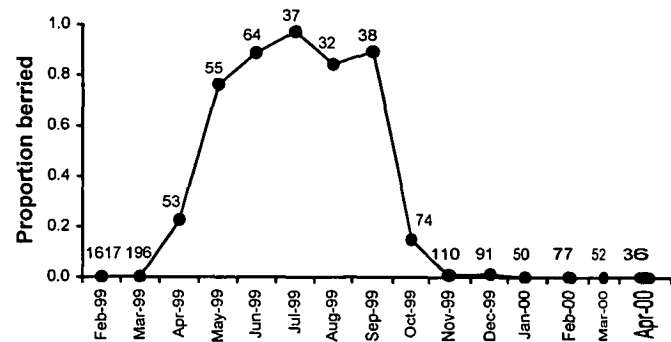


Fig. 4.5: Seasonal variation in the proportion of mature females carrying eggs. Numbers denote sample sizes.

Mating appeared to be synchronised in the population, with a high proportion of females mating in late April and May. Between May and September 87.3% of all mature females captured carried eggs (Fig. 4.5). Berried females first appeared in April, and the proportion of berried females increased steeply in May and peaked with 97.3% in mid-winter (July). Berried females were rare in spring, summer and autumn. The proportion of the male population involved in mating could not be determined but was assumed to be similar.

Sex ratios in trap catches varied with moult cycles (Fig. 4.6). During the male moult between August and October they were skewed towards females. After the male moult in spring when males resumed feeding, and until the middle of the female moult in autumn, males dominated the catches. During the second half of female moult, when mating took place, the sex ratio was close to 1:1.

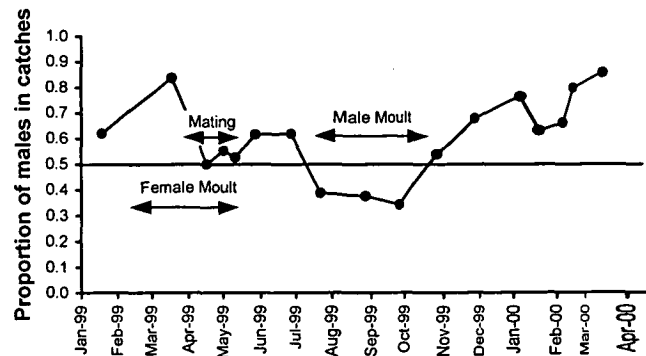


Fig. 4.6: Proportion of legal-sized male lobsters in catches from January 1999 to April 2000.

*Combined models of water temperature, moulting and mating*

Combining water temperature models with moulting and mating models improved the model fits to catchability, but also increased the number of parameters. Where appropriate, using the same parameter values for the different Gaussian curves of moulting, mating and associated compensation periods considerably reduced the number of parameters with only minor losses in the quality of fit.

Both optimum free and biologically-based models for the catchability of males incorporated four Gaussian curves for moulting, mating and subsequent compensation periods (Tables 4.1 and 4.5; Fig. 4.7). The optimum free model had only a slightly better fit than the optimum biologically-based model, but required 5 instead of 2 fitted parameters for the Gaussian curves. In addition to the identical amplitudes of the moulting, mating and mating compensation period and the amplitude of the moult compensation period, the mean dates of moulting and mating, and the identical duration of both periods had to be fitted in the free model.

Parameter estimates of the free and biologically-based models for males were similar. The estimate of the mean date of moulting in the biologically-based model was 13 days earlier than in the free model, while the mean dates of the associated compensation periods were similar. The estimates of the mean dates of mating were also similar in the two models, but the mean date of the associated compensation period was delayed by 14 days in the biologically-based model. Standard deviations of all Gaussian curves were slightly larger in the biologically-based model. Since these differences were small, both models provided a similar description of the data set. In combination with the water temperature model, these models accounted for 85% (free model) and 83% (biologically-based model) of the variation in catchability of males (Fig. 4.8).



Table 4.5: Moulting and mating components of optimum catchability models for male and female lobsters. The table shows sources and values of the parameters in each Gaussian probability density function  $f(x) = k * N(\mu, \sigma)$  representing moulting, mating and associated compensation periods given for the free and biologically-based models. The optimal models for females included only a combined moulting and mating period in each of the two years.

	Free model		Biologically-based model	
	Sources	Values	Sources	Values
<b>Males</b>				
<i>Moulting:</i>				
Mean date $\mu_O$	fitted	28 September	observed	15 September
Standard deviation $\sigma_O$	fitted	17.3 d	observed	21.8 d
Amplitude $k_O$	fitted	-1103.9	fitted	-1243.0
<i>Compensation period after moulting:</i>				
Mean date $\mu_P$	$= \mu_O + 3.92\sigma_O$	5 December	$= \mu_O + 3.92\sigma_O$	9 December
Standard deviation $\sigma_P$	$= \sigma_O$	17.3 d	$= \sigma_O$	21.8 d
Amplitude $k_P$	fitted	1964.5	fitted	2137.6
<i>Mating:</i>				
Mean date $\mu_S$	fitted	1 May	observed	7 May
Standard deviation $\sigma_S$	$= 0.5\sigma_O$	8.6 d	observed	10.9 d
Amplitude $k_S$	$= 0.5k_O$	-552.0	$= 0.5k_O$	-621.5
<i>Compensation period after mating:</i>				
Mean date $\mu_T$	$= \mu_T + 1.96\sigma_O$	4 June	$= \mu_T + 1.96\sigma_O$	18 June
Standard deviation $\sigma_T$	$= 0.5\sigma_O$	8.6 d	$= 0.5\sigma_O$	10.9 d
Amplitude $k_T$	$= -0.5k_O$	552.0	$= -0.5k_O$	621.5
Number of data points		17		17
Number of parameters		5		2
Sum of Squares		1697.4		2467.0
Adjusted $R^2$ incl. temperature model		0.85		0.83
<b>Females</b>				
<i>Combined moulting and mating 1999:</i>				
Mean date $\mu_O$	fitted	20 March	observed	15 April
Standard deviation $\sigma_O$	fitted	29.9 d	observed	21.8 d
Amplitude $k_O$	fitted	-4162.1	fitted	-3079.5
<i>Combined moulting and mating 2000:</i>				
Mean date $\mu_S$	fitted	12 March	$= \mu_O$	15 April
Standard deviation $\sigma_S$	fitted	54.2 d	$= \sigma_O$	21.8 d
Amplitude $k_S$	fitted	-7923.1	$= k_O$	-3079.5
Number of data points		17		17
Number of parameters		6		1
Sum of Squares		1212.1		9067.4
Adjusted $R^2$ incl. temperature model		0.76		0.34
When Jan 2000 excluded		0.84		0.47

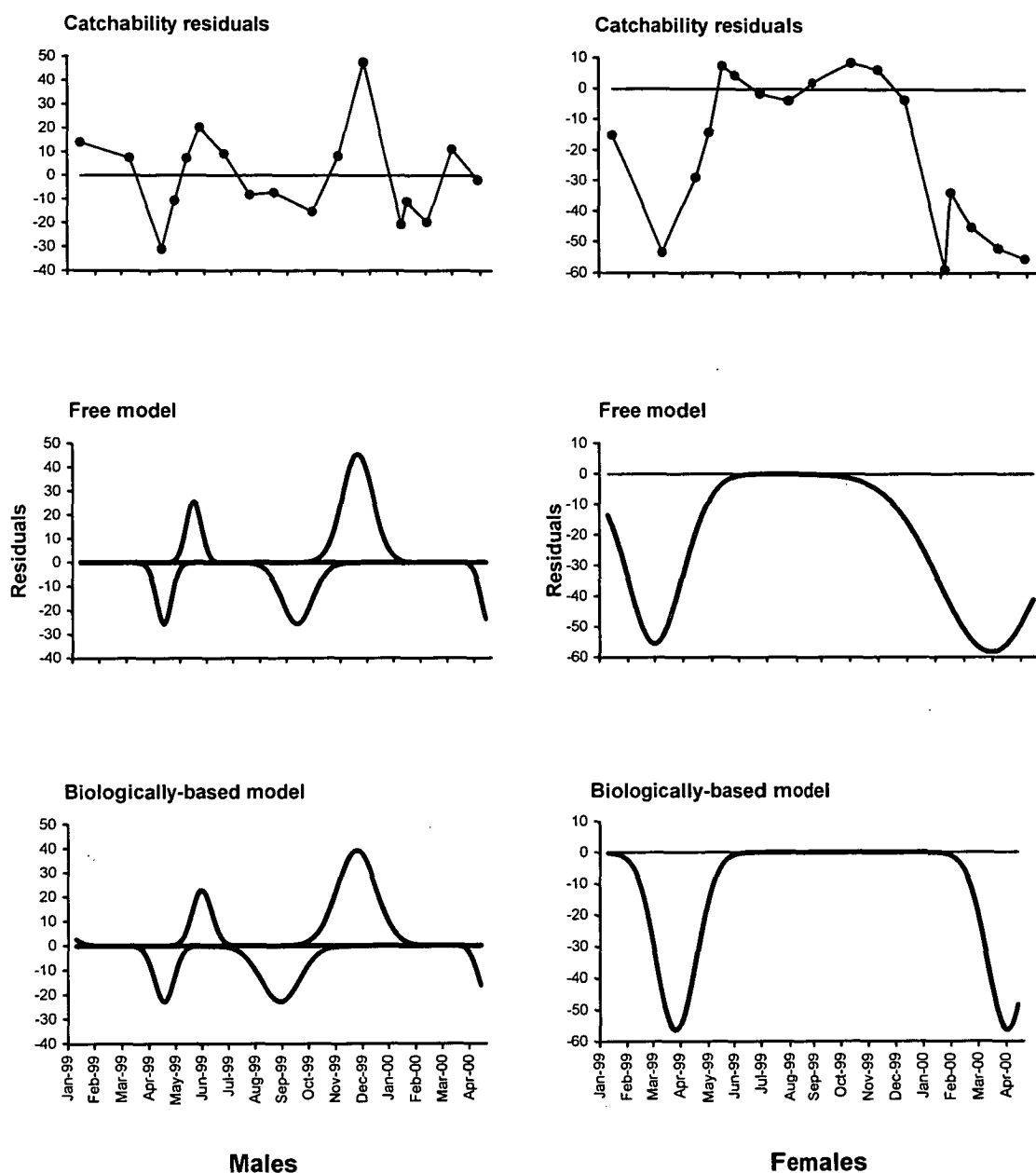


Fig. 4.7: Plots of residuals after the water temperature sine function has been applied to the catchability data for male and female lobsters. To these residuals free and biologically-based models describing moulting and mating events were fitted. Only the optimum models are shown. For males, the free and biologically-based models consist of two Gaussian curves with negative amplitudes representing mating and moulting, and two Gaussian curves with positive amplitude representing associated periods of compensation. For females, the free and biologically-based models consist of two Gaussian curves with negative amplitudes representing combined periods of moulting and mating in each of two years.

The general structure of the optimum biologically-based and free models for the catchability of females was also similar (Tables 4.2 and 4.5; Fig. 4.7). Both models consisted of two combined moulting and mating periods, i.e. one in each of two consecutive years. Models without a compensation period after the combined moulting and mating period performed better than models with a compensation period according to the AIC measure.

When added to the water temperature model (Fig. 4.8), the free model described 76% of the total variation. When the low catchability value in January 2000 was excluded, parameter values changed minimally, but the variation described improved to 84%. The January 2000 data point appeared as an outlier, possibly caused by locally inclement weather and high swells, both of which are known to affect the mobility and behaviour of lobsters. By adding the biologically-based model to the temperature model, only 34% of the total variation in catchability was described, increasing to 47% when the January 2000 outlier was excluded.

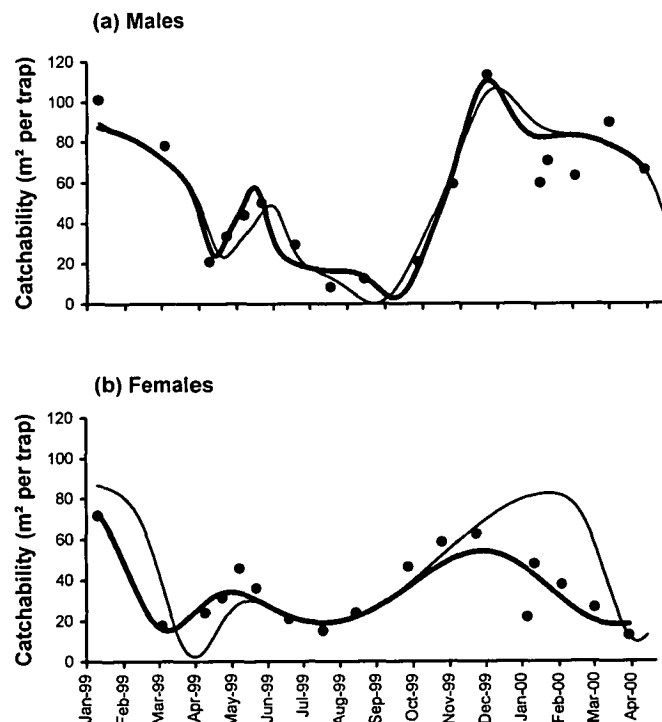


Fig. 4.8: Optimum free (heavy line) and biologically-based models (thin line) of catchability combining the effects of water temperature, moulting and mating for (a) male and (b) female lobsters. Circles indicate empirical estimates of catchability to which the models were fitted.

## Discussion

Models were developed to help understand possible factors causing seasonal and gender-specific variation in catchability of southern rock lobsters. The models were based on two factors that are plausibly the main sources of variation in catchability, viz. water temperature and the physiological cycles of moulting and mating. By adding Gaussian curves representing moulting, mating and associated compensation periods to a function describing water temperature, 85% of the annual variation in catchability of males were described. The model for catchability of females based on these two factors described 84% of the variation, but indicated that other factors play an important role in determining catchability. In this case, interannual variation of moulting and mating could account for this variation.

### *Effects of water temperature*

Water temperature was an important but insufficient parameter to predict catchability. Seasonal changes in water temperature accounted for 63% of the variation in catchability of male lobsters, but failed to adequately describe catchability of female lobsters for a full season. In summer and autumn, water temperature was a poor predictor of catchability of females.

Close correlations between catchability and water temperature, as found in the present study for males, have been reported previously. Monthly or seasonal water temperature is closely correlated with catchability of *H. americanus* outside the moulting period between September and April (McLeese and Wilder 1958; Paloheimo 1963). Other authors have reported correlations between water temperature and catch rates for clawed and spiny lobsters, however, they refer mainly to annual mean sea surface temperatures and annual catch rates of males and females combined, and do not address seasonal variation in catchability (e.g. Flowers and Saila 1972; Dow 1977; Fogarty 1988; Campbell et al. 1991; Evans et al. 1995).

*Effects of moulting and mating*

Catchability varied between sexes as well as seasonally. The gender differences correlated with the different timing of moulting during the year. Considerable improvements to the amount of variation in the data described by the models were achieved by adding Gaussian functions to the temperature models to describe moulting, mating and their associated compensation periods.

In males, the free model consisted of four Gaussian curves for moulting, mating and associated compensation periods and was similar to the biologically-based model. In the free model, the delay between moulting and mating and their respective compensation periods were shorter than in the optimal biologically-based model (the standard deviations were smaller). Since the temporal limits of moulting and mating in the biologically-based models were determined from monthly sampling surveys, the resolution of the estimates was relatively coarse and may have been biased. The large overlap of the Gaussian curves, similarities in the amount of variation described, and similar AIC values of the free and biologically-based models indicated that moulting and mating account for the residuals from the temperature model and play an important role in determining the overall catchability. This is also confirmed by the weekly food consumption rates of captive male *J. edwardsii* in New Zealand (Kelly et al. 1999), which were related to their moulting and mating cycle and follow closely the trend of catchability found in this study. In addition, our models support earlier findings in many lobster species suggesting that animals increase food consumption after moulting and mating to compensate for the lack of feeding during these periods (Lipcius and Herrnkind 1982; Zoutendyk 1988; Miller 1990; Kelly et al. 1999).

In females, the optimal description of catchability was produced by adding a single Gaussian function with negative amplitude, representing the combined periods of moulting and mating to the temperature function. This curve largely reduced the effect of water temperature when it was highest and can therefore explain the shift in the modal peaks between catchability and water temperature during summer.

While the structure of the free model for females was similar to that of the biologically-based model, it provided a notably better fit to the data and its parameter estimates differed substantially. By accounting for interannual variation in the timing

and duration of moulting and mating, the free model successfully captured the low catchability from January to May 2000. In contrast, the moulting and mating effects in the biologically-based model were constrained to the period from March to May and the model failed to describe the low values in January and February 2000.

This may have been caused by extrapolating inappropriately the timing and duration of moulting and mating from field observations in the first year to the second year, and/or overestimating the impact of water temperature in summer. Since catchability of females did not follow the trend of water temperature during summer and autumn, the temperature function was fitted to data between May and December, where it provided a good prediction of catchability. As a consequence, the temperature model may have overestimated catchability in summer. In addition, it performed the function of the expected compensation period following moulting and mating. This is in contrast to peak rates of weekly food consumption by captive female *J. edwardsii* in New Zealand just after mating in June and July, which suggest that females compensate for the lack of feeding during moulting and mating (Kelly et al. 1999). However, the resumption of food consumption in winter may be suppressed in our study area, because water temperatures after moulting and mating (ca. 10°C) were several degrees lower than at the study site in New Zealand (ca. 15°C; MacDiarmid 1989; Kelly et al. 1999).

Similar influences of moulting and mating on catchability have been described from other lobster fisheries. Catchability of male *J. lalandii* is depressed during moulting, and then increases markedly for at least two months after moulting along the west coast of South Africa (Newman and Pollock 1974; Pollock and DeB. Beyers 1979). In Maine, USA, *H. americanus* has a reduced catchability during moulting in June (Fogarty 1988). Further north in Nova Scotia, Canada, Tremblay and Eagles (1997) reported skewed sex ratios in traps during the moulting season of males and females similar to those reported here. In early summer, when males are less likely to be captured as they prepare to moult, the sex ratio is skewed towards females, while the female moult causes a high male-to-female ratio in late summer and autumn.

In addition to moulting and mating, factors such as the dietary composition and maternal broodcare can influence feeding behaviour and cause differences in catchability between males and females. Nevertheless, diets of male and female

lobsters have been found to be generally similar, although they can change with moulting activity (Ennis 1973; Joll and Phillips 1984; Mayfield et al. 2000). Maternal broodcare may alter the foraging behaviour of females, but females in this study were berried predominantly between April and October, during the period of the smallest differences in catchability between the two sexes.

### *Conclusions*

Despite frequent descriptions of seasonal environmental and physiological factors that influence catchability, few models consider these influences. In most cases models have been simple multiple linear correlations. Morgan (1974) correlated catchability of *P. cygnus* with a combination of temperature, salinity and moult factors, while temperature and moulting accounted for 66% of variation in monthly catches of the portunid crab *S. serrata* (Williams and Hill 1982). In both studies, no distinction between sexes was made and the reproductive cycle was not included. Our models are the first to include water temperature, moulting and mating in a combined model. In crustacean species where moulting of each sex occurs at different periods during the year, we have shown that separate models are required for each sex.

Our models were developed for a population in an unfished region where large males and females formed a substantial proportion of the population. In contrast, the size-frequency distribution in fished areas is usually truncated at the legal-size limit. Since the size of an animal is likely to influence its catchability (Miller 1989, 1995; Pezzack and Duggan 1995; Frusher and Hoenig 2001; Chapter 3), we expect catchability to differ in areas with a different population size structure. However, it is likely that effects of water temperature, moulting and mating can be found to influence catchability in a similar way as found in this study, since the seasonal pattern of catchability is largely independent of lobster size (Chapter 3).

**Chapter 5:**  
**Space-time variation in catchability of southern rock lobster**  
***Jasus edwardsii* in Tasmania explained by environmental,**  
**physiological and density-dependent processes**

(Accepted by the Journal of Fisheries Research)

**Abstract**

A seasonal catchability model, which had been developed previously for the rock lobster *Jasus edwardsii* population in a scientific reserve, was applied to catchability over several years in the two fishing regions off Tasmania. Catchability was estimated from commercial catch and effort data and fishery-independent estimates of exploitation rates. The seasonal catchability models describe the effects of water temperature, moulting and mating on catchability. They suggest that similar environmental and physiological processes underpin seasonal catchability in the two fishery regions, but that the relative importance of these factors varies considerably between the two regions. Physiological processes dominate the pattern of catchability in the north while water temperature contributes significantly to the model only in the south. Interannual variation in relative catchability was correlated with density-dependent processes. Full models described 72% of the total variation in catchability over 6 years in the south and 80% of the total variation over 4 years in the north.



Introduction

Catchability is used to scale catch rates to stock biomass and is therefore an important parameter in stock assessment models of many crustacean fisheries, including the southern rock lobster *Jasus edwardsii* fishery in Tasmania, Australia (Punt and Kennedy 1997). To estimate changes in relative catchability within a year, seasonal catchability models have been developed for the legal-sized population of male and female lobsters in a scientific reserve at Crayfish Point, Taroona, in the south-east of the state (Fig. 5.1; Chapter 4). These models are based on water temperature, moulting and mating, which previously have been found to influence catchability (McLeese and Wilder 1958; Morgan 1974, 1978; Chittleborough 1975; Branford 1979; Lipcius and Herrnkind 1982; Zoutendyk 1988; Kelly et al. 1999; Smith et al. 1999).

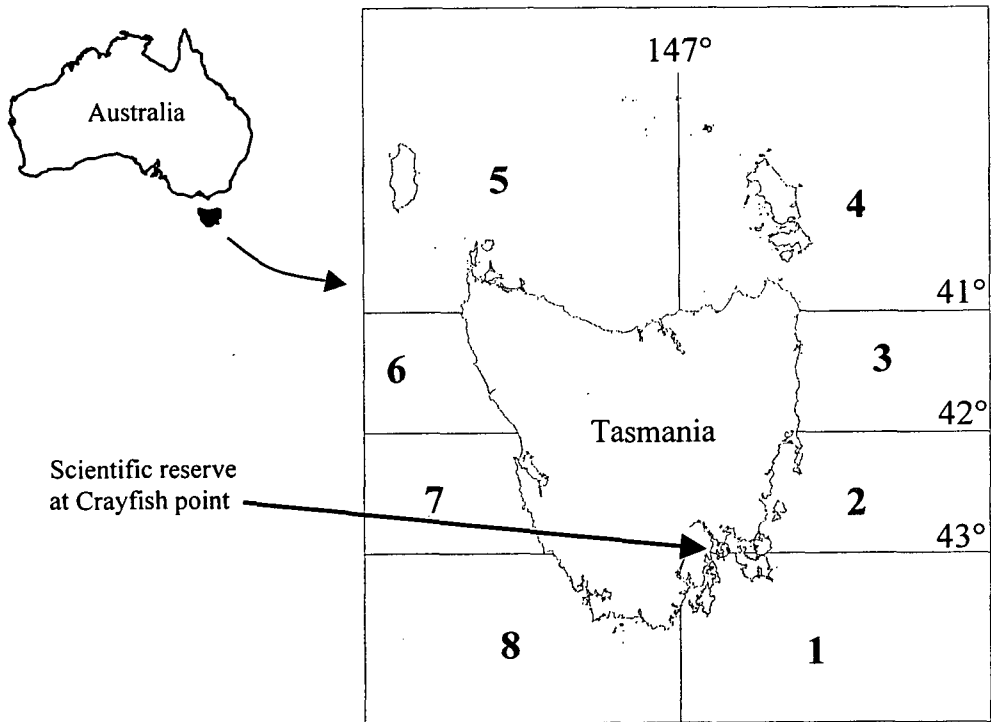


Fig. 5.1: Map of Tasmania, indicating the scientific reserve at Crayfish Point, Taroona, and the eight fishing areas of stock assessment for rock lobster.

Water temperature and physiological parameters such as growth rate, size at maturity, and the frequency, timing and duration of moulting and mating vary considerably among the fishery regions around Tasmania (Frusher 1997; Punt et al. 1997). Water temperatures in summer and winter are approximately 2°C warmer in the north than in the south. Growth rates differ substantially, with males and females growing over 4 times faster and reaching larger maximum sizes in the north than in the south of the state. Given these differences, it seemed highly likely that catchability would differ among regions.

Population density and size-frequency structure also vary among regions and years (Frusher 1997), and this too can affect catchability. Catchability may increase with decreasing population density, as the presence of a lobster in a trap can inhibit the entry of other lobsters and therefore reduce catch rates (Richards et al. 1983; Addison 1995; Miller and Addison 1995; Addison and Bannister 1998; Frusher and Hoenig 2001b). These behavioural interactions are also likely to depend on the population size-frequency structure, since catchability is known to increase with animal size and to change as large lobsters are removed by the fishery (e.g. Morrissey and Caputi 1981; Miller 1989, 1995; Pezzack and Duggan 1995; Tremblay et al. 1998, Tremblay 2000; Frusher and Hoenig 2001b; Chapter 3). This suggests that catchability varies between regions in Tasmania, because the population size structure is very different between areas in the north and the south of the state, where animals grow up to 200 mm and 120 mm carapace length (CL) respectively (Frusher 1997). However, size-specific effects on catchability in the Tasmanian fishery are still poorly understood.

The aim of this project was to develop predictive models of seasonal and interannual variation in catchability in the lobster fishery for different regions around Tasmania. By applying our catchability model developed for a population in a scientific reserve, where we measured catchability directly (Chapter 4), we investigated whether environmental and physiological processes are the main sources of variation in catchability in two commercially fished regions in the north and the south of the state.

## Material and methods

### *Estimates of relative catchability*

Regions in the southwest (stock assessment area 8; Fig. 5.1) and in the northwest (stock assessment area 5) of Tasmania were selected, since they represent extremes of the fishery with regard to environmental and physiological processes (Frusher 1997). Monthly catchability  $q$  of legal-sized male ( $\geq 110$  mm CL) and female lobsters ( $\geq 105$  mm CL) was estimated as the ratio of catch per unit effort to estimated population size, and was then standardised relative to the highest value within each fishing season.

For each fishing season from early austral summer in November to the following August, monthly catch rates were calculated from commercial catch and effort data. Daily catch and effort returns by each licence holder are mandatory and provide information of the geographical block fished, number of potlifts, depth, size of the catch in weight and numbers of animals. However, catch data collected by fishermen are not sex-specific. Males and females are captured from November until the end of April, when the fishery for females is closed. From May until the end of the season in August only males are retained. To standardise catch rates over the whole season in area 5, we used the proportion of legal-sized males captured in scientific catch samples of legal-sized animals (61.8% males in May,  $N = 940$ ; 49.0% males in September,  $N = 1379$ ) to estimate total catch rates between May and August. Catchability estimates in the northwest were thus not sex-specific. In the colder and deeper waters of area 8 further south, females do not reach legal size. Thus, catch data and estimates of catchability for this region are for legal-sized males only.

The number of legal-sized animals at the start of the season  $N_s$  was estimated by dividing the total number of animals captured  $C_t$  by the exploitation rate  $U_t$  for the same period:

$$N_s = C_t / U_t \quad (5.1)$$

Mean population size during each month  $N_x$  was calculated by subtracting all catches from preceding months plus half the catch of the month of interest:

$$N_x = N_s - (C_1 + C_2 + C_3 + \dots + C_{x-1} + (C_x / 2)) \quad (5.2)$$

Estimates of exploitation rates (required in equation 5.1), derived from change-in-ratio techniques in area 8 and multi-year tagging studies in area 5, were taken from Frusher et al. (1998) and Frusher and Hoenig (2001a) respectively. Both methods calculated fishing mortality for the legal-sized population of combined sexes each year. Although these two methods have never been compared directly, but been applied to dissimilar data sets, both methods have been assessed for variation in catchability which could bias estimates of exploitation rates (Frusher 2001; Frusher and Hoenig In press). Therefore we believe that these estimates are applicable for this study.

Exploitation rates at mid season (March) or at the end of each season (August) were available over 6 seasons in area 8 (1992/1993, 1993/1994, and 1995/1996 to 1998/1999) and over 4 seasons in area 5 (1992/1993 to 1995/1996). The open season was shortened or extended in three years. The fishing season of 95/96 started late (December), while the 97/98 and 98/99 seasons in area 8 were open until September. However, data for September were excluded from the analysis, since recruitment to the fishery was assumed during this month. September catch rates increased greatly compared with those in August, but a high proportion of the animals in the September catches had just moulted. Since new recruits make up a substantial proportion of the catches in area 8, we assumed that the population available to the fishery had increased in September compared with the months before.

#### *Correlation of seasonal catchability and temperature*

To determine the proportion of the variation in catchability described by water temperature, the monthly estimates of relative catchability were correlated with mean monthly water temperatures. Due to lack of direct measurements of water

temperatures, sea surface temperature (SST) near Maatsuyker Island in area 8 and near King Island in area 5 from NOAA satellite AVHRR imagery was used to indicate water temperature for the period between November 1989 and August 2000. Because estimates of SST can be biased downwards if there is significant cloud cover, water temperature was calculated as a 20-day median average of observations taken every 4 days to minimise the effects of short-term warmings and lowering of temperatures by cloud contamination. However, in area 8 where cloud cover can occur over extended periods, short-term drops in SST sometimes occurred over one or two data points (4-8 days) followed by rapid recovery. If a short-term temperature drop differed by more than 2°C from the temperature of the preceding or following data points, these data were treated as outliers and omitted from the analysis.

SST ranged from 9.6°C to 17.5°C in area 8 and from 11.3°C to 19.2°C in area 5. Because absolute changes in temperature with depth were similar at all times of the year, trends in SST were considered to adequately represent trends in water temperature experienced by the lobsters on the ground. Temperature profiles were measured directly on research cruises in October 1992, March and October 1993 in area 8, and in February and May 1993 and 1994 in area 5. They indicated similar absolute declines in water temperature with depth within regions throughout the year in waters less than 60 m depth, which is where most lobsters are captured. In area 8, waters at depths between 45 m and 80 m were 0.2°C to 1.8°C colder than at the surface in March, and 0.6°C to 1.7°C colder in October. In area 5, water temperatures between 30 m and 60 m were 0.3°C to 1.6°C colder than at the surface in February, and up to 0.8°C colder in May.

### *Models of relative catchability*

#### *(a) Model parameters*

The models of catchability used in this study combine a function to describe water temperature and Gaussian curves representing the effects of moulting, mating and subsequent compensation periods, similar to that described in Chapter 4.

Water temperature is represented by a sine function imposed on a linear trend for the 11-year period from November 1989 to August 2000 in each region:

$$\text{temperature } (^{\circ}\text{C}) = (a * x + b) + c * \sin ((d + x) * \pi / e) \quad (5.3)$$

where  $a$  and  $b$  are the slope and intercept of any linear trend,  $c$  is the amplitude,  $d$  is the phase shift relative to the date of the first data point,  $e$  determines the oscillation frequency of the sine function, and  $x$  denotes the number of days since the starting date at 10 November 1989. The linear trends in both regions were close to zero. The models accounted for 66% of the variation in water temperature in area 8, where SST strongly fluctuated presumably because of extensive periods of cloud cover, and 81% of the variation in water temperature in area 5 over the 11-year period.

The timing and duration of moulting and mating were estimated from independent biological data at Maatsuyker Island in area 8 and at King Island in area 5 (see Appendix 5A). Since only males contribute to catches in area 8, estimates of the male moult and mating parameters were used in the models for this region, where most males moult once a year between August and October. Mating was assumed to start in the middle of the female moult and end simultaneously as moulting (Chapter 4). However, while most females apparently moulted between March and the end of July, the timing of the female moult could not be determined more precisely. For the models, the female moult and mating in area 8 were thus assumed to be similar to that in the scientific reserve on the southeast coast, where females moult from March until May and mating takes place from mid April until the end of May (Chapter 4).

In area 5, where the size range of lobsters is greater than in area 8 in the south, the frequency, timing and duration of moulting depend on size. As a result, at least some individuals of the population moult over an extended period. Males smaller than 130 mm CL moult between October and March, while males greater than 130 mm CL moult earlier between September and December. Small males and some large males moult a second time between May and July. This timing falls within the period of mating and the main moult of females. Females smaller than 110 mm CL moult a second time between November and March, and some females larger than 110 mm

CL have a second moult between February and March. Two annual moults are therefore an important feature of this population with an extended period between September and March and a well-defined second moulting and mating period between May and July. To distinguish between the two periods in the remainder of the text, we refer to the first moulting period as ‘moulting’ and to the combined period of the second moulting and mating as ‘mating’.

Similar models as described in Chapter 4 simulated the effects of moulting and mating on catchability. Four Gaussian curves were used to represent the effects of moulting, mating and subsequent compensation periods when feeding resumes after moulting and mating (Chittleborough 1975; Lipcius and Herrnkind 1982; Zoutendyk 1988; Miller 1990; Kelly et al. 1999). Each Gaussian curve:

$$f(x) = k * N(\mu, \sigma) \quad (5.4)$$

was defined by the amplitude  $k$  of the effect as a scaling term used to fit the relative catchability data, the mean date  $\mu$  of the effect providing the seasonal timing, and the standard deviation  $\sigma$  of the effect in days related to the duration. Because moulting and mating were expected to have a negative impact on catchability, the amplitudes of their respective Gaussian curves were negative. Subsequent compensation periods were expected to have a positive impact on catchability and thus the amplitudes of their Gaussian curves were positive.

As in the original model developed to describe catchability in the scientific reserve (Chapter 4), the number of independent parameters needed was reduced by using identical parameters for the separate Gaussian curves relating to moulting, mating and their compensation periods. The ‘duration’ of moulting and mating was defined as equalling 3.92 standard deviations, i.e. they represented 95% of all events in a normal distribution function. Mating and its respective compensation period were assumed to have the same duration and complementary amplitudes, and the duration of the moulting compensation period was assumed to be the same as that of moulting. The amplitude of the moulting compensation period was fitted separately in all models, as moult compensation in the catchability model of the scientific reserve during the early austral summer had by far exceeded all other impacts of

moulting and mating. Compensation periods were assumed to immediately follow moulting and mating in a smooth transition. To represent this in the model, the mean dates of the compensation periods were delayed compared to the mean dates of moulting or mating by the sum of 1.96 standard deviations of each, so that both curves, representing the mating or moulting period and the subsequent compensation period, overlapped at their 95 percentile.

As in the original model (Chapter 4), we assumed that differences in the duration of moulting and mating in area 8 were caused by differences in duration rather than in synchronicity of moulting and mating in individuals. In the scientific reserve, moulting of males had been found to last twice as long as mating, which seemed to reflect the relative duration during which animals cease to feed. Feeding after ecdysis in male *J. edwardsii* does not resume for up to 4 weeks, and is also likely to cease for a similar period before ecdysis as in other lobster species (Lipcius and Herrnkind 1982; Zoutendyk 1988; Kelly et al. 1999). In contrast, the mating period is considerably shorter than the moulting process. Males court females for 1-11 days, although the period of reduced feeding is probably longer because males defend shelters during the mating period to attract copulation partners (MacDiarmid 1989; MacDiarmid 1994). Assuming that similar proportions of the population are involved in both events, the peak impact of moulting and mating will be identical. Thus, the amplitudes of the moulting and mating periods were related to one another according to the duration of their periods, e.g. if moulting lasted twice as long as mating, its amplitude was also double that of mating.

In area 5, the first moult is weakly synchronised and only a fraction of the population moults at any one time between September and March. Since the first moulting period and the second combined moulting and mating period were expected to have a similar overall impact on catchability, their amplitudes were set to be identical. However, the compensation period after the first moult relates only to animals moulting towards the end of the extended moulting period. While the proportion of these animals in the population was unknown, their moult duration was assumed to be similar to the second moult. To account for this, the amplitude of this moult compensation period was fitted separately and the duration set to be identical with that of the compensation period after the second moult.



### (b) Modelling seasonal variation in catchability

Models describing the seasonal component of catchability during the fishing season from November to August were fitted to monthly data over 6 years in area 8 ( $N = 59$  months) and over 4 years in area 5 ( $N = 39$  months). In all models, the intercept of the trend and the amplitude of the 11-year temperature sine function, and the amplitudes of the Gaussian curves, were fitted to the catchability data (Table 5.1). In 'biologically-based models', empirical estimates of mean dates and duration, derived from independent biological studies (Appendix 5A), were used to define the periods of moulting and mating within the model. Thus, beside the two parameters for the water temperature model, only 2 more parameters were needed to describe the identical amplitudes of the moulting, mating and mating compensation curves, and the amplitude of the moulting compensation curve. The performance of biologically-based models was compared to that of 'seasonal models', in which the 4 parameters for mean dates and duration of moulting and mating were fitted to the catchability data, i.e. they were not set by independent empirical observations. All fits were optimised using a least-square residual error procedure.

### (c) Modelling interannual variation in catchability

We ran four different 'annual models' to investigate the extent to which the interannual variation in water temperature and the timing of moulting and mating account for interannual variation in relative catchability (Table 5.1). In annual models 1 and 2, interannual variation in parameters of the water temperature function was used to describe the observed interannual variation in catchability. While it may have been optimal to test the influence of annual water temperature using different annual water temperature functions instead of the single function fitted to 11-year water temperature, the approach was not feasible due to the high number of parameters necessary.

Table 5.1: (a) General structure of models for lobster catchability in area 8 and area 5, and (b) sources of parameters used in the models. ‘Observed’ indicates parameters determined from independent biological or environmental data; ‘fitted’ indicates parameters estimated from fitting entire data set; and ‘fitted annually’ indicates parameters estimated from fitting the model to data for each year separately. For parameter values see Tables 5.5 and 5.6

(a) General model structure

	Water temperature	Moulting	Moulting compensation	Mating / second moult	Mating / second moult compensation
Basic structure:					
	$q = (a * x + b) + c * \sin((x + d) * \pi / e)$	$+ k_O * N(\mu_O, \sigma_O)$	$+ k_P * N(\mu_P, \sigma_P)$	$+ k_S * N(\mu_S, \sigma_S)$	$+ k_T * N(\mu_T, \sigma_T)$
Structure of models as applied in:					
Area 8:	$q = (a * x + b) + c * \sin((x + d) * \pi / e)$	$+ k_O * N(\mu_O, \sigma_O)$	$+ k_P * N(\mu_O + 3.92\sigma_O, \sigma_O)$	$+ k_O * (\sigma_S / \sigma_O) * N(\mu_S, \sigma_S)$	$- k_O * (\sigma_S / \sigma_O) * N(\mu_S + 3.92\sigma_S, \sigma_S)$
Area 5:	$q = (a * x + b) + c * \sin((x + d) * \pi / e)$	$+ k_O * N(\mu_O, \sigma_O)$	$+ k_P * N(\mu_O + 1.96(\sigma_O + \sigma_S), \sigma_S)$	$+ k_O * N(\mu_S, \sigma_S)$	$- k_O * N(\mu_S + 3.92\sigma_S, \sigma_S)$

(b) Tested models

Parameters of models	Biologically-based models	Seasonal models	Annual model 1	Annual model 2	Annual model 3	Annual model 4
<b>Water temperature</b>						
Gradient of trend $a$	observed	observed	fitted annually	observed	observed	observed
Intercept of trend $b$	fitted	fitted	fitted	fitted	fitted	fitted
Amplitude of sine function $c$	fitted	fitted	Fitted	fitted annually	fitted	fitted
Phase shift $d$	observed	observed	Observed	observed	observed	observed
Oscillation frequency $e$	observed	observed	observed	observed	observed	observed
<b>Moulting and mating</b>						
Moulting: Mean dates $\mu$	observed	fitted	fitted	fitted	fitted annually	fitted
Standard deviations $\sigma$	observed	fitted	fitted	fitted	fitted	fitted
Amplitudes $k$	fitted	fitted	fitted	fitted	fitted	fitted
Mating: Mean dates $\mu$	observed	fitted	fitted	fitted	fitted	fitted annually
Standard deviations $\sigma$	observed	fitted	fitted	fitted	fitted	fitted
Amplitudes $k$	fitted	fitted	fitted	fitted	fitted	fitted

As a more parsimonious approach, we varied just one parameter of the 11-year water temperature function. In annual model 1, the gradient of the trend in the water temperature function of the seasonal models was adjusted up or down as appropriate for each year. The origin of the trend line was set at the month with the least interannual variation in catchability, so that independent and model estimates of catchability varied least during the same month (February in area 8, August in area 5). In annual model 2, we fitted annual amplitudes of the sine function in the water temperature model to the observed variation in catchability.

Adjusting the parameters of trend and amplitude in the water temperature function to the interannual variation in catchability need not necessarily reflect actual interannual variation in water temperature. We tested this by correlating the annual parameters with a number of measures of annual water temperature. These included (i) the annual trend of residuals between measured water temperatures and the 11-year temperature function, and the sums of these residuals (ii) for the whole fishing season, and (iii) during summer or winter. We also correlated the gradient of the trend with the population density at the end of the season. Since the sampling unit is a fishing season, sample sizes of all correlations were low and correlations were conducted only for area 8 ( $N = 6$ ).

In two further annual models, variation in the timing of moulting (annual model 3) and mating (annual model 4) respectively was investigated to describe the observed interannual variation in catchability. The timing of moulting or mating and their linked compensation periods were allowed to vary annually and were fitted together with the parameters of the seasonal model.

Selection of the optimum model required a balance between number of parameters and closeness of the fit to data. The least-square estimate of Akaike's Information Criterion (AIC) was used to differentiate between models (Burnham and Anderson 1998). The model with the smallest AIC value was considered to be the best approximation to the information in the data relative to the other models considered.

## Results

### *Estimates of relative catchability*

Monthly catch rates, the total catch, and exploitation rates varied considerably among years. Exploitation rates varied between 0.58 and 0.88, total catches varied by 42%, and the estimated population of legal-sized lobsters available to the fishery at the start of the season varied by 21% (Table 5.2). Monthly catch rates in area 8 generally fell consistently from the start of the season until May and remained at low levels for the remainder of the season, but catch rates were up to twice as high in some years than in others (Fig. 5.2). The pattern of relative catchability in area 8 was relatively consistent during the first half of the season, with catchability peaking between November and March. It varied greatly in the second half of the season, but was usually lowest in April and May with some recovery between June and August.

Table 5.2: Total number of legal-sized lobsters captured during the season, exploitation rates at the end of the season and estimated total number of legal-sized lobsters available at the start of the fishing season in areas 8 and 5.

Area 8				Area 5			
Year	Total catch	Exploitation rates	Estimated population at start of season	Year	Total catch	Exploitation rates	Estimated population at start of season
92/93	569672	0.88	647355	92/93	303210	0.64	473766
93/94	377938	0.58	651618	93/94	306379	0.64	478718
95/96	655401	0.80	819251	94/95	282158	0.71	397406
96/97	566310	0.79	716848	95/96	284360	0.63	451365
97/98	460826	0.69	667864				
98/99	527922	0.66	803534				

In area 5, catch parameters and population estimates were more consistent between years (Table 5.2; Fig. 5.2). Relative catchability increased from the start of the season until March. Catchability was more variable during the first half of the season than in area 8, but consistently dropped in June and rose to its highest value in August.

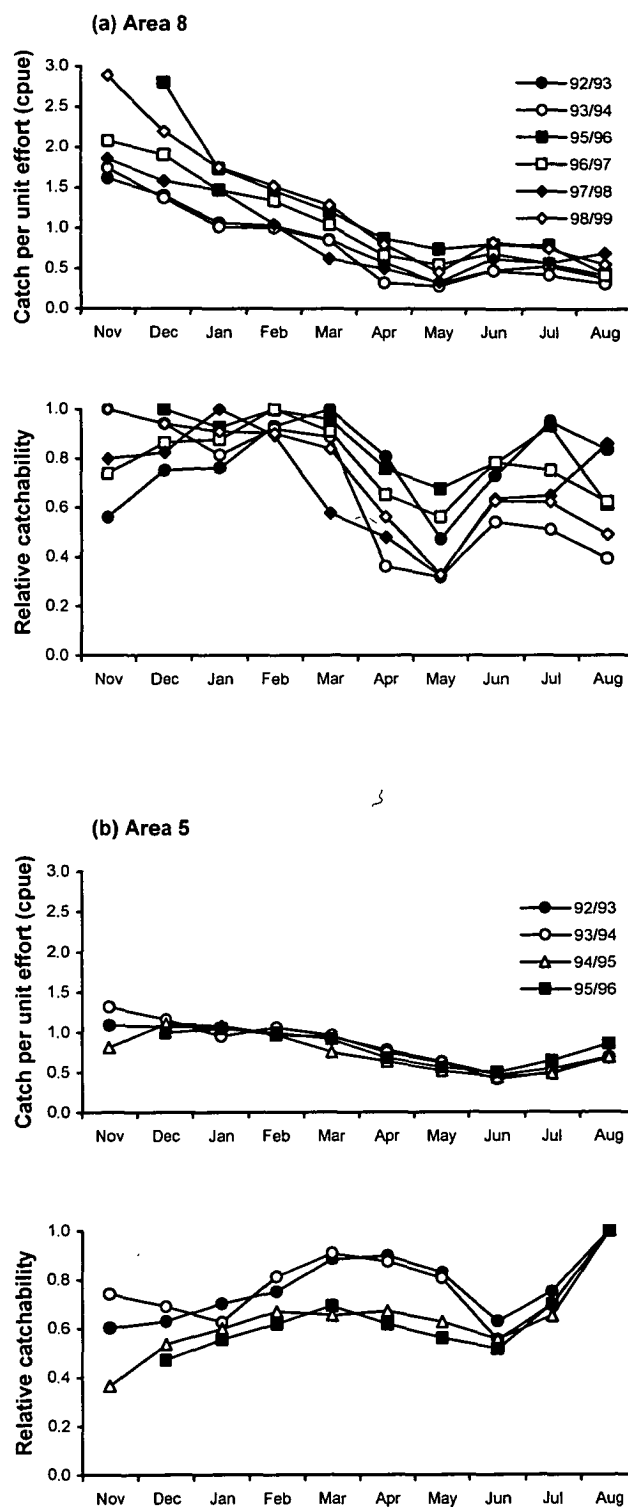


Fig. 5.2: (a) Catch per unit effort and estimated relative catchability of legal-sized male lobsters over the fishing season from November to August over 6 years in area 8. (b) Catch per unit effort and estimated relative catchability of legal-sized lobsters (sexes combined) over 4 years in area 5.

However, we may have generally overestimated catchability towards the end of each fishing season. The multi-year tagging method estimated exploitation rates of the population available to the fishery at the start of the season only. New recruits to the fishery during the fishing season after the two moulting periods were not accounted for and would have reduced the decrease in population size caused by the removal in catches, although the amount of recruitment was unknown. Nevertheless, our estimates were likely to represent the seasonal fluctuations in catchability to a large degree.

*Correlating water temperature with relative catchability*

Water temperature alone provided a poor description of relative catchability over a year. Mean monthly water temperature described 9-52% of the seasonal variation in catchability in different years in area 8, while in area 5 water temperature accounted for only 1-19% of the seasonal variation in catchability (Table 5.3).

Table 5.3: The amount of variation in relative catchability described by mean monthly water temperature in areas 8 and 5.

Area 8		Area 5	
Year	$R^2$	Year	$R^2$
92/93	0.09	92/93	0.13
93/94	0.32	93/94	0.19
95/96	0.52	94/95	0.01
96/97	0.26	95/96	0.02
97/98	0.24		
98/99	0.38		

*Models of relative catchability*

(a) Modelling seasonal variation in catchability

In area 8, the biologically-based model was a poor description of relative catchability (Table 5.4). Considerable improvements were achieved when the timing and duration of moulting and mating were allowed to be fitted in the seasonal model. Over the 6

years, the model described 50% of the total variation. Water temperature and the period of mating dominated the seasonal catchability model (Table 5.5; Fig. 5.3). The amplitude of the water temperature function and the standard deviation and amplitude of mating in the seasonal model were considerably larger than in the biologically-based model. Moulting and the compensation period after mating overlapped to a large degree from July until October and nearly neutralised one another, since their amplitudes were similar but with opposite sign. Because omitting either moulting or the compensation period after mating would not reduce the number of parameters in the model, both periods were retained in the model. The compensation period after moulting had only a limited positive effect due to its small amplitude, but it proved important in optimising the model.

Biologically-based and seasonal models in area 5 provided better descriptions of the variation in catchability than in area 8 (Table 5.4). The water temperature function acted simply as a scaling factor, since the amplitude of the sine function was zero and thus omitted in the optimal model (Table 5.5). The periods of the first and second moult and a compensation period after the second moult were pronounced (Fig. 5.3). The standard deviation of the first moult was shorter than that in the biologically-based model. Moult compensation had only minimal effect given that its amplitude was close to zero. It was therefore omitted from the model, improving the AIC. All parameters of the second moult and its compensation period after fitting the seasonal model were similar to those in the biologically-based model.

Table 5.4: Overall performances of the models for lobster catchability in areas 8 and 5. Given are sample size (*N*, number of months), number of parameters, sums of squares (SS), Akaike's Information Criterion (AIC), and adjusted *R*<sup>2</sup>.

Model	Area 8					Area 5				
	<i>N</i>	Parameters	SS	AIC	<i>Adj R</i> <sup>2</sup>	<i>N</i>	Parameters	SS	AIC	<i>Adj R</i> <sup>2</sup>
Biologically-based	59	4	1.71	-441.4	0.20	39	2	0.44	-313.6	0.48
Seasonal	59	8	0.99	-465.9	0.50	39	6	0.37	-312.9	0.53
Annual 1	59	14	0.48	-496.5	0.72	39	10	0.14	-343.3	0.80
Annual 2	59	13	0.70	-475.8	0.60	39	10	0.30	-313.0	0.56
Annual 3	59	15	0.52	-489.5	0.74	39	10	0.32	-309.6	0.57
Annual 4	59	13	0.97	-456.7	0.51	39	9	0.36	-37.7	0.52

Table 5.5: Parameters and their sources and values for the biologically-based and seasonal models of lobster catchability in areas 8 and 5. ‘Observed’ indicates parameters determined from independent biological or environmental data; ‘fitted’ indicates parameters estimated from fitting entire data set.

Parameters	Area 8				Area 5			
	Biologically-based model		Seasonal model		Biologically-based model		Seasonal model	
	Source	Value	Source	Value	Source	Value	Source	Value
<b>11-year water temperature model</b>								
$x = \text{Days since 10 November 1989}$								
Gradient of trend $a$	observed	-0.0000043	observed	-0.0000043	observed	-0.0000043	observed	-0.0000043
Intercept of trend $b$	fitted	0.70	fitted	0.79	fitted	0.78	fitted	0.75
Amplitude of sine function $c$	fitted	-0.08	fitted	-0.15				
Phase shift $d$	observed	158.4	observed	158.4				
Oscillation frequency $e$	observed	181.4	observed	181.4				
<b>Moulting and mating model</b>								
<i>Moult</i>								
Mean date $\mu_O$	observed	15 September	fitted	16 August	observed	15 December	fitted	12 December
Standard deviation $\sigma_O$	observed	21.8 d	fitted	25.8 d	observed	53.8 d	fitted	29.3 d
Amplitude $k_O$	fitted	-7.77	fitted	-27.25	fitted	-16.44	fitted	-11.91
<i>Moult compensation</i>								
Mean date $\mu_P$	$= \mu_O + 3.92\sigma_O$	9 December	$= \mu_O + 3.92\sigma_O$	25 November				
Standard deviation $\sigma_P$	$= \sigma_O$	21.8 d	$= \sigma_O$	25.8 d				
Amplitude $k_P$	fitted	11.99	fitted	6.69				
<i>Mating / second moult</i>								
Mean date $\mu_S$	observed	7 May	fitted	4 May	observed	15 June	fitted	14 June
Standard deviation $\sigma_S$	observed	10.9 d	fitted	24.81 d	observed	21.8 d	fitted	18.6 d
Amplitude $k_S$	$= k_O * (\sigma_S / \sigma_O)$	-3.88	$= k_O * (\sigma_S / \sigma_O)$	-26.22	$= k_O$	-16.44	$= k_O$	-11.91
<i>Mating / second moult compensation</i>								
Mean date $\mu_T$	$= \mu_S + 3.92\sigma_S$	18 June	$= \mu_S + 3.92\sigma_S$	9 August	$= \mu_S + 3.92\sigma_S$	8 September	$= \mu_S + 3.92\sigma_S$	25 August
Standard deviation $\sigma_T$	$= \sigma_S$	10.9 d	$= \sigma_S$	24.81 d	$= \sigma_S$	21.8 d	$= \sigma_S$	18.6 d
Amplitude $k_T$	$= -k_O * (\sigma_S / \sigma_O)$	3.88	$= -k_O * (\sigma_S / \sigma_O)$	26.22	$= -k_O$	16.44	$= -k_O$	11.91



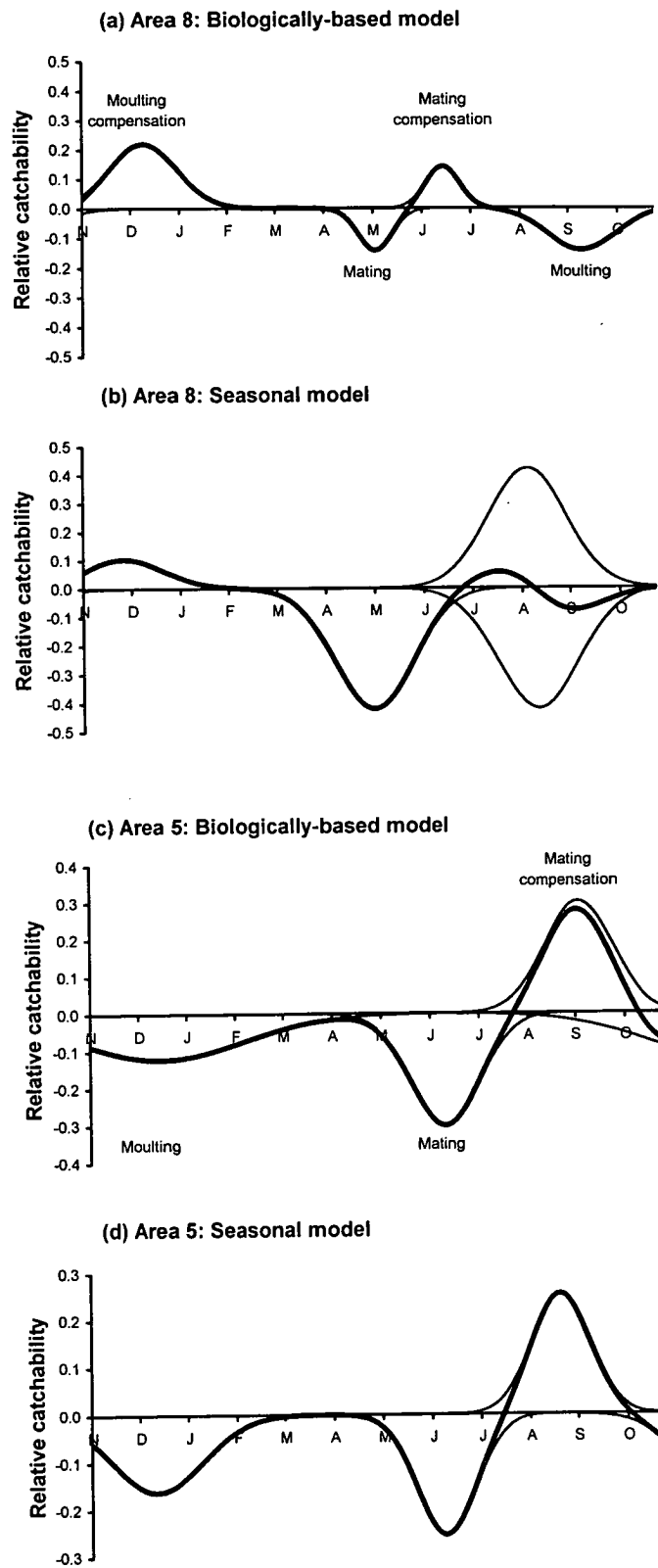


Fig. 5.3: Components for moulting, mating and associated compensation periods (thin lines), and overall effect (heavy lines) of the moulting and mating model in the (a) biologically-based and (b) seasonal model of area 8, and in the (c) biologically-based and (d) seasonal model of area 5. The overall effect closely follows the single components in all except the seasonal model of area 8.

## (b) Modelling interannual variation in catchability

In the two annual models where parameters of the water temperature function were adjusted annually, only varying the gradient of the trend greatly reduced the catchability residuals (annual models 1 and 2; Table 5.4). Varying the amplitude of the temperature function produced non-meaningful results, since the amplitude was of opposite sign for some years. The annual model 1 based on the seasonal model and an annual gradient of trend described 72% of the overall variation in catchability of area 8, and 80% of the overall variation in area 5 (Fig. 5.4; Tables 5.4 and 5.6). Despite the relatively high number of parameters compared to data points, these models were also considered to be best based on their minimised value of the AIC.

Table 5.6: Annual parameters (gradient of trend) in the annual model 1 of lobster catchability in areas 8 and 5.

	Area 8	Area 5
Year	Gradient of trend	Gradient of trend
92/93	0.00134	-0.00011
93/94	-0.00146	-0.00025
94/95		0.00070
95/96	0.00072	0.00076
96/97	0.00036	
97/98	-0.00003	
98/99	-0.00090	

However, the annual gradient of trend was not significantly correlated with any of the measures of interannual variation in water temperature (Table 5.7). Neither the annual trend of water temperature, nor elevated or lowered water temperatures over summer, winter or the whole year in relation to the 11-year water temperature function, were associated with the trend of the catchability curve. Thus, even though the gradient of trend is a parameter of the water temperature function, it was not related to interannual variation in water temperature. In contrast, the annual gradient in trend of the water temperature function was significantly correlated with the population size at the end of the season (Table 5.7). Similarly, the inverse relationship between absolute catchability and mean population size increased over the months and became significant at the end of the season from June to August.

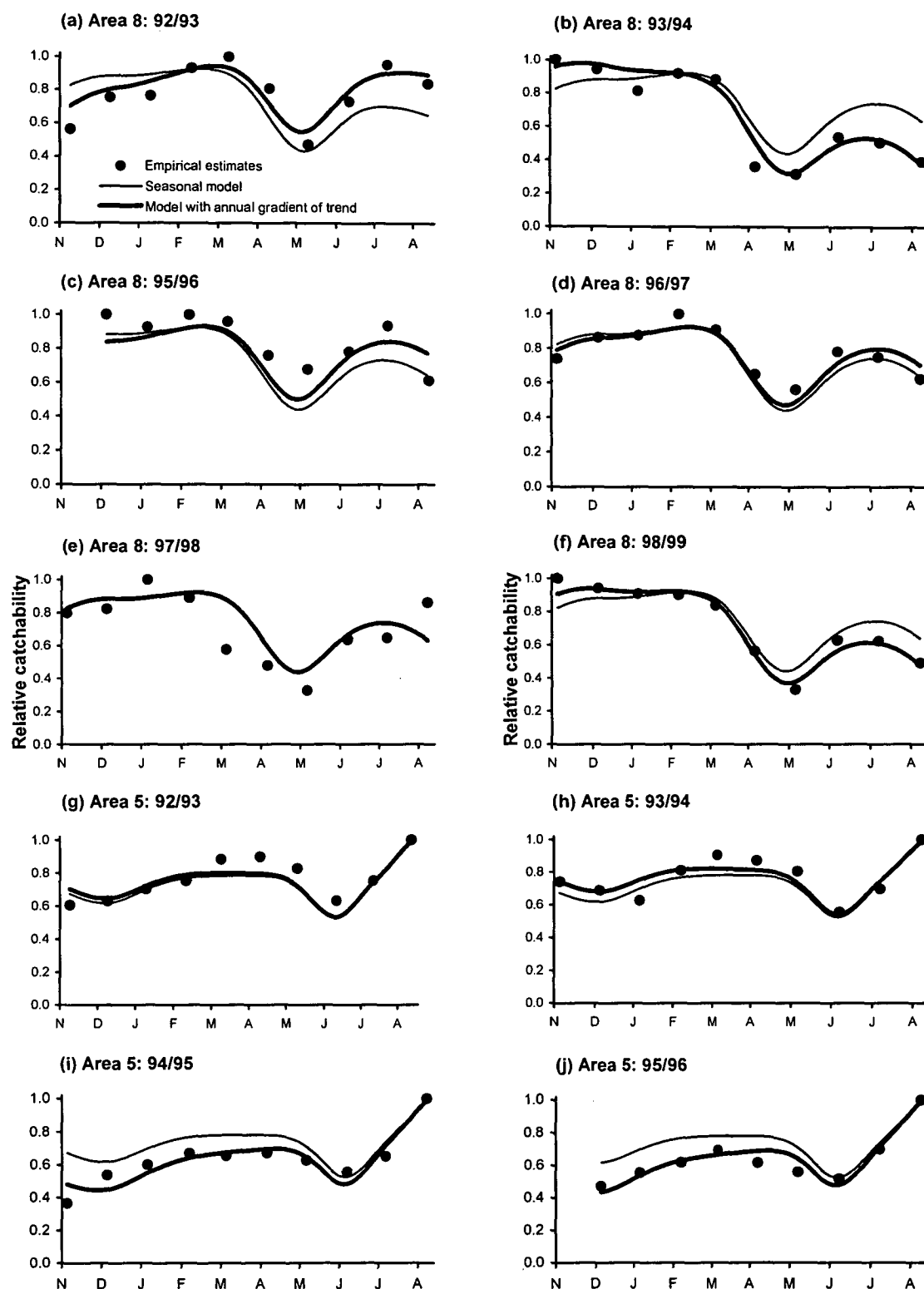


Fig. 5.4: Relative catchability of legal-sized male lobsters (area 8) and both sexes combined (area 5) estimated from fishery data and exploitation rates (filled circles), seasonal models (thin line) and models with annual gradient of trend (heavy lines) over 6 years in area 8 (a - f) and over 4 years in area 5 (g - j).

Table 5.7: Correlations of the annual gradient of trend in the water temperature function in area 8 with (a) measures of interannual variation in water temperature (annual trend and sum of water temperature residuals of the 11-year temperature function at Maatsuyker Island for different periods of the season); and (b) population density at the end of the season. (c) Correlation of absolute catchability with population size each month. Sample size  $N = 6$ , \* significant at 0.05 level, \*\* significant at 0.005 level.

Correlation	$R^2$	Slope	$F$	$P$
(a) Annual gradient of trend with water temperature				
(i) Annual trend of residuals	0.12	0.12	0.52	0.51
(ii) Sum of residuals of the whole fishing season	0.35	-0.000018	2.15	0.22
(iii) Sum of residuals of: November - March	0.52	-0.000038	4.23	0.11
April - August	0.09	-0.000015	0.38	0.57
(b) Annual gradient of trend with population size at the end of the season				
	0.93	-1.30E-8	54.17	0.002 **
(c) Absolute catchability with population size in:				
November	0.60	4.77E-12	4.50	0.12
December	0.00	3.13E-13	0.01	0.91
January	0.21	-3.68E-12	1.03	0.37
February	0.54	-8.49E-12	4.65	0.10
March	0.50	-1.12E-11	4.05	0.11
April	0.64	-1.24E-11	7.17	0.06
May	0.48	-7.40E-12	3.62	0.13
June	0.72	-9.99E-12	10.45	0.03 *
July	0.81	-1.61E-11	17.04	0.01 *
August	0.76	-1.35E-11	12.41	0.02 *

According to fishermen, males moulted early in area 8 at the end of the seasons 94/95, 95/96 and 97/98. Because of this, interannual variation in the timing of moulting and mating was investigated with two further annual models (annual models 3 and 4). Including the variation in annual timing of moulting in area 8 improved the overall model fit, describing 74% of the total variation in catchability (Table 5.4). However, the annual timing of moulting indicated from fitting the models varied far more than the observed range of one or two months reported by fishermen. The mean date of moulting in area 8 predicted by the models varied by 147 days between 1 May and 25 September. Consequently, the model predicted that moulting overlapped with mating in some years. In addition to the wider range of mean dates of moulting, the years with early moulting predicted in the models did not coincide with the observations of fishermen.

## Discussion

Our models of catchability suggest that environmental and physiological processes are the main sources of variation in catchability within fishing seasons in two commercially fished regions of Tasmania. Notably, the effects of these processes were region-specific. In both areas, density-dependent processes in addition to environmental and physiological processes seemed to be important in determining interannual variation in relative catchability.

### *Seasonal pattern of relative catchability*

Similar to our direct observations of catchability in a scientific reserve in southeast Tasmania (Chapter 2), relative catchability in both fishing regions followed a seasonal pattern during the fishing season from November to August, with peaks in each half of the fishing season. However, the seasonal pattern varied between regions in the timing and duration of the peaks.

Environmental and physiological factors were investigated as potential sources of the seasonal pattern in catchability and variation among regions. The seasonal models fitted to catchability followed the same structure as the model developed for the scientific reserve (Chapter 4), combining the effects of water temperature, moulting and mating. The models described 50% of the overall variation in catchability over 6 years in area 8, and 53% of the variation over 4 years in area 5. The predicted periods of moulting and mating in fitting the models overlapped with the range suggested by independent biological data. We therefore suggest that the model estimates effectively represent these physiological processes and may provide improved estimates of timing and duration in moulting and mating, given that the independent biological data were unable to give precise indications of timing and duration.

### *Regional differences of seasonal catchability models*

Strong correlations between catchability and seasonal water temperature arise commonly for lobsters and crabs (McLeese and Wilder 1958; Paloheimo 1963; Morgan 1974, 1978; Morrissy and Caputi 1981; Williams and Hill 1982; Yamakawa et al. 1994). Effects of water temperature were also evident in this study, however

they were region-specific. Seasonal differences in water temperature were more important in the south and contributed significantly to the models in area 8 and in the scientific reserve (Chapter 4), but not in area 5 in the north. The absolute lower temperatures during winter could have largely suppressed feeding in the south, while warmer winter temperatures may not have a similar effect on catchability in the north. Catchability in area 5 remained relatively low during the summer months and rose to maximum values in August, which was reflected by weak correlations with water temperature. However, the models of area 5 may have underestimated the influence of water temperature. Catchability was likely to be overestimated towards the end of the season in the north, since our estimates of population size did not account for new recruitment during the fishing season. As a result, the latitudinal differences in the effect of water temperature on catchability may have been exaggerated.

Changes in catchability in the seasonal model of area 5 are best described solely as effects of the two moulting periods and a compensation period after mating, which override any other effects. The timing and duration of moulting and mating were similar to that indicated from independent biological data. The first moulting period indicated by the model lasted from October to February, i.e. it was slightly shorter than the period when animals were observed to moult in the wild. The predicted second moulting and mating period followed closely the observed period from May to July. While the moult compensation period of the model developed for the population in the scientific reserve was a dominant feature (Chapter 4), the compensation period following the first moult in area 5 had a minimal impact and was omitted to optimise the model. Due to the extended moulting period, few animals moult towards the end and exhibit only a weak distinct compensation. In contrast, the compensation period after the second moult and mating in July and August had a strong effect on catchability. Although this was against the trends in the models for area 8 and the reserve population, it is similar to the massive peak in weekly food consumption rates observed just after mating in captive male *J. edwardsii* in New Zealand (Kelly et al. 1999).

In the models for area 8, mating was the key factor, while all other physiological effects were less important. The timing of mating from early March until late June

overlapped with the time period observed in the wild, however it was twice as long as expected from observations on mating in the scientific reserve. This could have been caused by the female-biased population structure prolonging the mating period in the south. Because only males reach legal size in this area, the sex ratio is strongly biased towards females. The relatively few remaining large males, which are more likely to copulate than smaller males (MacDiarmid 1994; MacDiarmid and Butler 1999), may mate with a much larger number of females than in a population with even sex ratio, such as in a no-take reserve (Chapter 2). Since males court females for an average of 5 days prior to egg-laying independent of animal size and progress of the mating season (MacDiarmid 1989), an extended mating season appears likely in this area.

Latitudinal trends in the timing of moulting and mating have been reported from *J. edwardsii* in New Zealand (MacDiarmid 1989), *J. lalandii* (Newman and Pollock 1974) and *Panulirus argus* (Lipcius and Herrnkind 1987). Similarly, in this study male lobsters moulted earlier in the south than in the north, which may have caused the apparently low importance of moulting and compensation after mating in area 8. The resulting proximity of moulting during which feeding activity decreases, and the mating compensation period during which feeding activity increases, may greatly reduce the impact of either at the population level.

Estimates of relative catchability in area 5 were not sex-specific. In the scientific reserve, where moulting of males and females is temporally separated within the year, differences between gender are an important feature of catchability (Chapter 2). However, large proportions of males and females in area 5 were found to moult twice during the year and at similar times. This suggests that differences in catchability between males and females are lower in the north than in the south.

#### *Interannual differences in catchability*

In both regions, catchability varied considerably between years. Inclusion of interannual variation in the gradient of trend in the water temperature function and in the timing of moulting considerably improved the model fits. However, the annual fluctuations were not well explained by annual variation in water temperature, moulting or mating. The interannual variation in the gradient of trend, despite being a

parameter of the water temperature function, was not significantly correlated with any measures of the interannual variation in water temperature. These results contrast with several other studies which have shown that annual catch per unit effort and yield are closely correlated with sea surface temperatures (Flowers and Saila 1972; Dow 1977; Fogarty 1988; Campbell et al. 1991; Robichaud and Campbell 1991; Evans et al. 1995).

In area 8, allowing the timing of moulting to vary improved the models in a similar way to adding annual gradients of trend. However, the resulting models were not biologically meaningful, as the timing of moulting varied to the extent that moulting overlapped completely with mating in some years. In addition, the years in which the models predicted early moulting did not coincide with years when fishermen observed early moults.

In contrast, interannual variation in seasonal catchability was correlated with density-dependent processes. In area 8, the annual gradients of trend was significantly correlated with population size at the end of the season, and the inverse relationship between absolute catchability and population size generally increased during the course of the fishing season and became significant towards the end of the season. Behavioural interactions between lobsters are known to reduce catch rates and the effects of these interactions are likely to increase with density (Richards et al. 1983; Addison 1995; Miller and Addison 1995; Addison and Bannister 1998; Frusher and Hoenig 2001b). However, it remains unclear whether interannual variation in population size is related to interannual variation in catchability by direct causal or indirect correlative processes.

Other factors may have contributed to the regional and interannual differences in catchability. The size-frequency distribution differs strongly between the fishing regions. Animals up to 200 mm carapace length (CL) are caught in the north, while animals larger than 120 mm CL are rare in the south. Since catchability has been shown to be size-specific (e.g. Morrissey and Caputi 1981; Miller 1989, 1995; Pezzack and Duggan 1995; Tremblay et al. 1998, Tremblay 2000; Frusher and Hoenig 2001b; Chapter 3), different catchability patterns, as found in the population of the fished regions in the north and south, may result. In addition, environmental factors like salinity and water motion, the soak time of traps, and distribution of



effort in fishing have been related to catchability and catch rates of crustaceans (Morgan 1974; Howard and Nunny 1983; Robertson 1989; Miller 1990; Yamakawa et al 1994; Miller and Addison 1995; Miller and Rodger 1996; Wallace et al. 1998). Since we used commercial catch and effort data over large areas for this study, these factors may have influenced our estimates of catchability, but were not considered in the models.

### *Conclusions*

In this study, seasonal and interannual variation in catchability of lobsters in two commercial fishing regions of Tasmania was modelled based mainly on the effects of water temperature, moulting and mating. In contrast to *Panulirus cygnus* in Western Australia, where year-to-year variation in catchability is low (Morgan 1974), catchability of *J. edwardsii* varied between years. While we failed to fully describe the interannual variation in catchability by environmental and physiological processes alone, interannual variation in catchability was correlated with density-dependent processes.

Developing the models in this study has greatly improved our understanding of the mechanisms apparently influencing catchability. However, before we can predict catchability in future years and in other fishing regions of Tasmania, we need to know the region-specific patterns of seasonal catchability and the relationship between density-dependent processes and interannual variation in catchability. This is also important, because the high variation in catchability of rock lobsters found in this study suggests that seasonal, regional and interannual variation in catchability of rock lobster be considered in stock assessments.

## **5A. Appendix:**

### **Timing and frequency of moulting at Maatsuyker Island and King Island**

#### **Material and methods**

The timing and frequency of moulting at Maatsuyker Island and King Island was determined from both research and commercial catch data. Research data at Maatsuyker Island was collected from July 1994 to March 2000 three times a year in February and March, July to September, and in November. Research and commercial catch data were available from November 1989 to September 2000 at King Island.

At Maatsuyker Island partial or complete regeneration of clipped pleopods between the tagging and recapture of a lobster was taken as an indication of a moult. A growth increment of 0 mm was assumed to indicate a moult without growth, and negative growth of -1 mm was interpreted as a measurement error. Data indicating negative growth greater than -1 mm per recapture period was omitted.

At King Island moult information had to be derived from growth data alone. Since small measurement errors are likely to occur, limits of growth increments were introduced to distinguish between moult and non-moult. A moult was assumed when the growth increment between capture and recapture of a lobster exceeded 1 mm. A growth increment of 0 mm indicated no moult, while growth increments of 1 mm or -1 mm were assumed to be measurement errors when the animals had not moulted. Data indicating negative growth greater than -1 mm per recapture period was omitted.

Since individuals were rarely captured several times during any one year, moult frequency had to be inferred from the comparison of the average growth increment per moult and the overall growth increment per year.

## Results

### *Maatsuyker Island*

#### (a) Moulting frequency and growth

A high proportion of the population moulted during the period of a year. Only 2.9% of males ( $N = 649$ ) and 9.7% of females ( $N = 167$ ) had not moulted when at large for a year. Unmoulted males were mainly large individuals greater than 100 mm carapace length (CL), while unmoulted females were of all sizes between 75 mm CL and 102 mm CL.

Animals with regenerated pleopods at large for less than a year were used to determine the growth increment per moult. To rule out double moults, animals at large for 160 days, which were highly unlikely to moult twice within that period, were compared to animals at large for 161-310 days. Growth increments of both males and females were not significantly different when animals at large for up to 160 days or for 161-310 days (Wilcoxon 2-sample test; males:  $N = 878$ ,  $Z = -1.76$ ,  $P = 0.08$ ; females:  $N = 379$ ,  $Z = -1.60$ ,  $P = 0.11$ ). Data of both groups in each sex were thus pooled.

Growth increments per moult were size-dependent for males, but not for females. Males smaller than 100 mm CL grew significantly more than males greater than 100 mm CL with an average of 5.5 mm and 3.2 mm increment per moult, respectively (Wilcoxon 2-sample test;  $N = 878$ ,  $Z = 13.07$ ,  $P < 0.0001$ ; Fig. 5A.1). No difference in growth increment per moult was found for females smaller or greater than 90 mm CL (Wilcoxon 2-sample test;  $N = 362$ ,  $Z = 1.37$ ,  $P = 0.17$ ). With an average increment of only 1.2 mm, females grew considerably less than males over each moult. However, the accuracy of this estimate is somewhat doubtful considering measurement errors of  $\pm 1$  mm.

Lobsters around Maatsuyker Island seem to moult mainly once a year. Annual growth increments for most males and females at large for a year can be explained assuming a single moult (Fig. 5A.1).

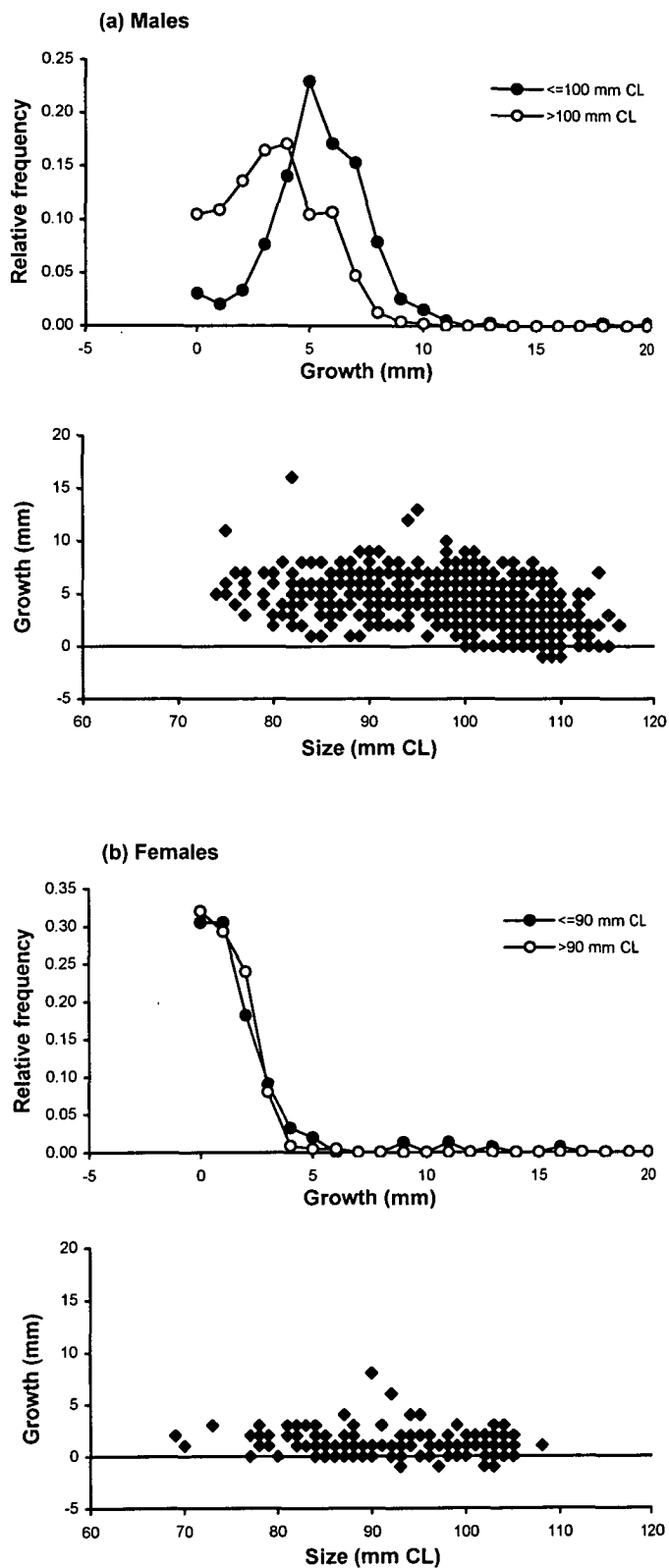


Fig. 5A.1: Relative frequency of growth increments (in mm) per moult at Maatsuyker Island for (a) male lobsters (filled circles: males  $\leq 100$  mm CL;  $N = 878$ ), and (b) female lobsters (filled circles: females  $\leq 90$  mm CL; open circles: females  $> 90$  mm CL;  $N = 362$ ); and growth increments (in mm) per carapace length (in mm) during one year at large for (a) male lobsters ( $N = 649$ ) and (b) female lobsters ( $N = 167$ ).

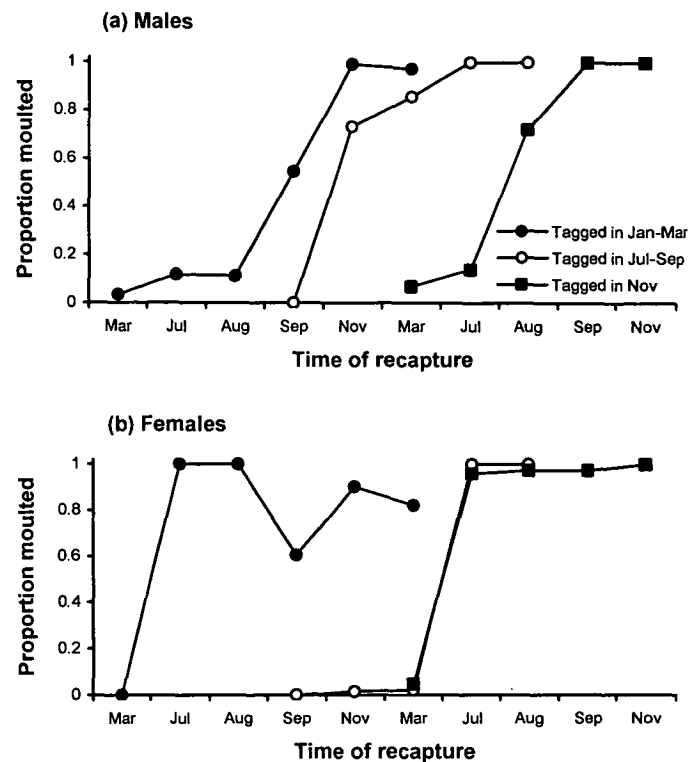


Fig. 5A.2: Proportion of lobsters that moulted between tagging and recapture in subsequent months at Maatsuyker Island derived from regeneration of clipped pleopods for (a) males ( $N = 2656$ ) and (b) females ( $N = 1322$ ). Filled circles: animals tagged between January and March, open circles: animals tagged between July and September, filled squares: animals tagged in November.

(b) Moulting timing and duration

Temporal resolution of timing and duration of moult for males and females was limited due to the low frequency of sampling periods during any one year. Males moulted mainly between August and October, but when tagged between July and September males moulted slightly later, and when they were tagged in November, they moulted slightly earlier (Fig. 5A.2). Females moulted between March and July, however the data do not allow more precise estimates of the timing and duration.

*King Island*

## (a) Moulting frequency and growth

Similar as at Maatsuyker Island, a high proportion of both males and females moulted during a year. However, research and fishery data differed in the proportion of the population moulting over a year. Research data from this area indicates that all of the 92 recaptured males and 96 recaptured females moulted when at large for a year as indicated by growth of more than 3 mm over this period. In data collected by fishermen, 1.1% of males ( $N = 88$ ) and 21.6% of females ( $N = 88$ ) had grown 1 mm or less, thus indicating no moult. Measurement errors as well as moult without growth may be the cause for the differences. A majority of the unmoulted females in the fishery data were of large size between 120-155 mm CL.

Growth increments of males and females were not significantly different, irrespective of whether animals were at large for up to 160 days or for 161-290 days (Wilcoxon 2-sample test; males:  $N = 315$ ,  $Z = -1.72$ ,  $P = 0.09$ ; females:  $N = 237$ ,  $Z = -0.71$ ,  $P = 0.48$ ). Again, data of both groups in each sex were pooled.

In contrast to Maatsuyker Island, growth increments per moult were size-dependent for females, but not for males. Growth increments of males were on average 10.3 mm per moult for all three size classes ( $\leq 100$  mm CL, 101-130 mm CL,  $> 130$  mm CL; Kruskal-Wallis test;  $N = 315$ ,  $\chi^2 = 1.27$ ,  $P = 0.53$ ; Fig. 5A.3). However, females smaller than 110 mm CL grew on average 8.8 mm per moult and significantly more than the females greater than 110 mm CL with a average increment of only 5.7 mm (Wilcoxon 2-sample test;  $N = 237$ ,  $Z = -7.10$ ,  $P < 0.0001$ ). Again, males of any size grew on average considerably more per moult than females.

Growth increments of animals at large for the period of a year are best explained assuming a size-dependent moult frequency. Most growth increments of males smaller than 100 mm CL indicated two moults. For males between 101-130 mm CL growth increments seemed to indicate either one or two moults, while for males larger than 130 mm CL increments could be explained by a single moult (Fig. 5A.3). Females followed a similar pattern, although with different size limits. Females

seemed to reduce moult frequency per year from two to one in growing larger than 100-110 mm CL.

(b) Moulting timing and duration

Not only the frequency but also the timing of moulting was size-dependent. This results in long periods when at least some individuals in the population are moulting. Males smaller than 130 mm CL moulted between October and March, males greater than 130 mm CL moult slightly earlier between September and December (Fig. 5A.4). Small and some large males moulted a second time between May and July. This timing falls within the period of the main moult for females. Females smaller than 110 mm CL moult a second time between November and March, and some females larger than 110 mm CL have a second moult between February and March. Two annual moults are therefore an important feature of this population with an extended period between September and March and a well-defined second moulting and mating period between May and July.

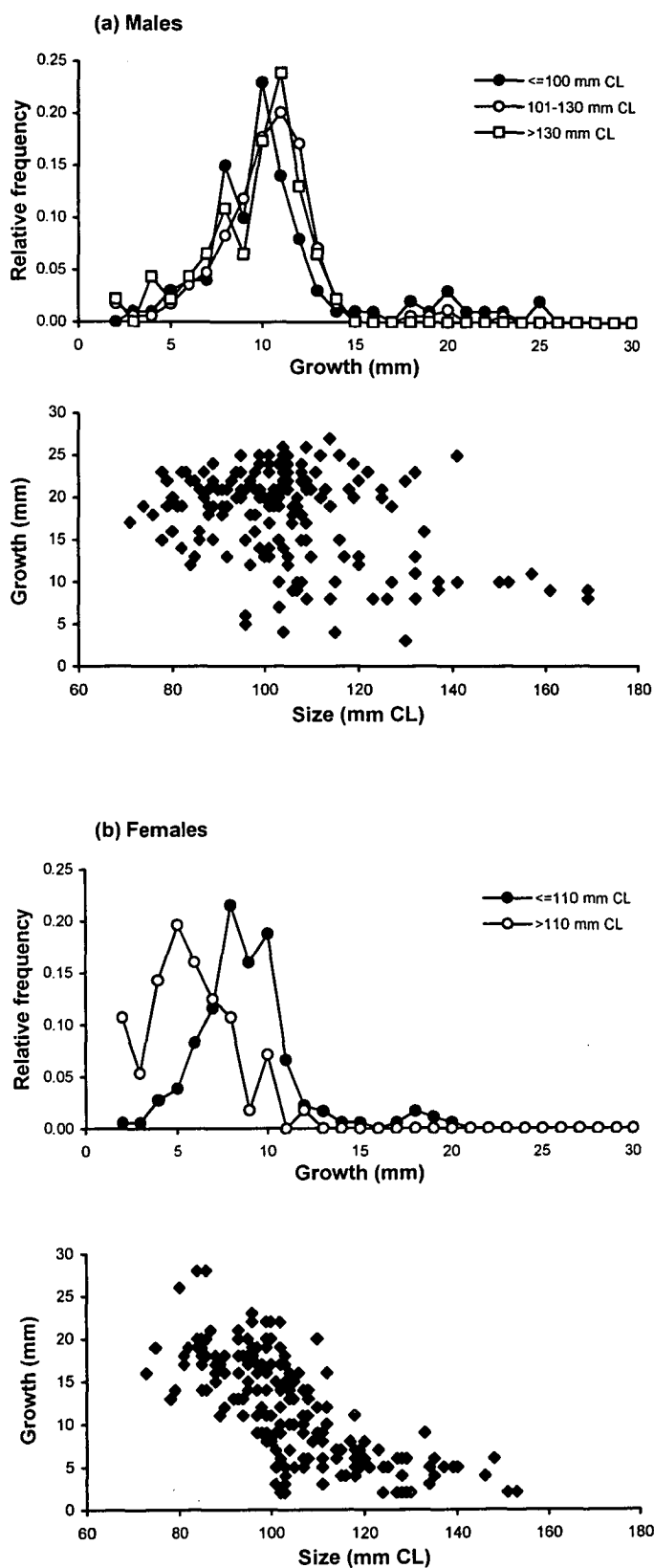


Fig. 5A.3: Relative frequency of growth increments (in mm) per moult at King Island for (a) male lobsters (filled circles: males  $\leq 100$  mm CL, open circles: males 101-130 mm CL, open squares: males  $> 130$  mm CL;  $N = 315$ ), and (b) female lobsters (filled circles: females  $\leq 110$  mm CL, open circles: males  $> 110$  mm CL;  $N = 237$ ); and growth increments (in mm) per carapace length (in mm) during one year at large for (a) male lobsters ( $N = 180$ ) and (b) female lobsters ( $N = 184$ ).



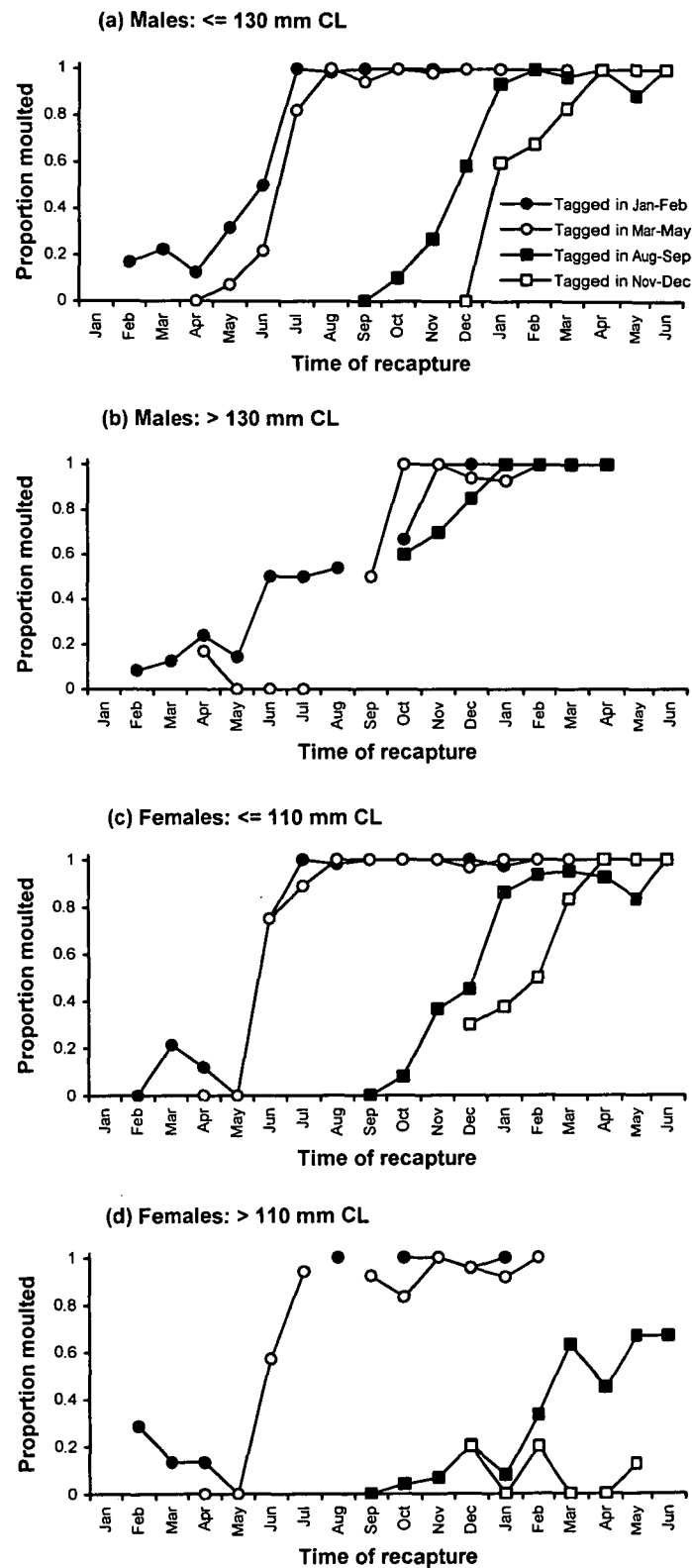


Fig. 5A.4: Proportion of lobsters that moulted between tagging and recapture in subsequent months derived from growth data for (a) males  $\leq 130$  mm CL ( $N = 1373$ ), (b) males  $> 130$  mm CL ( $N = 303$ ), (c) females  $\leq 110$  mm CL ( $N = 895$ ) and (d) females  $> 110$  mm CL ( $N = 659$ ). Filled circles: animals tagged between January and February, open circles: animals tagged between March and May, filled squares: animals tagged between August and September, empty squares: animals tagged between November and December.

## Chapter 6:

### Discussion

#### Introduction

Catchability of crustaceans and other harvested marine animals has been shown to vary with fishing practices, a wide variety of environmental and physiological parameters, and individual behaviour of animals (for reviews see Miller 1990 and Arreguín-Sánchez 1996). For the southern rock lobster *Jasus edwardsii* in Tasmania, we have investigated the influence of environmental and physiological effects, and intraspecific interactions on the variation in catchability with animal sex and size, season, region and year (Chapters 2 to 5).

Here, we integrate the results of these studies and discuss the implications of the variation in catchability for the stock assessment process. In many crustacean fisheries, population dynamics and stock assessments are aided by models, and seasonal catchability and relative selectivity are parameters in these models. In drawing this work together, we compare model estimates with independent estimates of catchability in the example of the stock assessment model for *J. edwardsii* in Tasmania (Punt and Kennedy 1997), and estimate qualitatively biases in the stock assessment in circumstances in which the model fails to represent catchability appropriately.

### Variation in catchability of *Jasus edwardsii* in Tasmania

Catchability of *J. edwardsii* was estimated in an unfished scientific reserve in Tasmania by comparing catch rates in trapping surveys with direct population density estimates obtained from underwater visual observations (Fig. 6.1; Chapter 2). Catchability varied with season depending on sex. Monthly catchability for both male and female lobsters declined in winter and was elevated in summer, but the magnitude of seasonal differences was greater in males than in females. Seasonal changes in catchability ostensibly depend mainly on a combination of environmental and physiological factors, and can be modelled by considering the effects of water temperature, moulting and mating (Chapters 4 and 5).

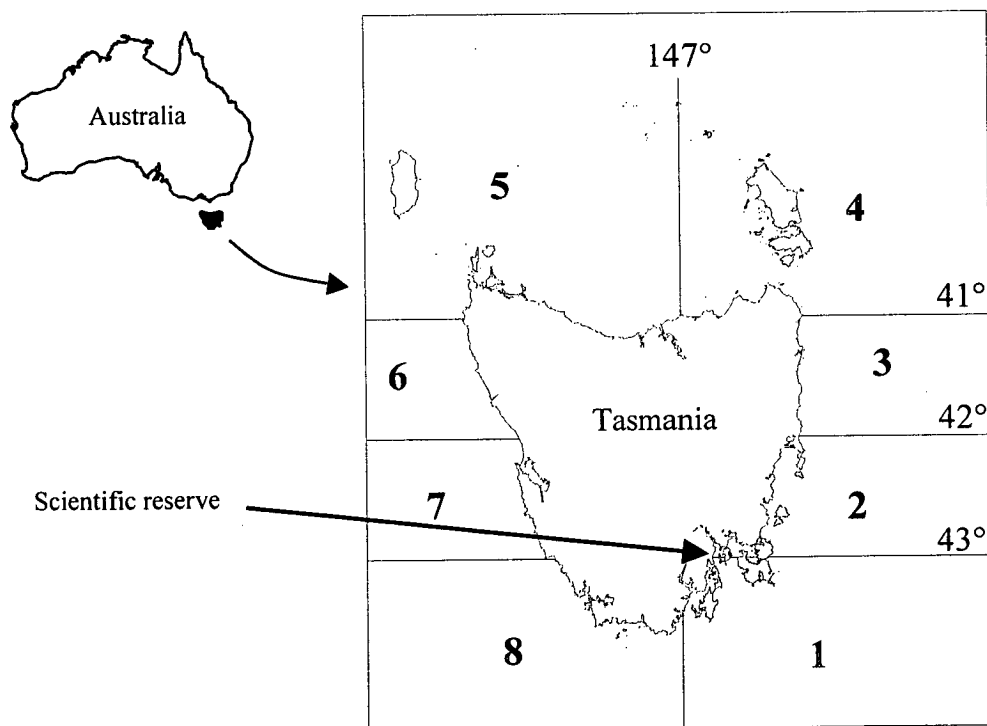


Fig. 6.1: Map of Tasmania and the eight fishing areas of stock assessment for rock lobster.

In a similar way, the effects of water temperature have been shown to influence catchability of the American lobster *Homarus americanus* (McLeese and Wilder 1958; Paloheimo 1963), and moulting was found to depress catchability in *J. lalandii* (Newman and Pollock 1974; Pollock and DeB Beyers 1979) and in *H. americanus* (Fogarty 1988; Tremblay and Eagles 1997). Multiple linear models have been developed incorporating both water temperature and moulting in the Western rock lobster *Panulirus cygnus* (Morgan 1974) and the portunid crab *Scylla serrata* (Williams and Hill 1982). However, none of these models consider separate sexes.

Sex is an important contributor to variation in seasonal catchability, when moulting is seasonally separated for male and female lobsters (Newman and Pollock 1974; Pollock and DeB Beyers 1979; Tremblay and Eagles 1997; Chapters 4). In colder southern waters of Tasmania, both sexes generally moult only once, with males moulting in early spring and females moulting just before mating in autumn (Chapter 4). Since catchability decreases during moulting and mating, and increases during the compensation periods immediately after moulting and mating (Chittleborough 1975; Lipcius and Herrnkind 1982; Zoutendyk 1988; Miller 1990; Kelly et al. 1999), the effects of these physiological processes on seasonal catchability are sex-specific. In the warmer northern waters of the state, most males and females moult twice at approximately similar times of the year. Thus, the sex-specific influence of moulting on catchability is expected to be smaller in these areas.

Catchability of the lobster population in the scientific reserve generally increased with animal size, although again the increase varied with sex and season (Frusher and Hoenig 2001b; Chapter 3). Catchability of medium-sized and large males was generally higher for males than for females in similar size classes. During moulting and mating, size-specific catchability did not increase, or even decreased, for larger animals. Similarly, in male and female *H. americanus* the magnitude of the increase in catchability with size differs between June and September depending on the moult stage (Tremblay 2000). The earlier moult of males seems to reduce catchability of large males in June compared with September, while large females show the reverse trend.

Likely mechanisms that underpin size-specific catchability are behavioural interactions arising from the presence of a large lobster in a trap inhibiting the entry

of smaller individuals, and the greater foraging range of large lobsters (Richards et al. 1983; Lawton 1987; Karnofsky and Price 1989; Miller 1990; Addison 1995; Addison and Bannister 1998; Frusher and Hoenig 2001b; Chapter 3). In the scientific reserve, negative correlations in the behavioural interactions between large and small animals varied with season and were weaker in summer. But it remained unclear, whether the actual intraspecific interactions between animals around traps varied, or whether the seasonal variation in negative correlation was the result of changes in feeding activity (Chapter 3). However, intraspecific interactions and size-specific foraging range do not seem to determine the seasonal pattern in catchability (Chapter 3). Similar patterns of catchability in most size classes indicate that catchability of all animals, independent of their size, is influenced by water temperature, moulting and mating (Chapter 4). Because of this and because effects of temperature, moulting and mating also influence catchability in other areas (Chapter 5), size-specific catchability is likely to vary with season in all regions around Tasmania. In addition, size-specific catchability depends on the size-frequency distribution of the population, which differs greatly between regions (Miller 1995; Frusher 1997; Tremblay et al. 1998; Tremblay 2000; Frusher and Hoenig 2001b). We therefore expect a distinct seasonal pattern of size-specific catchability in each region.

We found seasonal catchability to vary between regions around Tasmania (Chapter 5). Differences in water temperature and in the timing of moulting and mating play an important role in underpinning these differences. In contrast to the colder waters in the south of the state, the warmer water temperatures in the north of Tasmania have relatively little impact in restricting catchability in winter, and moulting and mating exhibit stronger influences on catchability in this area. In the north, moulting and mating also take place later in the year, so that their influence on catchability is delayed compared with that in the south.

Seasonal catchability was also found to vary considerably between years (Chapter 5). In contrast to *P. cygnus* in Western Australia, where variation in water temperature contributes to interannual variation in catchability (Morgan 1974), density-dependent processes seem to be associated with interannual variation in catchability in the south of Tasmania. However, it remains unclear whether this is a direct causal or indirect correlative relationship. If density-dependence is the direct cause of interannual

variation in catchability, then we would assume catchability to vary between years in all regions around Tasmania. This is because behavioural interactions, believed to be the underlying causes of density-dependence (Richards et al. 1983; Karnofsky and Price 1989; Addison 1995; Addison and Bannister 1998; Frusher and Hoenig 2001b), are likely to occur in all lobster populations. Since population densities and size-frequency distributions influence variation in behavioural interactions and vary both among fishing regions and interannually within regions (Frusher 1997), it is likely that these differences will also manifest as interregional and interannual variation in seasonal catchability.

### **Consequences for stock assessment**

Stock assessment models often incorporate parameter estimates of relative selectivity and seasonal catchability. Size-based estimates of relative selectivity are crucial in models which simulate the size-frequency structure of the population to estimate population parameters such as recruitment (Bergh and Johnston 1992; Johnston and Bergh 1993; Walters et al. 1993; Punt and Kennedy 1997; Walters et al. 1998). Seasonal catchability is a critical parameter in most stock assessments, since it is used to scale catch rates to stock size. However, while relative selectivity is often estimated independently from tag-recapture data (e.g. Frusher and Hoenig 2001b), robust estimates are rare for seasonal catchability. This parameter is therefore often considered as a 'nuisance' variable that is estimated indirectly (e.g. Walters et al. 1993; Punt and Kennedy 1997; Walters et al. 1998).

The accuracy of stock assessment predictions is expected to improve, if independent estimates of seasonal catchability are incorporated into the model, since independent estimates are likely to be more accurate than indirect estimates from stock assessment models. Independent estimates of catchability by direct observations, as provided in this study, can also be used to investigate the overall accuracy of the structure and parameter values in a stock assessment model. Catchability coefficients that are estimated indirectly in optimising the fit of stock assessment models are a composite of catchability and other factors not accounted for elsewhere in the model, and the similarity between independent estimates of catchability and those derived

from fitting the model can be used to evaluate the influence of these other factors. If the fishery-independent estimates of catchability are similar to estimates obtained in fitting the model, then other factors unrelated to catchability that influence the estimate of catchability coefficients from model fitting, are likely to be minor. This would indicate that the model structure and values of parameters used in the model accurately reflect the biological parameters and processes acting on the fished population.

However, the output of a stock assessment model can only be considered to be valid, if variation in selectivity and catchability with animal sex, season, region and year as described above is adequately represented in the model. Although models allowing for all sources of variation in selectivity and catchability will be rare, most models account for at least some variation. For example, in the stock assessment model for *J. edwardsii* in Tasmania relative selectivity is sex-specific and assumed to be known exactly in each of the eight fishing regions, however relative selectivity is assumed not to vary with season (Punt and Kennedy 1997; Punt et al. 1997). Catchability is assumed to vary seasonally among regions, but not to vary between years. In addition, estimates of monthly catchability are not sex-specific due to the lack of resolution in catch and effort data, which is used to estimate catchability. The lack of variation in seasonal selectivity and interannual catchability may result in bias in the predictions of the stock assessment. In the following we discuss the effects of variation in selectivity and catchability on stock assessments and in particular that for rock lobster in Tasmania. We also compare independent estimates of catchability with model-derived estimates to evaluate model parameters and the accuracy of the model predictions.

#### *Effects of seasonal variation in relative selectivity*

Dynamic stock assessment models fitted to the observed length distribution in the lobster population generally include relative selectivity, but only some consider area- and/or sex-specific selectivity (e.g. Bergh and Johnston 1992; Punt and Kennedy 1997; Walters et al. 1998). From the result of our study, we recommend area-specific selectivity where the size-frequency distribution varies between regions, since relative selectivity is likely to depend on the size-frequency distribution of the

population (see above). The great differences in selectivity between sexes found in the scientific reserve (Chapter 3) suggest that sex-specific components should be developed in size-structured stock assessment models.

None of the existing stock assessment models, including the Tasmanian rock lobster stock assessment model, accounts for seasonal changes in relative selectivity (e.g. Bergh and Johnston 1992; Walters et al. 1993; Punt and Kennedy 1997; Punt et al. 1997; Walters et al. 1998). Because selectivity is assumed to be largely gear-related, it is treated as a fixed effect and does not consider seasonal changes in the behaviour of animals. However, large seasonal changes in size-specific catchability and relative selectivity have been shown in *J. edwardsii* and *H. americanus* (Tremblay 2000; Chapter 3), and similar seasonal changes are expected in most lobster species. This is because physiological processes such as moulting, mating or subsequent periods of increased feeding (Chittleborough 1975; Lipcius and Herrnkind 1982; Zoutendyk 1988; Miller 1990; Kelly et al. 1999) fall within the fishing season (Newman and Pollock 1971; Morgan 1974; MacDiarmid 1989; Tremblay and Eagles 1997) and effect relative selectivity (Chapter 3).

Fixing selectivity at a single value throughout the season for particular size and sex categories imposes a potential bias in estimating the actual size-frequency distribution in the population, since catches of at least some periods during the season are likely to be misinterpreted. Unfortunately, it is rarely practical and feasible to estimate relative selectivity throughout the fishing season, and specific sampling periods have to be chosen instead. Bias in estimating the size-frequency structure of the population can then be reduced, when the selectivity is estimated during the periods which contribute to most of the total catch within a fishing season. In Tasmania, this is at the start of the season between November and March, when approximately 80% of the annual catch is harvested. However, if the distribution of fishing effort and catch change through the season, selectivity estimates may need adjustment. With the introduction of the quota system in 1998, fishermen in Tasmania began to delay their effort and catch more lobsters later in the season in winter, when lobsters fetch higher prices. If this shift is not accounted for, it is likely to yield misleading estimates of the size-frequency distribution of the population after the introduction of the quota system.



*Effects of seasonal variation in catchability*

Including seasonal variation in catchability in lobster stock assessment models is essential, because catchability has been found to follow distinct seasonal patterns related to the effects of water temperature, moulting and mating (Morgan 1974; Chapters 4 and 5). Area-specific catchability on a monthly or even fortnightly scale is incorporated in some stock assessment models (e.g. Walters et al. 1993; Punt and Kennedy 1997; Walters et al. 1998). However, since these models estimate seasonal catchability indirectly as a 'nuisance' variable from catch and effort data, model estimates do not necessarily represent 'true' estimates of catchability. In addition, because catch and effort data do not separate for sex, model estimates are usually not sex-specific, but represent catchability of the entire legal-sized lobster population.

Independent estimates of seasonal catchability from this study can provide more accurate parameters for the modelling process than model derived estimates. We can also compare our independent estimates of catchability of the legal-sized population with estimates of catchability derived in fitting the assessment model in three regions around Tasmania. Similar distinct seasonal patterns in independent and model-derived estimates of monthly catchability are found in areas 8 and 1, but are clearly different in area 5 (Fig. 6.2; Chapters 2 and 5).

In area 8, where only males contribute to the catches, the model estimates of catchability follow a similar trend and are well within the range of the interannual variation in independent catchability estimates for all years investigated (Fig. 6.2). This suggests that components other than catchability in the model-derived estimates are relatively small. However, the model estimates tend to be at the upper end of the range of independent catchability estimates particularly during the second half of the fishing season. Consequently, the stock assessment model may underestimate population size in this area, although a sensitivity analysis is needed to determine the extent of the bias.

The results for area 1 are similar to those for area 8. Estimates of catchability of legal-sized male and female lobsters from the scientific reserve are pooled to estimate catchability of the entire population (Chapter 2). These estimates are similar to those from the stock assessment model for all of area 1 except for the last two

months of the season (Fig. 6.2). Since the notable differences are restricted to the end of the fishing season, and the model estimates are similar to those in nearby area 8, it is likely that factors specific to the small population in the reserve, rather than additional components contributing to the catchability estimates in the model, caused these differences. Catchability in winter may have been reduced in the scientific reserve because of increased maximum catchability in the austral summer due to the higher proportion of large animals in the reserve (Chapter 3), and relative higher water temperatures in summer in the estuarine environment where the reserve is situated (Chapter 5).

In contrast to areas 8 and 1, the model-derived estimates for area 5 do not follow the trend of our independent estimates. Catchability predicted by the model is relatively flat throughout the season, and fluctuations showed no apparent trend (Fig. 6.2). Although water temperature seems to have limited influence on seasonal catchability in this region, distinct seasonal trends in catchability were found in the independent estimates due to the effects of moulting and mating (Chapter 5). If the trend in the independent estimates is correct, this suggests that the model-derived estimates for area 5 are influenced by inappropriate parameter estimates.

#### *Effects of regional variation in catchability*

Where environmental parameters and seasonal timing of physiological events vary between regions, accounting for area-specific seasonal catchability in the assessment of the fishery seems to be important (Chapter 5). This is acknowledged widely in that several stock assessment models are spatially explicit (e.g. Walters et al. 1993; Punt and Kennedy 1997; Walters et al. 1998). Since independent estimates of area-specific seasonal catchability requires independent estimates of stock size and involves a considerable sampling effort (Chapter 5), we developed models to predict catchability in other fishing regions. Unfortunately, it was impossible to extrapolate catchability estimates from one region to another, because the interactions between the components of moulting and mating, and thus the overall effects of these components, lacked a distinct latitudinal pattern (Chapter 5). It seems that each region needs to be sampled individually to obtain estimates of area-specific catchability.

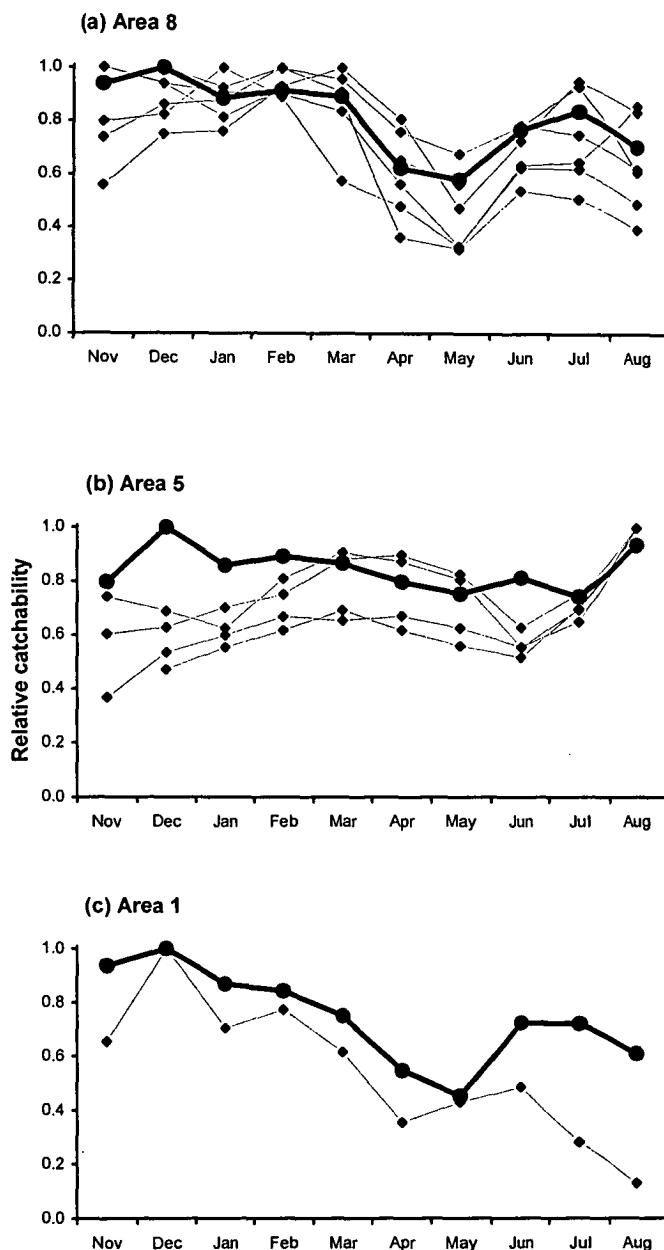


Fig. 6.2: Catchability estimates derived from the stock assessment model (heavy lines) and independent estimates (thin lines) derived from commercial catch and effort data and population estimates using the change-in-ratio technique in area 8, multi-year tagging methods in area 5, and direct underwater visual observations in area 1 (see Chapters 2 and 5). Multiple thin lines in plots represent different years.

Nevertheless, we can use the understanding of factors determining seasonal and regional catchability to investigate seasonal patterns and latitudinal trends in the catchability estimates derived from the stock assessment model. For *J. edwardsii* in

Tasmania, we expect some seasonal pattern in each region of the fishery due to the interaction between the effects of water temperature, moulting and mating. The lack of any apparent seasonal pattern in catchability estimated from the stock assessment model in area 5, for which model estimates of seasonal catchability are relatively invariant through the season (Fig. 6.3), and in area 6, for which estimates increase slowly between January and August, suggests inappropriate representation of catchability in the model. In area 6, this may reflect insufficient data to estimate the size-frequency distribution (S. D. Frusher, Tasmanian Aquaculture and Fisheries Institute, personal communication).

We also expect some latitudinal trends in catchability. Catchability is likely to be higher in the warmer northern waters of Tasmania than in the colder southern waters, since water temperature strongly influences absolute catchability (McLeese and Wilder 1958; Paloheimo 1963; Morgan 1974). This latitudinal trend is reflected in the area-specific estimates of catchability in the stock assessment model, except for areas 4 and 5 (Fig. 6.3). Consistently lowest catchability estimated in the model for these two areas suggests that parameter values used in the model or the model structure does not accurately reflect the biological parameters or processes acting on the fished population in the areas. This could be the case e.g. for growth by double moult which is common only in the north of the state.

#### *Effects of interannual variation in catchability*

Stock assessment modes for rock lobster rarely account for interannual variation in catchability and an identical pattern of seasonal catchability is applied to all years (e.g. Walters et al. 1993; Punt and Kennedy 1997; Walters et al. 1998). Because seasonal catchability can vary considerably between years (Chapter 5), stock size will be underestimated in some years and overestimated in others. If interannual variation in catchability varies directly with stock density (Chapter 5), then the effects of density-dependence may be stronger in some regions and weaker in others, since different population density and size-frequency distribution will influence the degree to which behavioural interactions will contribute to catchability variation. However, the overall effects of regional-specific interannual variation in stock assessments remain unclear without a sensitivity analysis.

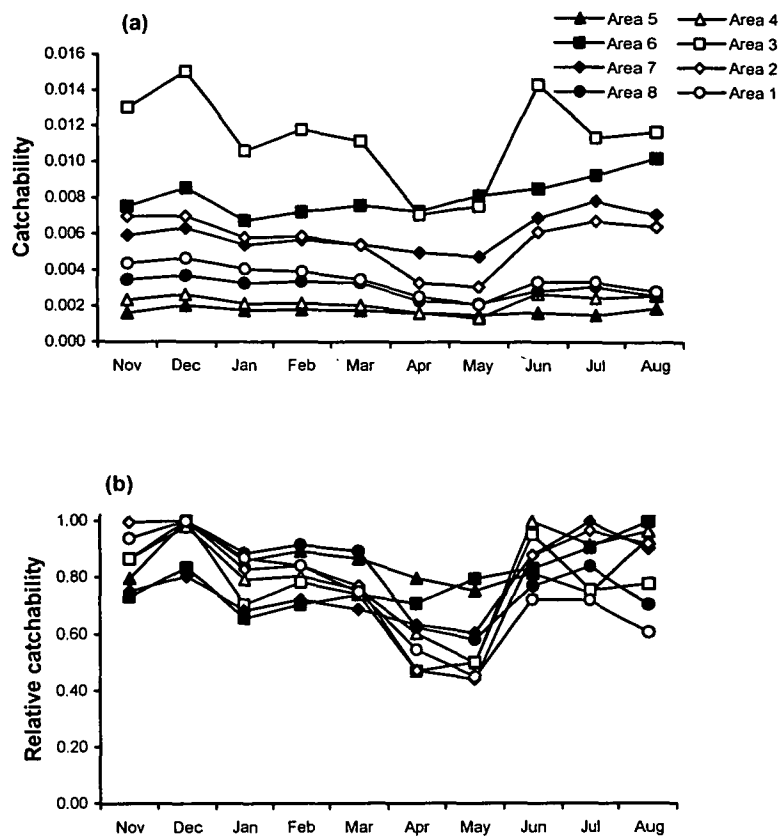


Fig. 6.3: Estimates of (a) absolute and (b) relative catchability from the stock assessment model in the 8 stock assessment areas. Estimates of relative catchability are standardised to the interval  $[0,1]$  for each year.

## Conclusions

Many stock assessment models account for some variation in catchability. For *J. edwardsii* in Tasmania most of the variation in catchability with animal sex and size, season, region and year found in this study is represented in the structure of the current stock assessment model. However, seasonal catchability is only estimated indirectly by the model and independent estimates of catchability can not be used with the current model structure. Allowing independent estimates of catchability as parameters in the model is a necessary step in the process to improve the model. Nevertheless, comparing model estimates with independent estimates of catchability is valuable in its own right to evaluate qualitatively the accuracy of catchability estimated by the model.

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In this study, we greatly improved our understanding of the mechanisms determining seasonal and size-specific catchability by modelling environmental and physiological effects. If our models are combined with a better knowledge of the region-specific patterns of seasonal catchability and of the relationship between density-dependent processes and interannual variation in catchability, predictions of catchability around Tasmania will be considerably more robust than present indirect estimates.

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